

A password for species recognition in a brood-parasitic bird

Mark E. Hauber*, Stefani A. Russo and Paul W. Sherman

Department of Neurobiology and Behavior, Cornell University, Ithaca, NY 14853, USA

Recognition of conspecifics is an essential precursor of sexual reproduction. Most mammals and birds learn salient features of their parents or siblings early in ontogeny and later recognize individuals whose phenotypes match the mental image (template) of relatives closely enough as conspecifics. However, the young of brood parasites are reared among heterospecifics, so social learning will yield inappropriate species recognition templates. Initially, it was inferred that conspecific recognition in brood parasites depended on genetically determined templates. More recently it was demonstrated that learning plays a critical role in the development of parasites' social preferences. Here we propose a mechanism that accommodates the interaction of learned and genetic components of recognition. We suggest that conspecific recognition is initiated when a young parasite encounters some unique species-specific signal or 'password' (e.g. a vocalization, behaviour or other characteristic) that triggers learning of additional aspects of the password-giver's phenotype. We examined the possibility that nestlings of the obligate brood-parasitic brown-headed cowbird (*Molothrus ater*) could use a species-specific vocalization, the 'chatter', as a password. We found that six-day-old nestlings responded (begged) significantly more frequently to playbacks of chatters than to other avian sounds and that two-month-old fledglings approached playbacks of chatters more quickly than vocalizations of heterospecifics. Free-living cowbird fledglings and adults also approached playbacks of chatters more often than control sounds. Passwords may be involved in the ontogeny of species recognition in brood parasites generally.

Keywords: begging; brood parasite; cowbird; discrimination; imprinting; phenotype matching

1. INTRODUCTION

The grossest blunder in sexual preference, which we can conceive of an animal making, would be to mate with a species different from its own [...]. Fisher (1958)

Species discrimination is obviously essential for sexual reproduction. Surprisingly, therefore, most mammals and birds do not recognize conspecifics from birth, but rather learn species characteristics (ten Cate *et al.* 1993; Laland 1994; Irwin & Price 1999) during early associations with their parents or siblings (e.g. Clayton 1988; Grant & Grant 1997; Kendrick *et al.* 1998). Such 'imprinting' (Lorenz 1937; Bateson 1966; Salzen 1998; ten Cate & Vos 1999) involves the formation of an internal representation of salient phenotypic attributes, i.e. a recognition 'template'. Later on, juveniles recognize individuals whose phenotypes match those mental images closely enough as conspecifics (Lacy & Sherman 1983; Sherman & Holmes 1985; Reeve 1989). Learning from parents or siblings is a reliable mechanism because all mammals and most birds provide parental care and young are typically reared in groups, so exposure to conspecifics is a predictable aspect of ontogeny.

However, in some circumstances such social learning will predictably yield inadequate or misleading recognition templates (Holmes & Sherman 1982; Hauber & Sherman 2000). In particular, obligate brood parasites are reared by heterospecifics, so learning the phenotypes of foster parents or nest mates (assuming the nest was parasitized only once) will result in species misidentification (Sherman 1999). Yet obligate brood parasites are

numerous (more than 90 species, i.e. 0.01 of all birds) (Payne 1977; Rothstein 1990; Ortega 1998; Rothstein & Robinson 1998; Davies 2000) and they can obviously recognize sexually compatible mates. How do brood parasites acquire their species-recognition template?

At present, we know very little about the ontogeny of the production and perception components of species recognition in brood parasites (e.g. the cues and templates) (Sherman *et al.* 1997). Initially, recognition templates were thought to be determined genetically (Tinbergen 1951; Hamilton & Orians 1965). More recently, West & King (1987) argued that, as with all behaviours, both genetic and environmental factors are involved in the ontogeny of appropriate species preferences in parasitic birds. Subsequently, it was discovered that the early social environment indeed affects choices of social partners and mates in some brood-parasitic species such as indigo birds (*Vidua chalybeata*) (Payne *et al.* 2000) and great-spotted cuckoos (*Clamator glandarius*) (Soler & Soler 1999).

These results raise an interesting paradox about brood parasites. On the one hand, social learning will predictably yield inappropriate species-recognition templates. On the other hand, early social experiences affect subsequent species recognition. How can these facts be reconciled? Here we present a new hypothesis and supporting evidence that point towards a resolution.

The idea is that the recognition process is initiated by exposure to some unique species-specific attribute, such as a vocalization, behaviour or other physical characteristic. This cue will have to identify its bearer as a conspecific unambiguously—essentially it will be a 'password'. Similar to movement in classical imprinting (Lorenz 1937; Salzen 1998), this password will trigger learning by the naive individual of other aspects of the phenotype of the

*Author for correspondence (meh20@cornell.edu).

password giver, thereby enabling it to form a recognition template that incorporates multiple cues. This new, multi-component template will facilitate more accurate recognition and also enable discrimination of conspecifics under different ecological circumstances (e.g. at a distance by sight alone, in occluded habitats by sound alone, etc.).

