b i o l o g y
letters

Social learning of a brood parasite by its host

William E. Feeney and Naomi E. Langmore

Supplementary data	"Data Supplement" http://rsbl.royalsocietypublishing.org/content/suppl/2013/06/11/rsbl.2013.0443.DC1.html
References	**This article cites 15 articles, 6 of which can be accessed free** http://rsbl.royalsocietypublishing.org/content/9/4/20130443.full.html#ref-list-1
Subject collections	Articles on similar topics can be found in the following collections behaviour (688 articles) cognition (136 articles) ecology (721 articles) evolution (730 articles)
Email alerting service	Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click **here**

To subscribe to *Biol. Lett.* go to: **http://rsbl.royalsocietypublishing.org/subscriptions**

b i o l o g y
letters

Research

CrossMark
click for updates

Author for correspondence:
William E. Feeney
e-mail: william.e.feeney@gmail.com

Royal Society Publishing
Informing the science of the future

Animal behaviour

Social learning of a brood parasite by its host

William E. Feeney and Naomi E. Langmore

Research School of Biology, Australian National University, Canberra, Australian Capital Territory 0200, Australia

Arms races between brood parasites and their hosts provide model systems for studying the evolutionary repercussions of species interactions. However, how naive hosts identify brood parasites as enemies remains poorly understood, despite its ecological and evolutionary significance. Here, we investigate whether young, cuckoo-naive superb fairy-wrens, *Malurus cyaneus*, can learn to recognize cuckoos as a threat through social transmission of information. Naive individuals were initially unresponsive to a cuckoo specimen, but after observing conspecifics mob a cuckoo, they made more whining and mobbing alarm calls, and spent more time physically mobbing the cuckoo. This is the first direct evidence that naive hosts can learn to identify brood parasites as enemies via social learning.

1. Introduction

Social learning facilitates the rapid transmission of adaptive information [1], and is particularly valuable when opportunities for learning through personal experience are limited [2]. One such context is recognition of brood parasites. Parasitic cuckoos lay their eggs secretively, rapidly and at times when hosts are unlikely to be near their nest [3], providing little opportunity to learn directly about the threat they pose. Yet, recognition of cuckoos is of critical importance, because parasitism imposes severe costs on host reproductive success [3], and recognition of an adult cuckoo can result in successful deflection of parasitism [4], or more accurate decisions about rejection of cuckoo eggs and chicks [5,6].

Few studies have investigated the mechanisms by which hosts recognize adult brood parasites [4]. Langmore *et al.* [7] showed that recognition of cuckoos is learned in superb fairy-wrens, *Malurus cyaneus*; individuals at parasitized sites mobbed cuckoos intensively, whereas at nearby unparasitized sites they showed no response to cuckoos. Reed warblers, *Acrocephalus scirpaceus*, mob cuckoos more intensively after seeing their neighbours mob a cuckoo [8,9], and mobbing intensity is influenced more by social cues than personal experience [10]. Although reed warblers clearly modify their defences against brood parasites in response to social cues, it is unclear whether social learning alters their perception of parasitism risk or facilitates recognition of cuckoos as a threat [8]. Here, we show that naive superb fairy-wrens learn to recognize cuckoos as a threat through observation of mobbing by conspecifics.

2. Material and methods

Cooperatively breeding superb fairy-wrens are common hosts of brood parasitic Horsfield's bronze-cuckoos, *Chalcites basalis*, and occasional hosts of shining bronze-cuckoos, *Chalcites lucidus* [11]. Superb fairy-wrens are resident, whereas the cuckoos are breeding migrants to southeastern Australia [11]. Fairy-wrens produce two distinct alarm calls when mobbing: a general 'mobbing' alarm, and a 'whining' alarm which has been observed only in the context of cuckoo mobbing [7]. Unlike reed warblers [12], they do not modify mobbing of cuckoos in relation to parasitism risk [7].

2

Table 1. Responses (mean $\pm$ s.e.) of naive ($n = 11$) and experienced superb fairy-wrens to presentation of cuckoo and control specimens during pre-training, post-training and training trials (mean length pre- and post-training trials = 41.18 ± 15.59 s, mean length training trial = 300 ± 0 s). Italics indicates statistical significance.

	naive individuals				experienced groups
	pre-training trial	post-training trial	Friedman's test on call rate or % time less than 0.5 m (χ^2)	p	training trial
cuckoo					
alarm calls	0 (± 0)	54.18 (± 30.75)	4	*0.006*	324.10 (± 57.80)
whining calls	0 (± 0)	18.18 (± 9.88)	7.36	*0.045*	239.64 (± 80.81)
per cent of time less than 0.5 m	0.91 (± 0.91)	62.27 (± 13.22)	6.4	*0.01*	79.21 (± 11.92)
honeyeater					
alarm calls	22.64 (± 6.83)	17.18 (± 10.12)	1	0.32	185.82 (± 53.80)
whining calls	3.27 (± 3.27)	0 (± 0)	1	0.32	27.18 (± 25.15)
per cent of time less than 0.5 m	19.70 (± 12.06)	13.12 (± 8.26)	1	0.65	30.85 (± 12.43)

