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First contact: A role for adult-offspring social association in the species recognition system of brood parasites

Mark E. Hauber

Department of Neurobiology and Behavior, Cornell University, Ithaca, NY 14853-2702, USA; current address: Department of Integrative Biology, Museum of Vertebrate Zoology, University of California, Berkeley, CA 94720-3140, USA (e-mail: hauberm@socrates.berkeley.edu)

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Social parasites typically develop in the absence of close relatives and receive parental care from foster parents. How do these parasitic offspring later recognize their kin or conspecifics as compatible social or sexual partners? Recent evidence suggests that association of fledgling obligate brood parasitic birds with adults of their own species may be more frequent than previously thought. This early social contact has been implicated to function in cuing species-typical behaviors, including conspecific recognition. I tested assumptions and predictions of this "first contact" hypothesis using field observations and laboratory choice trials with brown-headed cowbirds (*Molothrus ater*). In support of the "first contact" scenario, playback experiments in the field indicated that female cowbirds were predictably detected near fledgling cowbirds. In the laboratory, adult cowbirds of both sexes spent consistently more time in the proximity of conspecific juveniles than adult hosts. Independent, hand-reared juvenile cowbirds also showed consistent biases in spatial preference for female cowbirds over hosts, even in the absence of prior conspecific experience. This preference for conspecific stimuli by juvenile parasites may have been mediated not only by phenotypic but also by behavioral cues in choice trials because the heterospecific social stimuli more frequently directed aggressive behaviors at the young cowbirds than did conspecific stimuli. These findings support the claim that, against conventional wisdom, adult brood parasites may play a role in the earliest stages of social development of conspecific young. Returning to parasitized broods to facilitate the conspecific recognition of their own offspring is likely to increase the fitness of, and represent a form of parental care by, territorial female cowbirds because most parasitic fledglings encountered within their breeding range are predictably their progeny.

Introduction

By definition, interspecific social parasites are raised by foster parents and typically develop alone or in the presence of unrelated brood mates (Payne 1977, Davies 2000). Therefore, early social learning (i.e., the characteristic ontogenetic path for kin- and species recognition in most avian species: Sherman *et al*. 1997, Irwin & Price 1999, ten Cate *et al*. 1999) by young parasites would predictably yield misleading information about the traits of conspecifics (Holmes & Sherman 1982, Hauber & Sherman 2001). How do developing parasites recognize compatible social partners and mates upon independence from their hosts? Despite much interest in the behavioral and physiological adaptations of brood parasitic birds to their unusual life history, published data on the early social development of most obligate brood parasites, especially the non-songbird species including the European cuckoo (*Cuculus canorus*), the South American black-headed duck (*Heteronetta atricapilla*), and the African honeyguides, is scarce (Ortega 1998, Davies 2000).

Parasites may follow an ontogeny of conspecific recognition that is independent of early social experiences (King & West 1977), using perhaps perceptual filters of their sensory systems that are under strong genetic control (Hamilton & Orians 1965, Ortega 1998, Davies 2000). Alternatively, they may use self-referent phenotype matching to learn about their own traits and later associate with individuals that carry similar characteristics or tags (Sherman 1991, Hauber *et al*. 2000, Mateo & Johnston 2000, Riolo *et al*. 2001). Both of these hypotheses are supported for brown-headed cowbirds (*Molothrus ater*) because observational evidence from the field and experimental results from laboratory trials demonstrated that the lack of early social experience with conspecifics in this parasite does not preclude subsequent contact with conspecifics as their preferred social and sexual partners (King & West 1977, Rothstein & Fleischer 1987, Graham & Middleton 1989, Hauber *et al*. 2000, Hauber *et al*. 2001).

When a specific phenotypic cue, the plumage color of the developing parasites, was manipulated by dyeing feathers, Hauber *et al*. (2000) found that social preferences of two-month old hand-reared brown-headed cowbirds were altered. That young cowbirds preferentially associate with others that are similar in appearance (e.g., due to their sex and/or age: Ortega *et al*. 1996, Farmer & Holmgren 2000) to themselves was also indicated by other studies of captive cowbird flocks (Freeberg 1999, Smith *et al*. 2002, White *et al*. 2002). The plumage-manipulation experiment provided critical support for self-referencing and falsified predictions of the non-learning hypothesis (Hauber & Sherman 2001; M. E. Hauber & P. W. Sherman unpubl. data) suggesting that, even at this early age, social choices by cowbirds are malleable.