We investigated the possibility that a particular vocalization of the obligately parasitic brown-headed cowbird (*Molothrus ater*, hereafter simply cowbird) might serve as a password for initiating species discrimination. Cowbirds are common North American icterids (Lanyon & Omland 1999) that parasitize many different species of passerines (Lowther 1993). Anecdotal observations on the time-course of species recognition in cowbirds has suggested the possibility of a password mechanism: juveniles begin associating with conspecifics soon after leaving their foster parents (Woodward 1983; Lowther 1993), juveniles learn various aspects of conspecifics' phenotypes, such as auditory courtship displays, following initial encounters (e.g. Rothstein & Fleischer 1987) and the accuracy of cowbird species recognition improves after lengthy social associations (West *et al.* 1996). Male cowbirds that were housed with canaries (*Serinus canaria*) during their first winter were more likely to court canaries than were male cowbirds that had been housed with conspecifics (Freeberg *et al.* 1995); thus, species recognition is malleable following initial encounters.

Cowbirds possess a variety of unique vocalizations (Rothstein *et al.* 1988, 2000; Lowther 1993). One of these, the 'flight whistle', is a male sexual vocalization that is learned from conspecific adults after a male has attained sexual maturity (Rothstein & Fleischer 1987; O'Loughlen & Rothstein 1993). Thus, flight whistles cannot serve as passwords for juvenile species recognition. Another vocalization, the 'perched song', develops spontaneously in hand-reared males and is recognized by naive females (King & West 1977; West & King 1988). Perched song is also a sexual vocalization and it is rarely made in mid-summer when fledgling cowbirds begin joining flocks (Rothstein & Fleischer 1987; O'Loughlen & Rothstein 1993). Moreover, neither adult cowbirds in the field (Dufty 1982; Yökel 1989) nor hand-reared juveniles in the laboratory are attracted to playbacks of perched songs (Graham & Middleton 1989). Apparently perched song also is not a password.

There is another species-specific vocalization, the 'chatter', that is attractive to adult cowbirds (Dufty 1982; Rothstein *et al.* 2000). Chatters are made by both sexes during social interactions, throughout the breeding season and across the species' range (Rothstein *et al.* 2000). Exposure to conspecifics is not necessary for an individual to begin chattering and there are no clear patterns of geographical variation in the acoustic structure of this call (i.e. no dialects) (Burnell & Rothstein 1994), thereby implying that it is not learned from social partners (Rothstein *et al.* 2000). We investigated whether the chatter could serve as a password for cowbird species recognition by monitoring and recording the behavioural responses of naive nestlings and fledglings to various conspecific and heterospecific vocalizations and the responses of free-living juveniles to playbacks of chatters.

2. METHODS

We studied the responses of juvenile cowbirds in three contexts.

(a) *Nestling begging*

Fifteen nestling cowbirds (five in 1997, six in 1998 and four in 1999) were located in the nests of song sparrows (*Melospiza melodia*) and eastern phoebes (*Sayornis phoebe*) near Ithaca, NY (Hauber 2000; Hauber & Russo 2000). Seven nestlings were left undisturbed in the host nests and eight were removed after zero to two days (mean \pm age s.e. = 0.75 ± 0.37 days) and hand-reared in isolation from adult avian stimuli. When hand- or field-reared nestlings were five to seven days old (5.6 ± 0.94 days), we videotaped their responses to playbacks of a randomized series of conspecific and heterospecific vocalizations including (i) chatters of cowbirds (from females in 1997, males in 1999 and females and males in 1998), (ii) non-chatter vocalizations of cowbirds (perched songs in 1997 and 1999 and perched songs and flight whistles in 1998), and (iii) vocalizations of various heterospecifics including the songs of yellow warblers (*Dendroica petechia*) and wood thrushes (*Hylocichla mustelina*) in 1997, the songs of eastern phoebes and red-winged blackbirds (*Agelaius phoeniceus*) in 1999 and the songs and alarm calls of song sparrows and tree swallows (*Tachycineta bicolor*) in 1998. Four stimulus tapes were used each year with different recordings of each vocalization type. For controls, we videotaped the responses of three- to six-day-old (5.1 ± 0.94 days) song sparrows ($n=11$) from six nests that had been parasitized by cowbirds to the same stimuli. All playback vocalizations were recorded from Peterson (1983) and Elliott *et al.* (1997).