Experiments were conducted in Campbell Park [13,14], Canberra, Australia, during September–November 2012. Parasitism of superb fairy-wrens by Horsfield's bronze-cuckoos at this site occurred in 8/14 years (1999–2012, 0–37% of nests in which eggs were laid each year, $n = 1201$ nests). In 2011, parasitism was rare (4%, $n = 167$ nests) and localized, which provided an opportunity to identify 'cuckoo-naive' juvenile superb fairy-wrens (that hatched, and were colour banded late in the 2011 breeding season, and had not shared the environment with cuckoos).

To test whether superb fairy-wrens acquire a mobbing response to cuckoos through social learning, we used freeze-dried specimens of (i) shining bronze-cuckoos and (ii) white-plumed honeyeaters *Lichenostomus penicillatus* (a harmless heterospecific control; [7]). Shining bronze-cuckoos are morphologically similar to Horsfield's bronze-cuckoos and elicit a highly aggressive response from superb fairy-wrens, whereas honeyeaters elicit a low-level response, even when placed near a fairy-wren nest [7]. The purpose of the honeyeater control was to investigate whether repeated presentations could affect response to a stimuli through sensitization [1]. We used two specimens of each species, which we swapped between trials to control for model effects.

Only cuckoo-naive individuals in a breeding group with 'cuckoo-experienced' individuals (that have previously shared habitat with breeding cuckoos) were used in experiments, and one naive individual was tested per breeding group (11 individuals). All experiments were conducted during late nest building, when cuckoos monitor host nests and are mobbed by their hosts (W. E. Feeney & N. E. Langmore 2012, personal observations).

At least 30 min prior to each experiment, a camouflaged hide was set up 10–25 m from the nest of the focal group, and the model was placed on a perch within a protective cage of wire mesh approximately 2 m from the nest [7]. The cage was covered with a camouflage cloth, which was pulled from the cage to reveal the model to the naive individual or group. Each trial comprised three treatments: (i) presentation of the model to the naive individual at a time when it was alone (pre-training), (ii) presentation of the model to the entire group (training) and (iii) presentation of the model to the (previously) naive individual, again when it was alone (post-training; methods similar to 1), and a cuckoo and control trial was conducted on each territory. When possible, all three treatments for a given trial were accomplished in 1 day, and the following trial was conducted on the following day. The order of trials was alternated between groups. Further, Langmore *et al.* [7] found no effect of presentation order (cuckoo or honeyeater) on response, so any change in response is likely a result of learning rather than carry-over aggression.

Pre- and post-training trials commenced when the naive individual came within 2 m of the model and no other group members were in sight. Training trials commenced when at least one experienced group member came within 2 m of the model. In all cases, the naive individual approached within 5 m of the model within 30 s of an experienced individual, after which the training trial continued for 5 min. For each focal individual, the length (s) of the pre- and post-training trials for the cuckoo and honeyeater were standardized according to the length of the shortest trial (a trial ceased if another fairy-wren approached; average trial length = 41.18 ± 15.59 s). A minimum of 90 min was allowed between training and post-training trials for carry-over aggression to diminish.

The number of mobbing and whining calls were recorded using a Marantz PMD661 solid-state recorder and an Audio-Technica condenser microphone, and distance between the focal bird and the model (time spent < 0.5, 2, 5, and 10 m from the model; [7]) was simultaneously dictated onto the recording. Number and type of call were extracted using RAVEN PRO v. 1.3 [15], statistical analyses were conducted in R v. 2.13.2 [16] and mixed-effects models were conducted using the 'lme4' package [17]. Our data violated assumptions of mixed-effects models, so we used conservative Friedman's tests to test whether response (number of whining and mobbing alarm calls, and proportion of trial spent mobbing) by the naive individual changed following training by their group. We used linear mixed-effects models to test whether group mobbing of cuckoos was more intense than to honeyeaters with model type, trial order and model replicate as a fixed effects, and group identity as a random effect. Trial order and model replicate were non-significant and were removed from final models.

Raw data can be found in the electronic supplementary material.