The developmental pathways of conspecific recognition in other sensory modalities, including vocal cues that are known to play an important role in juvenile brown-headed cowbirds' social preferences (King & West 1977, Rothstein *et al*. 2000, Hauber *et al*. 2001), remain unclear. As one possibility, several studies suggested that natural or experimental variation in the social environment of some young parasites affected aspects of their species typical behaviors, including perhaps their subsequent choices of social partners and mates across several brood parasitic bird species (e.g., presence or absence of adult conspecifics in the social environment of fledgling brown-headed cowbirds: White *et al*. 2002; species composition of winter flocks of yearling cowbirds: Freeberg *et al*. 1995; presence of conspecific nestling and/or adult parasites at nests parasitized by great spotted cuckoos, *Clamator glandarius*: Soler & Soler 1999; mimicry of or preference for host species' song by, respectively, males or females of *Vidua* spp.: Payne 1973, Payne *et al*. 2000). These observations from cowbirds, cuckoos, and indigobirds imply significant malleability and outline a potentially critical role for learning not just from self but also from early social partners in the developmental pathways of parasitic species recognition.

Brown-headed cowbirds (hereafter simply 'cowbirds') are a widespread, highly social North American obligate brood parasitic species. Young cowbirds join flocks of conspecifics soon after becoming independent of their foster parents (Woodward 1983, Hauber *et al*. 2001). Previous studies showed that hand-reared naïve cowbirds approached models of male conspecifics preferentially in the presence of heterospecific stimuli (Graham & Middleton 1989) and preferred the proximity of a cage with a conspecific female rather than an empty cage (Hauber *et al*. 2000). These findings suggest that juvenile cowbirds are able to recognize and discriminate conspecific adults even in the absence of or limited prior social experience with other cowbirds (King & West 1977). This is not surprising because in some populations of cowbirds adult conspecifics leave the breeding grounds before juveniles become independent of hosts and hence are unable to join flocks of conspecific adults (Rothstein & Fleischer 1987, O'Loghlen & Rothstein 1995).

That naïve parasites are able to recognize conspecifics in the field and the laboratory does not eliminate a potential role and fitness benefit for some adult parasites to cue or facilitate conspecific recognition by juveniles under natural conditions (Hahn & Fleischer 1995, Hahn *et al*. 1999, Hauber *et al*. 2001, White *et al*. 2002). In another brood parasite, the great spotted cuckoo in the Mediterranean basin, the absence of adult or nestling conspecifics was associated with a reduced probability of juvenile cuckoos being detected in conspecific groups (Soler & Soler 1999). In turn, the aggregation of fledgling parasites was beneficial because it resulted in increased provisioning by host parents (Soler *et al*. 1995).

Adult cowbirds in many populations are site faithful throughout much of the breeding season, with female cowbirds showing > 50% exclusive spatial use and access to host nests within their breeding areas which they also defend from same sex conspecific intruders (i.e., breeding territory: Dufty 1982b, Darley 1983, Alderson *et al*. 1999, Hahn *et al*. 1999, Raim 2000 but *see* Elliott 1980 for geographic variability). In an extensive genetic study in the northeastern USA, Hahn *et al*. (1999) demonstrated that radio-tagged resident female cowbirds were related at above chance levels to the parasitic offspring that were located and sampled for DNA within the females' respective breeding territories. Mechanistically, therefore, mother cowbirds may be able to interact with those of their genetic young that fledged from host nests, especially if these nests had been parasitized during the early part of the breeding season (Hahn & Fleischer 1995). Tests of genetic relatedness between local adult males and juveniles have not yet been published but are likely to be less tightly correlated because of the male-biased operational sex-ratio of adult cowbirds and the frequent absence of male cowbirds from their mates' breeding territory (Lowther 1993).

Socialization with adult conspecifics is likely to be adaptive for juvenile cowbirds and they typically join other cowbirds within weeks after fledging from the host nests (Woodward 1983, Hauber *et al*. 2001). Functionally the nature and the context of the benefits from this early flocking with conspecifics remains unclear, but the possibilities include foraging in the safety within larger flocks, locating communal nocturnal roosts more rapidly, establishing dominance hierarchies at an earlier age, crystallizing conspecific recognition templates by incorporating more cues, and learning a greater repertoire of cultural vocal and courtship traits from the local song dialect (West & King 1988, O'Loghlen & Rothstein 1995, Freeberg *et al*. 1995, West *et al*. 1996, Freeberg 1999, Hauber *et al*. 2000, Hauber *et al*. 2001, Smith *et al*. 2002, White *et al*. 2002).