To conduct a playback session, a nestling was removed from its host nest (in the field) or the rearing nest (in the laboratory), placed in a simulated nest in a room by itself and deprived of food for 45–65 min in order to standardize motivation (hunger level) (Kedar *et al.* 2000). Then a video camera and the playback apparatus were switched on, the observer left the room and, following an initial period of 2 min of silence, the various stimuli were presented from a loudspeaker (Radio Shack™ AMX 40–168) located 0.5 m away. Subsequent stimuli were separated by 30–120 s of silence. The peak intensities of playback stimuli were measured with a type 41/34 B&K 0.5-inch (1 inch = 0.0254 m) microphone at 0.5 m. Only one playback session was conducted on each nestling.

Videotapes of each trial were viewed four or more weeks later by observers who were 'blind' as to the type and timing of the playbacks (because the tapes were viewed without sound, displaying only the time-stamp for each recording). Begging (raising the head and opening the beak) was chosen as the response behaviour because it was unambiguous and easily quantified. Using these data, the numbers of playbacks of each stimulus class to which nestlings begged within 3 s following the playback were calculated. For analyses, responses were expressed as proportions. Thus, a nestling that only responded to a female cowbird's chatter among eight playback stimuli, including two chatters, one by a male and the other by a female, received an 'average score' of 0.125 responses per stimulus and a 'specific score' of 0.5 responses per chatter stimulus. In order to estimate the extent of preferential responses to particular stimuli, we also calculated the difference between the specific score and the average score for each playback type separately. Using the above example, this 'discrimination score' for chatters would thus have been $0.5 - 0.125 = 0.375$. This value

indicates a preference for chatters because the random expectation is zero.

(b) *Fledglings' choices*

Twelve nestling cowbirds (three in 1998 and nine in 1999) were removed from parasitized nests just before fledging (i.e. ≤ 11 days) (Lowther 1993) and hand-reared in visual isolation from all other birds and auditory isolation from adult cowbirds (Hauber *et al.* 2000). The five surviving nestlings from experiment (a) were also transferred to this study and treated similarly. We did not know whether the field-reared chicks had ever heard vocalizations (i.e. the chatters) of adult cowbirds. The hand-reared chicks had previously heard playbacks of cowbird sounds, but they had been exposed to heterospecific and conspecific vocalizations in equal proportions and they had not been differentially rewarded with food after begging to any sounds. At fledging, all cowbirds ($n = 17$) were placed in individual cages and given *ad libitum* access to food and water.

Fledglings' preferences for conspecific or heterospecific vocalizations were assessed when they were 60–80 days old (mean \pm s.e. = 65.9 ± 1.1 days), at which age they are independent of their foster parents in nature (Woodward 1983). Tests were conducted in a 5 m \times 5 m \times 5 m room that was divided into four symmetrical sectors with markings on the floor. Two identical, triangular-shaped cages (0.9 m \times 0.6 m \times 0.5 m), each with a protruding perch, were placed in adjacent corners of the room. One of the cages contained a speaker (Radio ShackTM AMX 40–168) and the other contained a similar-looking box. The perch attached to the cage with the real speaker was designated the 'noisy perch' and the one in the cage with the mock speaker was the 'silent perch'. Cowbird chatters and song sparrow songs were played back in a continuous stream for 600 s (1998) or 300 s (1999). The stimulus vocalizations were recorded from Elliott *et al.* (1997) and matched for relative peak intensities. The order in which vocalizations were presented and the sides of the room from which tapes were played were determined in a balanced random manner.

To begin a trial, a fledgling was placed in a small box on the wall opposite the cages. After 2 min the speaker was turned on and the bottom of the box was released, forcing the cowbird to fly. The time it spent in each sector of the room was recorded continuously from behind one-way mirror. Each fledgling was tested twice (1999) or three times (1998) with each stimulus type. Individuals were rested for ≥ 4 h between subsequent trials.

We computed the time that elapsed between the start of a trial and a bird's first entry to the sector of the room closest to the noisy perch for each fledgling. Maximum latencies (601 s in 1998 and 301 s in 1999) were assigned to trials in which the fledgling never entered the sector nearest the noisy perch. In order to compare data across years, latencies were averaged between trials within each playback type for each fledgling and relative latencies were calculated as the ratio of the latency to the total observation time.

(c) *Field attraction*

In 1999 we broadcast chatters ($n = 121$) in the field in order to see whether they would attract free-living cowbirds. For controls we played back chatter-like vocalizations of two related icterids, namely eastern meadowlarks (*Sturnella magna*) ($n = 21$) and red-winged blackbirds ($n = 15$), as well as red-winged blackbird songs ($n = 9$) and music (song clips) ($n = 5$). Playbacks were conducted from 23 June to 16 July 1999, at which point the earliest locally hatched cowbirds were 40–60 days old; this is

the age at which cowbirds typically join conspecific flocks (Woodward 1983; Graham & Middleton 1989). We positioned a tape player (Radio ShackTM CTR 69 Tape Recorder) at each playback site 5–10 m from an observer who sat motionless in a car. Adult and fledgling cowbirds approached occupied vehicles without apparent hesitation.

