Current Biology
Dispatches

Animal Behavior: The Raised-by-Wolves Predicament

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https://doi.org/10.1016/j.cub.2019.09.064

Social learning poses a particular problem for brood parasites, which are raised by adults of another species. Brood-parasitic cowbirds use a password, a simple signal that aids the young in identifying appropriate models for learning of their species' behaviors.

For millennia, stories have been told of human infants raised by wolves or other animals, under conditions that preclude social learning from other humans [1]. Although such reports are questionable, better verified cases of severe social deprivation exist, such as the deliberate isolation of a child by its parents [2]. One general consequence of severe social deprivation in human infants is that language development is greatly impaired, such that normal speech may never be acquired, even if social isolation is ended [3]. These effects of social deprivation constitute one line of evidence (albeit a grim one) showing that humans are vocal learners. Outside of humans, vocal learning is best known in songbirds, a group comprising thousands of species within the perching bird order Passeriformes. In songbirds, the details of at least one category of vocalization, namely song, are typically learned from adult conspecifics [4]. Within the songbirds, however, a parallel to the raised-by-wolves predicament is routinely experienced by a small subset of species, those that are obligate brood parasites. In these species, adults never undertake parental care and instead always lay their eggs in the nests of other species, leaving their young to be raised to independence by the host adults. How then are the young of brood parasites able to develop songs typical of their own species? A new study by Matthew Louder, Mark Hauber and colleagues [5] in this issue of *Current Biology* tests one proposed answer to this question: the password hypothesis.

According to the password hypothesis, a simple, non-learned cue is used to trigger species recognition, thus allowing a naïve young animal to focus its attention on appropriate models for social learning. The hypothesis was originally proposed [6] for the brown-headed cowbird (*Molothrus ater*), an obligate brood parasite that parasitizes hundreds of host species over a wide range in North America (Figure 1). As is typical for songbirds, male brown-headed cowbirds raised in isolation produce abnormal versions of the species' song [7], whereas males with appropriate social experience produce normal songs, incorporating additional details indicative of the song's geographic origin [8]. A candidate for a password cue in this species was identified in the female chatter call [6], a particularly simple vocalization consisting of a single note type repeated in a series [9]. Chatters are often given by females in immediate response to male vocalizations [9], and thus could serve as a cue to the occurrence of male cowbird song as well as to the presence of adult female cowbirds. In a previous test of the password hypothesis, it was shown that both six-day-old nestling cowbirds and two-month-old juveniles respond preferentially to female chatter relative to control sounds, the nestlings by begging more and the juveniles by approaching more readily [6]. A subsequent study demonstrated neural responses to chatter, with both juvenile and adult cowbirds showing greater expression of the immediate early-gene ZENK in their auditory forebrains in response to female chatter compared to control sounds [10]. In addition, female cowbirds respond with courtship displays preferentially to songs that they have previously heard paired with chatter [11].

In their study, Louder and colleagues [5] provide a definitive test of the password hypothesis in brown-headed cowbirds, showing that the chatter password can open the door for learning even the songs of a different species. In a first experiment, young male cowbirds were hand-reared in social isolation and then tutored daily for 30 days with songs recorded from canaries (*Serinus canaria*). One set of males heard each canary song paired with a recording of cowbird chatter, while a second set of males heard canary songs paired with a control sound, the coo of a mourning dove (*Zenaida macroura*). At the end of training, the cowbirds were recorded and their songs compared back to the canary training songs using spectrogram cross-correlation [12]. Mean correlation values were in general low, indicating that none of the cowbirds produced accurate copies of canary songs. Nevertheless, correlation values were significantly higher for the experimental males than for the controls, demonstrating that the young cowbirds learned songs that were paired with chatter better than those that were not paired. As a further test of the effects of pairing song with the password, both sets of subjects in this experiment were played the canary songs used in their training and then sacrificed for measurement of gene expression levels. A number of genes from the auditory forebrain showed differences, in particular upregulation of genes linked to nervous system development in those birds that had been trained with chatter-paired canary songs relative to the controls. Exposure to songs linked to the password thus caused just the sort of transcriptional changes that might be involved in song learning and memory.

Figure 1. Young brood parasites are raised by another species.
A juvenile brown-headed cowbird (left) is fed by an adult Carolina wren. The young of brood parasites such as cowbirds are raised by adults of other species, which limits their opportunities for social learning of species-typical behaviors such as song. (Photo: © David Kinneer.)

In a second experiment, Louder and colleagues [5] tested whether chatter calls also function to focus attention of female cowbirds on particular songs. Here, the subjects were juvenile female cowbirds that had been raised with no exposure to cowbird song. Each subject was trained for 14 days with both a canary song paired with cowbird chatter and a canary song paired with dove coos. Then each subject was played either its chatter-paired canary song or its coo-paired canary song prior to measurement of gene expression levels in the auditory forebrain. Attention was directed in particular to six genes that prior work with zebra finches (*Taeniopygia guttata*) had singled out as possible markers of song familiarity, in that expression of these genes increases in response to hearing song but less for familiar song than for novel song [13]. In the female cowbirds, expression of all six of these genes was lower in response to chatter-paired canary song than in response to the coo-paired canary songs, and for four of the genes the differences were statistically significant. These four genes and others that were differentially expressed in this experiment are involved in neural processes, such as memory formation. These genomic responses indicate that the young female cowbirds also learned the canary song that had been paired with the proposed password better than they learned the control canary song.

Password-triggered song learning in female cowbirds may have an indirect effect on male song learning. Male cowbirds are known to be influenced in song development by adult female cowbirds, even though these females do not sing [14]. Females apparently exert their influence on males via a visual signal, a rapid wing stroke, which they give in response to preferred songs; males respond in turn to the wing stroke by increasing production of those songs that elicit it [15]. By this mechanism, females stimulate males to include elements in their songs that they would not otherwise incorporate.

Louder and colleagues [5] suggest that password-like mechanisms might operate not only in brood parasites but also in species with more conventional life histories, in which young are raised by adults of their own species. In some non-parasitic species, young males have been shown to have an innate predisposition to learn their own species' song in preference to heterospecific songs [16,17]. In one such species, the white-crowned sparrow (*Zonotrichia leucophrys*), juvenile males are strongly influenced in their choice of song models by the presence of an initial, pure-tone whistle, so much so that adding a whistle to a heterospecific song will cause young males to learn that song [18], in much the same way that Louder and colleagues [5] have shown for cowbird chatter. Genetically encoding the rules for recognizing a simple password such as a whistle or chatter may be easier than encoding recognition of all the features of a complex song. Thus, many songbirds, whether brood parasites or not, may use a password mechanism to guide social learning towards appropriate models.

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