Adult cowbirds may therefore bestow fitness benefits upon juvenile conspecifics if they reduce the time that it takes for fledgling parasites to search for conspecifics. For example, adults may seek out and preferentially associate and interact with juvenile cowbirds. Alternatively, independent parasitic fledglings may approach adult conspecifics that, unlike adults of most host species (Ortega 1998), do not respond aggressively to and tolerate young cowbirds. Once "first contact" is established, juveniles may follow these adults to communal foraging and roosting sites and receive the potential benefits of early socialization with conspecifics.

The first contact hypothesis is feasible for several of the mentioned parasitic species because territorial adult cuckoos and cowbirds have been anecdotally observed at parasitized nests (Soler *et al*. 1995, Sheppard 1996, Dearborn *et al*. 1998, Soler & Soler 1999). It is therefore possible that, despite conventional wisdom, the early social environment of some brood parasitic young predictably includes adult

Fig. 1. A typical nesting site of eastern phoebes under the deck of a suburban house at Ithaca, NY. Insert: a parasitic cowbird egg is easily noticed among parasitized phoebe eggs because of its distinctive spotting (photo credits: Mark E. Hauber).

conspecifics (Hahn *et al.* 1999, Soler & Soler 1999). If, for example, female cowbirds usually return to nests they had parasitized (as suggested by Hahn & Fleischer 1995) and identify themselves to their chick via a 'password' (i.e., a cowbird-specific vocalization, behavior, or physical characteristic, Soha & Marler 2000), this could induce the chick to learn the entire cowbird-specific phenotype (e.g., plumage patterns, bill morphology) from an unambiguously appropriate model (i.e., its mother). Recently, Hauber *et al.* (2001) suggested that the cowbird 'chatter,' a species-specific contact call most often emitted by territorial females and in-stress males (Dufty 1982a, Rothstein *et al.* 1988, Rothstein *et al.* 2000, Burnell & Rothstein 1994), may function in such a password-like manner because both hand-reared and wild juvenile cowbirds preferentially approached chatter playbacks over control vocalizations.

In this study I report the findings from several field and laboratory experiments that were conducted with adult and juvenile brown-headed cowbirds. These results address critical assumptions and predictions of the "first contact" hypothesis. To determine whether (1) adult, especially female, cowbirds predictably form a part of the early social environment of developing parasites and (2) at which developmental stage adult (female/mother)–juvenile association is likely to occur in parasitic cowbirds, I used videotaping and auditory playbacks in the field to detect adult cowbirds in the proximity of parasitized nests. I predicted that female cowbirds would be more likely to be detected near parasitized than non-parasitized host nests during the fledgling stages of parasitic young. To examine whether adult and juvenile cowbirds preferentially associate and interact with conspecifics, I observed captive cowbirds' spatial and behavioral association with conspecifics in the presence of heterospecifics using a simultaneous laboratory choice paradigm. I predicted that both adult and socially inexperienced juvenile cowbirds should preferentially associate with conspecific juveniles and adult females, respectively.

Methods

Study species and field site

The brown-headed cowbird is a common obligate brood parasitic species throughout much of North America (Lowther 1993). Cowbirds breed between between late April and July in Ithaca, NY (42°24´N, 76°30´W), Northeastern USA, and they parasitize a wide variety of species, ranging from flycatchers to warblers and sparrows (Hauber & Russo 2000). The general environs of the research site and methods are described in Hauber (2002). For the field portion of this study I monitored nesting attempts of Eastern phoebes (*Sayornis phoebe*, hereafter simply 'phoebes') during the 2000 and 2001 breeding seasons. Phoebes near Ithaca frequently nest on human-made structures, such as under eaves (Fig. 1) and bridges, and are frequently hosts for cowbirds (i.e., each year > 25% of first nesting attempts are parasitized: Hauber 2001, Hauber 2002).