Playbacks were conducted using a 30 s endless-loop stimulus tape containing a continuous stream of vocalizations and each playback lasted 300 s. Two different tapes were used for each stimulus type and comprised different examples of vocalizations recorded from Elliott *et al.* (1997). Although the natural history of juvenile cowbirds (e.g. habitat preferences and social environment) immediately after they leave their foster parents is poorly known (Woodward 1983), undoubtedly they encounter many different avian sounds both simultaneously and in temporal and spatial isolation. In order to approximate this acoustic environment, we did not equalize the duty cycles of the various playbacks (e.g. by manipulating the natural duration of the stimuli) and we presented stimuli sequentially (Strausberger & Horning 1998; Wagner 1998).

Playback sites were chosen arbitrarily whenever suitable cowbird habitat was encountered beside a country road (e.g. woodland edges, open grasslands and horse and cow pastures). No attempt was made to determine whether cowbirds were present before conducting a trial. The type of playback stimulus was determined randomly. After starting the tape loop, the time at which cowbirds first approached the speaker was recorded and their ages and sexes were identified visually based on plumage characteristics (Lowther 1993). An 'approach' was defined as entry (e.g. flying or walking) into an imaginary half sphere surrounding the tape player with a radius of 3 m. Spatial proximity was chosen as the response behaviour because we were interested in whether chatter calls facilitate joining of cowbird flocks. Only one playback was conducted per site and sequential sites were more than 500 m apart in order to minimize the chances of repeatedly attracting the same birds. For analyses, each trial (site) was considered to be independent.

We continued the experiment in 2000 following the previous year's methods. Between 6 and 22 June we broadcast amplitude-matched vocalizations of the following stimuli in a randomized order (single playbacks of 5 min at each site more than 500 m apart, with two tapes of each stimulus type): chatters ($n = 60$), perched songs ($n = 30$) and flight-whistles ($n = 30$) of brown-headed cowbirds and chatter-like calls of shiny cowbirds (*Molothrus bonariensis*) ($n = 30$), red-winged blackbirds ($n = 30$) and eastern meadowlarks ($n = 30$).

In 2000 we also expanded our playback protocol in order to see whether juvenile cowbirds that could hear playbacks would be attracted to chatters. Between 26 June and 15 July, we located free-living juvenile cowbirds along roadsides ($n = 15$) and played either cowbird chatters ($n = 9$) or heterospecific vocalizations (chatter-like sounds of red-winged blackbirds ($n = 3$) or songs of song sparrows ($n = 3$)) to them. Each type of vocalization was broadcast for 5 min and whether or not the focal juvenile approached the speaker was recorded. As before, playback sites were located more than 500 m apart and used once in order to avoid pseudoreplication, with one exception; at one site a playback was first conducted to an unbanded juvenile and, two weeks later, to a colour-banded juvenile.

All data are reported as means \pm s.e. and statistical tests were two-tailed. We used χ^2 -tests for analysing categorical data and non-parametric statistics for testing for heterogeneity among proportional response variables.