3. Results

Cuckoo-naive superb fairy-wrens were unresponsive to cuckoo models in the pre-training trials (table 1). However,
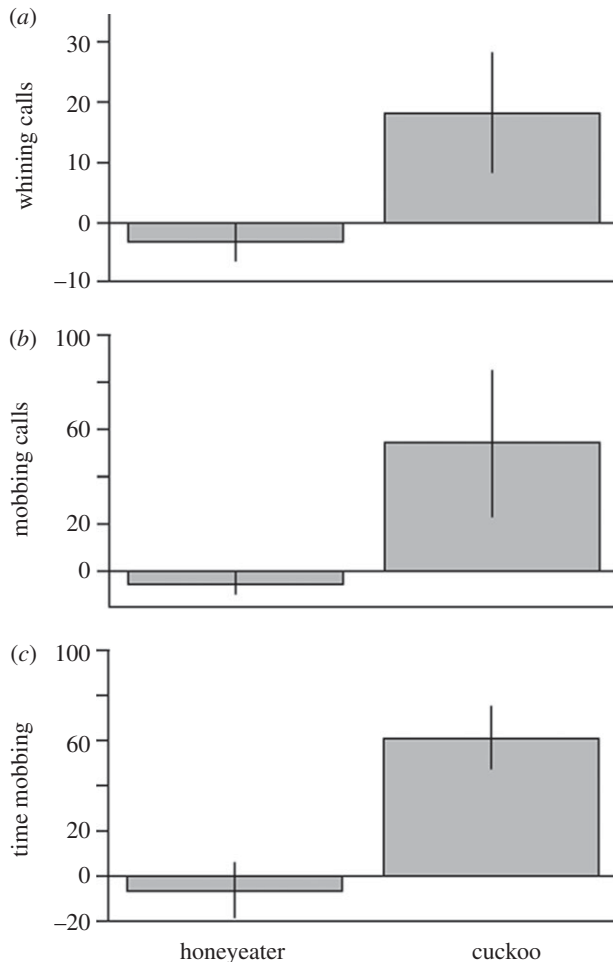
Figure 1. Change in response of naive superb fairy-wrens ($n = 11$) to honeyeater and cuckoo models following training. 'Whining calls', and 'mobbing calls' refer to the number of calls, and 'time mobbing' refers to the proportion of time spent within 0.5 m of the model by the naive individual. Error bars denote s.e.

Figure 2. Mobbing of a cuckoo model by a previously naive male superb fairy-wren and a female superb fairy-wren in Campbell Park, Australia. (Online version in colour.)

following training by group members, these individuals produced significantly more whining and mobbing alarm calls and spent significantly more time within 0.5 m of the model in response to the cuckoo (table 1; figures 1 and 2).

During the training trial, groups were more aggressive to cuckoos than honeyeaters (LME on number of whining calls, $Z = -35.16$, $p < 0.001$; mobbing calls, $Z = -20.05$, $p < 0.001$ and proportion of time spent within 0.5 m by the closest group member, $Z = -25.53$, $p < 0.001$, table 1), and whining and mobbing alarm calls produced in the post-training trials always occurred following whining and mobbing alarm calls being produced by at least one experienced group member in the training trial.

Repeated presentations did not have an effect on the response of cuckoo-naive fairy-wrens to honeyeaters between pre- and post-training trials (table 1 and figure 1), suggesting that the increased aggression to cuckoos after training was a result of social learning rather than a change in sensitivity as a result of repeated presentations.

Two naive individuals whined briefly as they approached the honeyeater (table 1). Both individuals received the honeyeater treatment after the cuckoo, so these were likely to be brief moments of mistaken identity. Naive individuals produced more mobbing alarms in response to the honeyeater than the cuckoo during the pre-training trial (Friedman's test, $\chi^1 = 7$, $p = 0.008$). This is probably because honeyeaters were familiar, whereas cuckoos were novel and their level of threat was unknown.

4. Discussion

Naive superb fairy-wrens were initially unresponsive to cuckoo models. However, following a single observation of the responses of their group to a cuckoo model, they produced an aggressive response while separate from their group. By contrast, they showed no change in response to the honeyeater control between pre- and post-training trials. These results indicate that social learning is a mechanism by which this species can rapidly recognize and respond to a novel threat.

Our results are consistent with theoretical predictions about social learning. First, social learning should occur when cues from conspecifics are both reliable and specific [10]. Superb fairy-wrens produce a 'whining' alarm call exclusively in response to cuckoos, and are likely to use it reliably because it recruits group members and neighbours to assist in mobbing of cuckoos (W. E. Feeney & N. E. Langmore 2011, unpublished data). Thus, it provides a highly reliable source of information to naive individuals. Second, animals should rely on social learning when personal learning is more costly, such as when learning about predators [10]. The costs of successful brood parasitism are greater even than those of nest depredation; the host not only loses its entire brood, but also invests substantial time and energy in rearing

the parasite. Thus, naive individuals pay a significant cost for failing to recognize and defend against brood parasites. Finally, social learning should occur rapidly if it is to provide an advantage over personal learning [18]. This was the case in our study; a single observation by a naive individual of an attack on a cuckoo by their group was sufficient for social learning to occur. This is consistent with studies showing one-event social learning of predators by birds [19], and rapid social acquisition of fear responses more generally [18].