Video recordings of host nests

To determine if female cowbirds return to parasitized nests during the nestling stage of parasitic young, I visually monitored 15 parasitized phoebe nesting attempts at 12 parasitized phoebe nests in 2000 using video cameras placed at ≥ 2 m from parasitized phoebe nests. During the nestling stage of parasitic cowbirds (ages 0–10 days after hatching, Lowther 1993) I recorded video footage of parasitized nests and their proximity of ≥ 1 m radius. Recordings were taken throughout daylight hours and lasted until the battery or the film ran out (≤ 1.5 hours). I also monitored non-parasitized nesting attempts with video cameras using the same methods. While videotaping at and around the nest is of limited value when assessing the proximity of adult cowbirds to parasitized nests, the specific hypothesis that was tested by this portion of the study (i.e., that the cowbird mothers come back to their nests: Hauber *et al.* 2000, Hauber *et al.* 2001) predicted that female cowbirds would land on the nest itself to show their visual phenotype to their nestling young. Because phoebe nests are deep cups and, when parasitized, most contain only a single cowbird egg (Hauber 2001), the young cowbirds would not be able to look at other conspecifics throughout the major part of the nestling period unless an adult physically landed on the nest structure. Hence, video footage of the nest itself was deemed sufficient to address predictions of the hypothesis. In addition, I took notes the sources of sounds that were recorded by the video footage.

I assumed that because of the proximity of all monitored nests to human activities the presence of video cameras did not represent a significant disturbance for either hosts or parasites. Accordingly, the examination of the footage indeed showed that phoebe parents typically resumed their feeding trips within 5 min. of set-up. Video tapes were viewed at regular speed ≥ 5 months following the breeding season by an observer whose primary task was to record phoebe feeding rates (M. E. Hauber & K. Montenegro unpubl. data) but who also looked and listened for the presence of adult cowbirds at the focal nests.

Chatter playbacks

Although videotapes can provide direct evidence for association between adult females and their nestlings, they are not suited to examine potential association between mobile adults and fledgling parasites. Therefore, I used a playback paradigm as a surrogate measure of whether adult cowbirds occurred in the vicinity of phoebe nests. The rationale behind this indirect measure of adult detection was that fledgling cowbirds, after they leave their hosts' nests, are still dependent on the parental care of their foster parents for several days (Woodward 1983). Young, dependent cowbirds are likely to remain near their natal nests, especially because most of their hosts are territorial passerines (Lowther 1993). If so, adult female cowbirds could interact with fledged offspring near parasitized nests.

To quantify if adult cowbirds were near parasitized nests, I conducted 5 min. playback sessions using continuous streams of several examples of female and male cowbird chatter calls recorded in northeastern North America from (Eliott *et al.* 1997) on two RadioShack loop-tapes. Vocalizations from one or the other tape were broadcast ≤ 5 m of active phoebe nests at consistent amplitudes. Both male and female cowbirds are attracted to conspecific chatters and they often vocalize in response to these playbacks (Dufty 1982b, Hauber *et al.* 2001). Rothstein *et al.* (2000) reported that cowbird detectability increases by several folds when using chatter playbacks compared to conventional point counts (but *see* Miles & Buehler 2000). Preliminary observations showed that adult cowbirds approached chatter playbacks at the typical experimental volumes from ≤ 50 m away. In turn, female cowbirds' breeding territories are > 50 m in radius (Dufty 1982b, Darley 1983, Alderson *et al.* 1999, Hahn *et al.* 1999, Raim 2000; pers. obs.). Therefore, a pattern of repeated approaches to chatter playbacks can be taken as an indicator of greater spatial proximity to the playback site than predicted by chance. Another explicit assumption behind using detectability to chatters as a surrogate measure of adult cowbirds' distance from parasitized nests is that if cowbirds were closer to parasitized nests overall they would be more likely to hear and, thus, approach playbacks. For instance, according to this logic, if adult cowbirds spent more time near parasitized nests during the incubation than the nestling stage of parasitic young, more trials during the incubation than the nestling stage should detect cowbirds. Such results would support, but, obviously, not imply that the function of why adult cowbirds approach playbacks near host nests is to associate with their young!