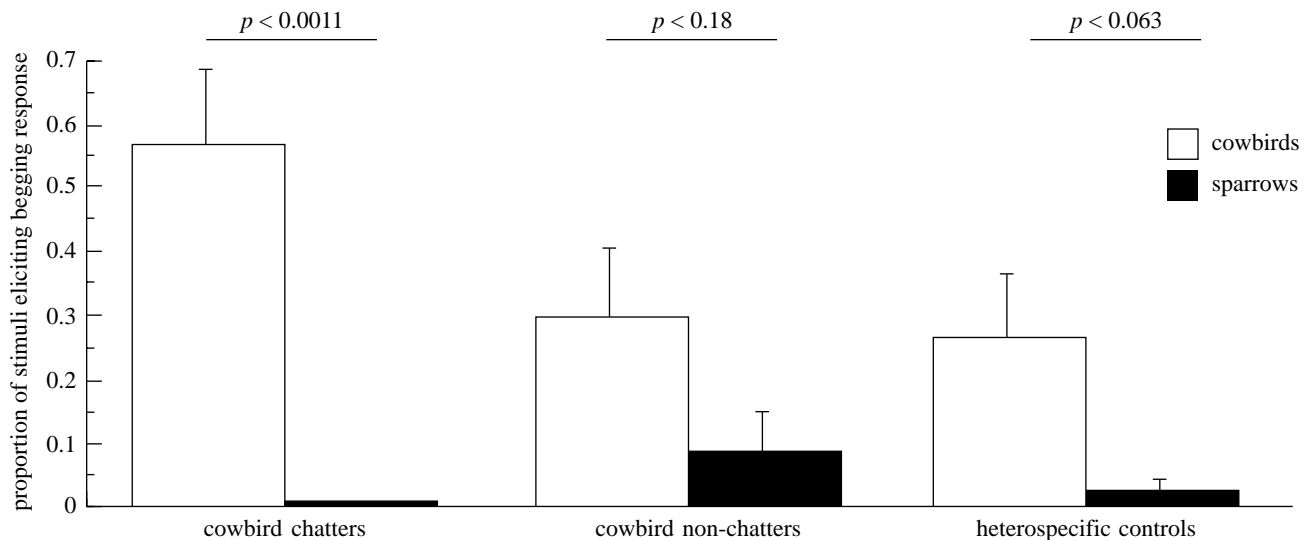


Figure 1. Mean (+s.e.) proportions of playbacks followed by begging (responses per stimulus type) of nestling brown-headed cowbirds (field- and hand-reared nestlings combined, $n = 15$) and song sparrows (naturally reared in parasitized nests, $n = 11$) in response to (i) chatters of male and female cowbirds, (ii) other vocalizations of cowbirds (male songs and flight whistles), and (iii) vocalizations of various heterospecifics (Mann–Whitney U -tests).

3. RESULTS

(a) Nestling begging

Nestling cowbirds begged in response to avian vocalizations equally often regardless of whether they had been raised by their natural hosts or by hand (0.393 ± 0.079 responses per stimulus, $n_{\text{natural host}} = 7$; and 0.312 ± 0.155 responses per stimulus, $n_{\text{hand rearing}} = 8$) (Mann–Whitney U -test, $p > 0.284$). Nestlings' specific responses to chatters also did not differ between rearing conditions (0.643 ± 0.143 responses per chatter, $n_{\text{natural host}} = 7$; and 0.500 ± 0.189 responses per chatter, $n_{\text{hand rearing}} = 8$) (Mann–Whitney U -test, $p > 0.617$). We therefore combined the data from field- and hand-reared chicks for subsequent analyses.

Nestling cowbirds were more responsive to playbacks than nestling song sparrows. Ten of the 15 cowbird chicks (0.67) begged following any acoustic stimulus, but only 3 of the 11 (0.27) song sparrow chicks did so ($\chi^2 = 3.97$, $p < 0.048$) and nestling cowbirds begged to a higher proportion of stimuli per trial than did song sparrow nestlings (average scores, 0.35 ± 0.088 responses per stimulus, $n_{\text{cowbird}} = 15$; and 0.034 ± 0.018 responses per stimulus, $n_{\text{sparrow}} = 11$) (Mann–Whitney U -test, $p < 0.0084$).

The responses of individual nestling cowbirds to conspecific chatters were consistently higher than their responses to cowbird non-chatters and heterospecific vocalizations (specific scores, $n_{\text{cowbird}} = 15$ and Friedman ANOVA, $p < 0.032$) (figure 1). In contrast, nestling song sparrows responded infrequently to all playbacks, regardless of type (specific scores, $n_{\text{sparrow}} = 11$, Friedman ANOVA, $p > 0.36$) (figure 1). In the most specific comparison, nestling cowbirds that had been reared in song sparrow nests responded to chatter playbacks significantly more often than did their host nest mates (0.393 ± 0.079 responses per chatter, $n_{\text{cowbird}} = 7$; and 0.0 ± 0.0 responses per chatter, $n_{\text{sparrow}} = 11$) (Mann–Whitney U -test, $p < 0.0004$).

The discrimination scores of cowbird nestlings ($n = 15$) for chatter playbacks were consistently positive (0.054 ± 0.020 , $p < 0.026$), while their scores were not significantly different from zero for cowbird non-chatter vocalizations (-0.013 ± 0.014 , $p > 0.35$) and heterospecific acoustic stimuli (-0.042 ± 0.023 , $p > 0.101$) (Wilcoxon signed-rank tests). This indicates that nestling cowbirds preferentially responded to chatters but not to other vocalization types.

In this experiment, the playback stimuli varied in duration (1.3 ± 0.35 s) and peak amplitude (71 ± 1.7 dB SPL). Chatters (1.6 ± 0.19 s and 71 ± 1.0 dB) were not at the limits of these variations. A *post hoc* pairwise comparison of the stimulus durations and relative peak amplitudes revealed no significant differences between stimuli that did and did not elicit responses from nestling cowbirds (differences, 0.489 ± 0.288 s, $p > 0.138$ and 0.56 ± 0.369 dB, $p > 0.213$, respectively) (Wilcoxon signed-rank tests). This implies that it was the acoustic structure rather than either the duration or volume of the chatter call that triggered the nestling cowbirds' begging responses.