Three other studies provide evidence of social learning in cuckoo hosts [8–10]. These studies demonstrated that mobbing of cuckoos by reed warblers is a phenotypically plastic response that is modified through social learning. However, it was unclear whether social learning led only to a change in perceived risk of parasitism or involved refinement of a template for cuckoo recognition [8]. Unlike reed warblers, fairy-wrens do not face high risks through mobbing of cuckoos, which may explain why they do not reduce their mobbing response to cuckoos with decreased risk of parasitism [7]. The absence of such phenotypic plasticity in mobbing response clarifies the role of social learning in cuckoo recognition. Our evidence that superb fairy-wrens acquire information about the threat posed by cuckoos through social learning supports the suggestion that a similar process may operate in other brood parasite hosts such as reed warblers [8].

References

1. Curio E. 1978 The adaptive significance of avian mobbing. *Z. Tierpsychol.* **48**, 175–183. (doi:10.1111/j.1439-0310.1978.tb00254)

2. Thornton A, Clutton-Brock T. 2011 Social learning and the development of individual and group behaviour in mammal societies. *Phil. Trans. R. Soc. B* **366**, 978–987. (doi:10.1098/rstb.2010.0312)

3. Davies NB. 2000 *Cuckoos, cowbirds and other cheats*. London, UK: T. & A.D. Poyser.

4. Feeney WE, Welbergen JA, Langmore NE. 2012 The frontline of avian brood parasite–host coevolution. *Anim. Behav.* **84**, 3–12. (doi:10.1016/j.anbehav.2012.04.011)

5. Langmore NE, Cockburn A, Russell AF, Kilner RM. 2009 Flexible cuckoo chick-rejection rules in the superb fairy-wren. *Behav. Ecol.* **20**, 978–984. (doi:10.1093/beheco/arp086)

6. Davies NB, Brooke MDL. 1988 Cuckoos versus reed warblers: adaptations and counteradaptations. *Anim. Behav.* **36**, 262–284. (doi:10.1016/s0003-3472(88)80269-0)

7. Langmore NE, Feeney WE, Crowe-Riddell J, Luan H, Louwrens KM, Cockburn A. 2012 Learned recognition of brood parasitic cuckoos in the superb fairy-wren *Malurus cyaneus*. *Behav. Ecol.* **23**, 798–805. (doi:10.1093/beheco/ars033)

8. Davies NB, Welbergen JA. 2009 Social transmission of a host defense against cuckoo parasitism. *Science* **324**, 1318–1320. (doi:10.1126/science.1172227)

9. Thorogood R, Davies NB. 2012 Cuckoos combat socially transmitted defenses of reed warbler hosts with a plumage polymorphism. *Science* **337**, 578–580. (doi:10.1126/science.1220759)

10. Campobello D, Sealy SG. 2011 Use of social over personal information enhances nest defense against avian brood parasitism. *Behav. Ecol.* **22**, 422–428. (doi:10.1093/beheco/arq225)

11. Brooker MG, Brooker LC. 1989 Cuckoo hosts in Australia. *Aust. Zool. Rev.* **2**, 1–67.

12. Welbergen JA, Davies NB. 2009 Strategic variation in mobbing as a front line of defense against brood parasitism. *Curr. Biol.* **19**, 235–240. (doi:10.1016/j.cub.2008.12.041)

13. Langmore NE, Adcock GJ, Kilner RM. 2007 The spatial organization and mating system of Horsfield's bronze-cuckoos, *Chalcites basalis*. *Anim. Behav.* **74**, 403–412. (doi:10.1016/j.anbehav.2006.09.019)

14. Langmore NE, Kilner RM. 2007 Breeding site and host selection by Horsfield's bronze-cuckoos, *Chalcites basalis*. *Anim. Behav.* **74**, 995–1004. (doi:10.1016/j.anbehav.2007.02.028)

15. Bioacoustics Research Program. 2008 *Raven Pro: interactive sound analysis software*. Ithaca, NY: The Cornell Lab of Ornithology.

16. R Development Core Team. 2011 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

17. Bates D, Maechler M. 2009 lme4: linear mixed-effects models using S4 classes. See http://lme4.r-forge.r-project.org/.

18. Griffin AS. 2004 Social learning about predators: a review and prospectus. *Anim. Learn. Behav.* **32**, 131–140. (doi:10.3758/bf03196014)

19. Maloney RF, Mclean IG. 1995 Historical and experimental learned predator recognition in free-living New-Zealand robins. *Anim. Behav.* **50**, 1193–1201. (doi:10.1016/0003-3472(95)80036-0)