Playbacks were conducted repeatedly at each site during the incubation stage of cowbird eggs (0–10 days after clutch completion and the onset of incubation, developmental stage I), the nestling stage (11–20 days, developmental stage II), the fledgling stage (21–30 days, developmental stage III), and the early independent stage (31–40 days, developmental stage IV) of young cowbirds (developmental stages after Woodward 1983, Lowther 1993). Playbacks took place both at parasitized phoebe breeding attempts and during the equivalent time periods at non-parasitized phoebe nests, throughout daylight hours, using an unconcealed tape-player, and with an observer sitting in a nearby car. Previous experiments showed that cowbirds, both males and females, readily approached such playback setups (for a different set of chatter playback data *see* Hauber *et al.* 2001). Preliminary observations also suggested that cowbirds in Ithaca, NY, occured in the vicinity of their potential breeding grounds throughout the day (based on radio tracking and locating color banded females: personal observations). Also, exploratory multiple regression analyses of the data presented here showed no relationship of date or time of day with the likelihood of detecting cowbirds for either sex (all $p > 0.2$).

No attempt was made to detect cowbirds in the vicinity of nests before the onset of playbacks. As the *a priori* devised response measure of detectability (Hauber 2001), I determined whether male and female cowbirds entered an imaginary 3 m half sphere centered around the tape deck during the duration of the playback. This appeared to be a reliable measure of detectability because in 81% of the cases in which adult cowbirds could be heard vocalizing during the playback sessions, at least one adult cowbird entered the ≤ 3 m vicinity of the tape player. To quantify detection levels, I calculated the number of female and male cowbirds detected during each playback and averaged these values across all playback sessions at each nest for each developmental period. This means, for instance, that if I detected one female and two male cowbirds during the first one of two playback sessions at a parasitized phoebe nest on "Besemer Lane" during the nestling stage and I detected no female cowbirds and two male cowbirds during the second playback, the female and male cowbird detectability scores for "Besemer Lane nestling stage" would be 0.5 and 2, respectively. The number of playback sessions varied at each nest and among developmental stages, but there was no significant relationship between frequency of playbacks and cowbird detectability for either sex (all $p > 0.4$, Spearman rank correlations, developmental stages I: 1.27 ± 0.182 playbacks per nest site, II: 1.59 ± 0.127 playbacks, III: 1.73 ± 0.156 playbacks, IV: 1.31 ± 0.108 playbacks, parasitized and non-parasitized nest sites combined, for number of sites *see* Fig. 1). Therefore, in exploratory analyses I also used categorical data to examine whether or not adult cowbirds were at least once detected (response measure: yes/no) during each developmental stage at either parasitized or non-parasitized nests. In each of the statistical analyses nesting sites were considered independent data points because the average nearest neighbor distance among the monitored phoebe nests was > 2 km, implying that each parasitized host nest was inside the breeding territory of a different female cowbird.

Sample sizes are indicated for each analysis separately and varied because some nesting attempts failed due to predators or inclement weather or had to be excluded because of human interference. Even though this study examined directional predictions of specific hypotheses focused on adult female cowbirds, many of these were not critical tests. Therefore, all statistical tests were two-tailed. The a level was set at 0.05 and analyses were carried out using Stativew® 5 (SAS Institute, Inc.).

Instead of video recordings and multiple chatter playbacks per site, in 2001 I modified the playback protocol at parasitized phoebe nests. I carried out a single 5-min. chatter playback per site between 8:00–11:00 EST (methods as above) at parasitized host nests during either the 10-day long nestling period (developmental stage II) or early fledgling stage (III) to detect adult cowbirds. This method was chosen so as to avoid experimental artifacts due to order effects (e.g., habitation or sensitization) that may have arisen during the multiple playbacks per site in 2000. To determine if female cowbirds were more likely to be detected near parasitized nests than predicted by chance throughout the landscape of this study site, I also compared detection scores with previously published detection levels derived from the same one-site one-5 min. chatter-playback methodology (Hauber *et al.* 2001).

Laboratory trials with adults

To determine if adult cowbirds approached juvenile conspecifics preferentially, I examined the responses of captive females and males to juvenile conspecific and heterospecific stimuli in a simultaneous choice paradigm in July 2000. Captive adults were > 2 year old and included both wild-caught (≤ 3 years prior to this study) and hand-reared individuals (that socialized with the rest of flock for ≥ 1 year). The flock was kept indoors in a mixed-sexed flock of cowbirds and zebra finches (*Taeniopygia guttata*) under natural light conditions. Members of this flock at the time of the experiments appeared to be in breeding condition, as indicated by frequent singing, intraspecific aggression and occasional egg-laying on the floor and in artificial nests (personal observations), and were allowed *ad lib* access to food of mixed seeds and turkey starter, water, and calcium and grit supplements.