(b) Fledglings' choices

The relative latencies of fledgling cowbirds in approaching a speaker broadcasting cowbird chatters versus song sparrow songs did not vary between 1998 and 1999 (difference, -0.110 ± 0.139 , $n_{1998} = 5$ and -0.257 ± 0.125 , $n_{1999} = 12$) (Mann–Whitney U -test, $p > 0.341$). Therefore data from the two years were combined.

Thirteen out of 17 fledgling cowbirds (0.76) approached the source of chatter playbacks closely (i.e. they landed on the noisy perch or in the section of the test room containing it) and 9 out of 17 (0.52) approached the source of song sparrow songs closely. This difference was not significant ($\chi^2 = 2.06$, $p > 0.14$). However, fledgling cowbirds approached chatter playbacks with significantly shorter latencies than heterospecific vocalizations: the

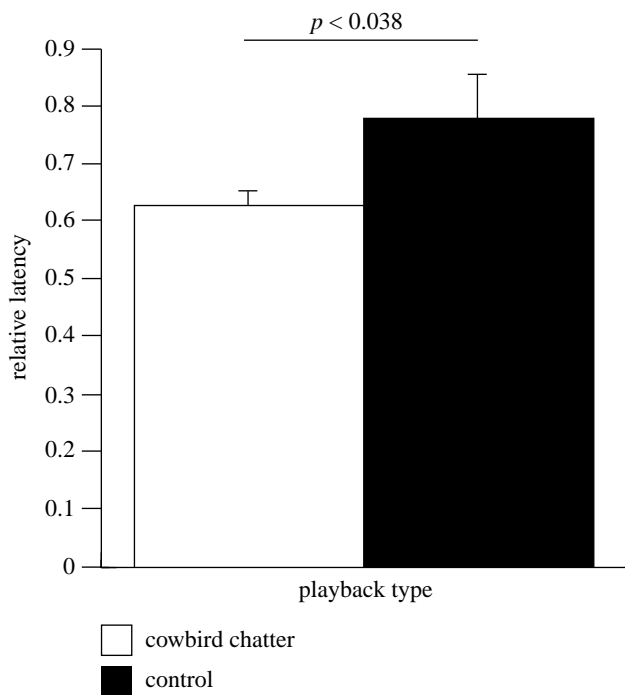


Figure 2. Mean (+ s.e.) relative latencies of hand-reared juvenile brown-headed cowbirds ($n = 17$) to approach speakers playing cowbird chatters versus song sparrow songs closely (control vocalizations) during sequential stimulus presentations in the laboratory (Wilcoxon signed-rank test).

difference in the relative latencies until the first close approach to either call was -0.214 ± 0.096 , which is significantly less than the random expectation of zero (one-sample Wilcoxon test, $p < 0.038$) (figure 2).

(c) **Field attraction**

In 1999 juvenile cowbirds approached the loudspeaker in only 9 out of 171 field playbacks (0.05). All nine responses were to cowbird chatters. Thus, juvenile cowbirds were significantly more likely to approach speakers broadcasting chatters than heterospecific sounds (i.e. 9 out of 121 versus 0 out of 50 control trials) ($\chi^2 = 3.93$, $p < 0.047$). The relative peak amplitudes of the various playback sounds were not related to juvenile cowbird approaches ($n = 171$) (logistical regression, $p > 0.80$).

The juveniles that were attracted to field playbacks had probably had previous experience with chattering adult cowbirds. Their behaviour may also have been influenced by adult flock mates that were attracted to chatter playbacks. In one instance in 1999 juvenile cowbirds arrived at the site of the chatter-playing tape in a mixed-sex flock containing adult conspecifics and another time a juvenile appeared after an adult male cowbird had already approached the speaker. However, the other seven times when juvenile cowbirds approached speakers playing chatters they were not accompanied by adult conspecifics.

Adult cowbirds were also differentially attracted to conspecific chatters. In 1999, adults (unaccompanied by juveniles or individuals of unknown age) approached the speaker in 13 out of 108 chatter playback trials (0.28) versus zero out of 36 playbacks of chatter-like calls of the two related icterids ($\chi^2 = 4.22$, $p < 0.040$). Similarly, in

2000, adult cowbirds appeared at 6 out of 60 conspecific chatter playback trials (0.10) while they were never seen at playbacks of other conspecific vocalizations (perched songs, zero out of 30 and flight whistles, zero out of 30). Adult brown-headed cowbirds did not approach the chatters of shiny cowbirds (zero out of 30) or chatter-like calls of other icterids (red-winged blackbirds, zero out of 30 and eastern meadowlarks, zero out of 30) (overall $\chi^2 = 23.5$, $p < 0.0003$).