Each adult cowbird was tested in choice trials (10 min per trial) with no more than two trials per day (follwing Hauber *et al.* 2000, Hauber *et al.* 2001). The test chamber (5 × 5 × 5 m) contained two identical cages (0.9 × 0.6 × 0.5 m) placed in adjacent corners of the room without a visual obstruction. Both cages had identical perches on which a stimulus bird (inside the cage) and the test bird (outside the cage) could rest. These were the only perches available for test birds to rest above ground. There were two sets of stimulus pairs: the first set comprised of a juvenile-plumaged female cowbird (i.e., < 3 months of age) and an adult, male song sparrow (*Melospiza melodia*). Both stimuli were trapped in the field the day before the onset of experiments using playbacks of conspecific vocalizations (chatters or songs, respectively). Adult cowbirds were tested individually in six separate trials each for their discrimination among this first set of stimuli. To control for side effects, the presentation sides of stimulus birds were switched in a balanced random manner between subsequent trials of each adult cowbird. The second wild-caught stimulus set comprised of a juvenile-plumaged male cowbird and a male red-winged blackbird (*Agelaius phoeniceus*). All test birds were again tested in six separate trials each with randomly switched sides of stimulus presentation. The juvenile cowbirds but not the heterospecifics were subsequently kept in captivity, allowed to molt, and sexed upon molt, while the sparrow and the blackbird were sexed by plumage and song and returned to the wild.

Prior to a trial, each test bird was placed in a cardboard box attached to the wall opposite the cages. At the beginning of a trial, the bottom portion of this box fell out, forcing the cowbird to take flight. The observation room was *a priori* (Hauber *et al.* 2000) divided into symmetrical sections to designate the location of the bird at all times. The behavior and the position of the birds were monitored through a one-way mirror and recorded on an event-recorder. 'Choice-time' was scored by determining the duration when the adult cowbird entered one of two pre-assigned areas nearest to either stimulus and 'proximity time' for each trial to a stimulus was determined by calculating the proportion of total choice-time spent near the juvenile cowbird. For each individual I determined whether they had been exposed to both stimulus types during prior trials (e.g., subject "BB" only approached one and the other stimuli in trials 1 and 2) and calculated the average of proximity times near the juvenile cowbird from all subsequent trials (e.g., trials 3–6) for "BB". Response measures were also averaged for each subject from trials with the two different stimulus pairs. This method yielded a single data point of spatial preference for each study subject, thereby avoiding concerns of pseudoreplication (also *see* Hauber *et al*. 2000). During each trial I also recorded the rate of aggressive strikes (pecks s^{-1}) that either the subject or the stimulus birds delivered while in the proximity of each other and calculated an average rate of this behavior across all twelve trials for each adult cowbird.

Laboratory trials with juveniles

To determine if juvenile cowbirds approach adult female conspecifics preferentially, I examined the responses of hand-reared juvenile cowbirds to conspecific adults and heterospecific using the simultaneous choice paradigm described above. Nestling cowbirds were taken from host nests prior to fledging (≤ 10 days of age) throughout the breeding season in 2001, and hand-reared in visual but not acoustic isolation from other avian stimuli (for methods *see* Hauber *et al*. 2000). When ~ 2 month old and prior to fall molt, I used these hand-reared subjects (n = 10) in experiments with the following stimulus pair in the choice chamber: adult female cowbird vs. adult male phoebe (n = 2 stimulus pairs, 3 trials each for a total of 6 trials per subject). These juveniles were not socially naïve, because they had one of two types of prior social experience in the choice chamber: (A) a total of 1 hr with a male vs. female zebra finch stimuli (n = 2 stimulus pairs) followed by a total of 1 hr. with a female zebra finch vs. adult female cowbird stimuli (n = 2 stimulus pairs) or (B) a total of 1 hr with a male vs. female zebra finch stimuli (n = 2 pairs) followed by a total of 1 hr. with a zebra finch vs. adult male phoebe stimuli (n = 2 pairs). One subject never approached the proximity of both stimuli throughout its 6 trails and was excluded. The responses of the juvenile cowbirds in the subsequent choice tests did not differ statistically depending on prior social exposure ($U = 8.0$, $p > 0.62$, Mann-Whitney test, $n_A = 4$, $n_B = 5$ juvenile cowbirds). Therefore, these juvenile cowbirds' responses were pooled together in subsequent analyses. Specifically, I calculated a single preference score towards adult female cowbirds for each juvenile subject as described above. During each trial I again recorded the rate of aggressive strikes (pecks s^{-1}) that either the subject or the stimulus birds delivered while in the proximity of each other and calculated an average rate of this behavior across all six trials.