The cowbirds' generally low response rates to our field playbacks may have been due, at least in part, to our procedure of conducting trials without locating cowbirds in advance, i.e. in many cases no fledgling or adult cowbirds probably even heard the broadcast chatters. However, when juvenile cowbirds were known to be in the vicinity (i.e. in the late-summer trials in 2000), they approached the speaker in seven out of nine trials (0.78) when it was playing chatters, but never approached when it was playing heterospecific vocalizations (zero out of six trials) ($\chi^2 = 8.75$, $p < 0.0031$).

4. DISCUSSION

Interest in recognition systems, in particular those of species in which social learning will provide misleading or inappropriate recognition templates, has surged recently (e.g. Petrie *et al.* 1999; Mateo & Johnston 2000; reviewed by Sherman 1999; Hauber & Sherman 2000). An obvious example of those circumstances is parasitism and studies have begun to examine the ontogeny of host and conspecific recognition in brood-parasitic birds (e.g. Soler & Soler 1999; Gibbs *et al.* 2000; Hauber *et al.* 2000; Payne *et al.* 2000). In the best-known example, early exposure to the songs of host species results in both mimicry of hosts by adult male viduine finches and preferences for host songs by adult female finches (Payne 1973; Payne *et al.* 2000). These preferences enable the parasitic females to find both host and conspecific males, but host-like vocalizations alone do not provide a sufficient conspecific recognition template. Once in proximity, male and female viduine finches require other cues, such as song syllables or plumage, in order to identify each other (Payne 1973). These characteristics may function in a password-like manner.

Juveniles in many brood-parasitic species begin to flock with conspecifics well before they mature sexually, e.g. great-spotted cuckoos (Soler *et al.* 1995a) and cowbirds (Lowther 1993). Recently, Soler & Soler (1999) reported that exposure to conspecific adults or siblings is necessary for juvenile cuckoos to join flocks, implying that social learning is involved in the development of species recognition. However, they did not investigate how young cuckoos initially discriminate adult conspecifics from heterospecific foster parents, i.e. what aspects of an adult's phenotype cue juveniles to learn the appropriate conspecific recognition template.

This is the issue that we addressed. We hypothesized that the cowbird's species-specific chatter might serve as an initial password that unambiguously identifies the chatterer as a conspecific. Consistent with this, nestling cowbirds preferentially responded to chatters but not to other conspecific and heterospecific vocalizations early in their development, while nestling song sparrows showed

no such discrimination (figure 1). As fledglings, cowbirds continued to discriminate and they approached speakers broadcasting chatters more quickly than speakers playing heterospecific vocalizations (figure 2). Finally, free-living juvenile and adult cowbirds sometimes approached playbacks of conspecific chatters, but they never approached playbacks of other conspecific and heterospecific vocalizations, including the chatter-like calls of a congeneric cowbird and related icterids.

In our experiments, nestling cowbirds were more likely to respond to playbacks overall than similar-aged nestling song sparrows (figure 1). Greater responsiveness to a general set of stimuli may enable the parasites to compete effectively with heterospecific nest mates through more intensive begging and posturing whenever the foster parents arrive (Dearborn 1998; Lichtenstein & Sealy 1998). However, the cowbirds' vigorous and preferential responses to conspecific chatters indicated that begging is not triggered equally by all vocalizations. Differential responsiveness to chatters suggests that there may be a special function for early auditory discrimination of this vocalization.

How can five- to six-day-old cowbirds benefit from responding preferentially to chatters? There are two possibilities. On the one hand, chatters might be acoustically similar to the begging solicitation calls of the most important cowbird host species, so nestlings respond quickly in order to ensure that they are fed. Unfortunately, no comparative acoustic information is available about the begging solicitation calls of the many different cowbird hosts, so we cannot evaluate this possibility. On the other hand, nestlings' responses may indicate their perceptual selectivity for chatters (Dooling & Searcy 1982; Whaling *et al.* 1997). If adult female cowbirds return to nests they parasitized (as do great-spotted cuckoos) (Soler *et al.* 1995*b*; Soler & Soler 1999) and chatter at their chick, the juvenile could form an unambiguous species-recognition template by learning their mother's phenotypic traits. Consistent with this, (i) the eyes of nestling cowbirds open by the time discrimination of chatters occurs (five to six days post-hatching), potentially enabling them to learn their mother's physical features, (ii) nestlings respond to adult chatters by raising their heads, opening their eyes and looking up (begging) toward the sound source, and (iii) female cowbirds sometimes associate with their own young soon after fledging (Hahn & Fleischer 1995). However, it is doubtful that female cowbirds routinely revisit their own nestlings (Lorenzana & Sealy 1998), although circumstantial evidence suggests that they sometimes do (e.g. Sealy 1994; Arcese *et al.* 1996; M. E. Hauber, personal observation). Even if females do not always attempt to return or die before being able to do so, juveniles' perceptual selectivity for chatters would still enable young to locate chattering individuals in flocks of conspecifics shortly after achieving independence from host parents. Thus, the password hypothesis does not depend on the mother's return.

In previous experimental work with hand-reared cowbirds, Graham & Middleton (1989) found that fledgling parasites did not discriminate between cowbird chatters and red-winged blackbird calls. However, these authors examined the responses of fledglings that were approximately one month younger than our test subjects and they used simultaneous playbacks, measured time

spent perching near playback speakers but not latency to approach or time spent on the ground nearby and studied relatively few birds ($n = 4$ for chatter/heterospecific trials). In contrast, we studied a larger sample of older fledglings ($n = 17$) and opted for a sequential presentation of chatters and songs of song sparrows in order to ensure that our subjects responded to the specific playback stimuli rather than an interaction of simultaneously presented vocalizations (Wagner 1998). We also recorded subjects' locations continuously (whether on a perch or on the ground), because we had found that juveniles often walked toward speakers in previous experiments using the same test chamber (Hauber *et al.* 2000).

The password hypothesis predicts that recognition of conspecifics is initially triggered by a specific cue, but it is silent about the ontogeny of this early perceptual selectivity. Although we removed some nestlings from parasitized nests soon after hatching, it is still possible that *in ovo* or early post-hatching exposure to conspecific chatters occurred and influenced their preferences (e.g. Lickliter & Lewkowitz 1995). In the absence of such early social exposure, nestling cowbirds' preferences for chatters might be determined genetically through the architectural design of perceptual filters in their auditory system (Marler 1997). Alternatively, nestlings' preferences might develop through an interaction of genetic and learning processes (West & King 1987), for example during experiences with parasitic nest mates in multiply parasitized nests (Soler & Soler 1999; Hauber 2000) or via self-referent phenotype matching (Sherman 1991; Hauber & Sherman 2000; Hauber *et al.* 2000; Mateo & Johnston 2000). However, multiple parasitism occurs too unpredictably in cowbirds (Lowther 1993; Hauber 2000) to be a reliable mechanism. Self-referencing is a possibility (Graham & Middleton 1989; Sherman *et al.* 1997) and the results of a previous experiment (Hauber *et al.* 2000) showed that naive cowbirds associated preferentially with individuals whose plumage colour matched their own. Although no experiments assessing self-referencing of vocalizations have been performed, it is feasible because the waveforms of adult cowbird chatters and fledgling begging calls are similar (Woodward 1983; Burnell & Rothstein 1994) and the nestlings' own begging calls have peak frequencies (Broughton *et al.* 1987) that are most similar to the adult chatters among our playback stimulus set.

Once conspecific discrimination initially occurs additional cues may be added to the species-recognition template. For example, a password-like mechanism of species recognition was recently demonstrated in white-crowned sparrows (*Zonotrichia leucophrys oriantha*) (Soha & Marler 2000). In this species, a short, species-specific vocalization cues young males to recognize and predictably imitate only songs (including experimentally constructed heterospecific songs) that are preceded by this 'whistle'.

Likewise, in cowbirds chatters may be necessary but not sufficient for species recognition. Hahn & Fleischer (1995) suggested that adult female cowbirds may seek out their independent offspring, perhaps introducing themselves to the juveniles with chatters and behavioural cues (e.g. 'a preening invitation display') (Rothstein 1977) as well, perhaps, as plumage characters (Graham & Middleton 1989; Hauber *et al.* 2000). Finally, continued

social experience with flock mates and learning of cultural traits (e.g. vocal dialects) clearly influences subsequent species and mating preferences of juvenile cowbirds (Rothstein & Fleischer 1987; Freeberg *et al.* 1995; O’Loghlen & Rothstein 1995; West *et al.* 1996; Freeberg 1999).

Juvenile cowbirds normally begin associating with conspecifics soon after leaving their foster parents (Woodward 1983; Lowther 1993). Chatters are reliable, error-proof cues about whom to associate with because cowbirds forage in single-species flocks in mid-summer (Lowther 1993; M. E. Hauber, personal observation). However, learning additional cues, such as plumage and vocalizations, is likely to be adaptive during the subsequent stages of cowbird life history. For example in late-summer and, in particular, on the wintering grounds cowbirds join large, mixed-species flocks with other blackbirds (Lowther 1993; Ortego 2000), within which auditory cues alone may be difficult to discern due to the sheer number of vocalizing conspecifics and heterospecifics (up to more than 10^6 birds) (Ortego 2000).

In general, conspecific recognition requires the use of unambiguous initial cues, such as the traits of parents and siblings. Passwords may be particularly important for recognition of conspecifics or kin in species where the young are typically first exposed to heterospecifics or a mixture of kin and non-kin. Identifying the vocal, chemical and visual traits that serve as passwords and their role in the development of conspecific recognition templates will contribute to our understanding of learning ontogenies and how social and self-referent cues are used in recognition systems generally.

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