Cowbirds appear to adapt easily to being kept in captivity and perform species-typical behaviors even in unfamiliar environments (e.g., the choice-chamber used in the laboratory trials: personal observations). No subject or stimulus bird died during or shortly after experimentation or suffered visible injuries. All methods used in this study had been approved by university and governmental agencies.

Results

Video-recordings

I obtained 67.6 hours of footage (mean age of nestling cowbirds: 7.8 days, with 4.5 hours per nesting attempt) of parasitized phoebe nesting attempts (n = 15). No adult (female or male) cowbirds were either observed or heard vocalizing to give chatters in the vicinity of parasitized phoebe nests in this sample. Similarly, no adult cowbirds were detected (seen or heard) during an additional 34.9 hours of recordings at non-parasitized phoebe nests (n = 11).

Chatter playbacks

Exploratory analyses on categorical data (*see* Methods) suggested that cowbird detectability was generally low (Fig. 2) and did not vary consistently with developmental stages for either female cowbirds at non-parasitized nests ($\chi^2 = 2.1$, $p > 0.54$) or males at both non-parasitized ($\chi^2 = 2.3$, $p > 0.52$) and parasitized nests ($\chi^2 = 5.6$, $p > 0.13$). However, developmental

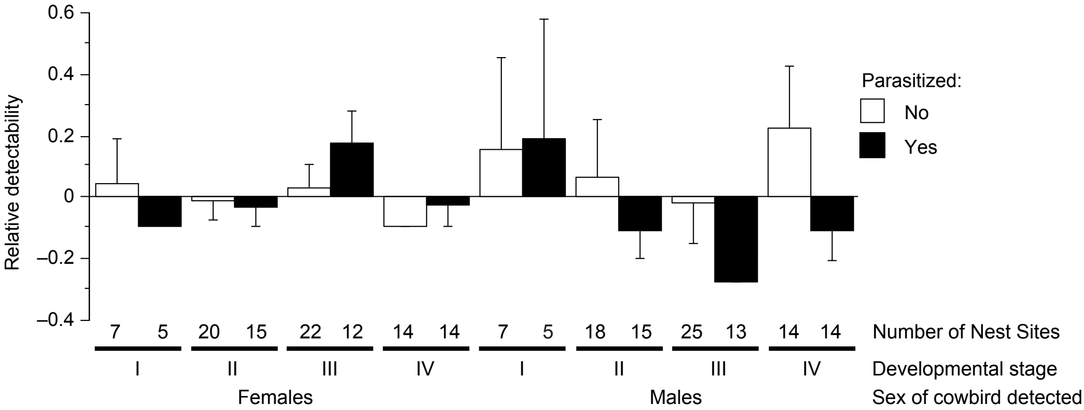

Fig. 2. Relative detectability scores of adult cowbirds during 5 min. chatter playbacks at nests of eastern phoebes. Actual values – mean values (averaged for all nests and developmental stages for each sex; female cowbirds: 0.098 detections per trial per nestsite, male cowbirds: 0.27 detections per trial per nestsite) are presented for each 10 day developmental period after clutch completion. Positive values indicate greater than average detectability. For definitions of developmental stages: *see* Methods. Means ± SE are presented.

stages appeared to be related to whether or not female cowbirds were detected near parasitized nests ($\chi^2 = 13$, $p < 0.0057$): most female but not male detections occurred at parasitized nests during the 21–30 day developmental stage III (i.e., early fledgling stage of juvenile cowbirds, Fig. 2). This statistically significant variation of female detectability with developmental stage at parasitized nests still remains significant even after a correction that takes into consideration that the data on the responses of female and male cowbirds to a playback session at each nesting attempt were collected simultaneously (i.e., $\alpha_{\text{corrected}} = 0.0125$). Interestingly, adult female cowbirds were more likely to be detected during this developmental stage near those parasitized phoebe nesting attempts at which at least once during repeated nest checks of 10 min. duration I was also able to locate by sight the fledged, colorbanded juvenile cowbird (6 of 8 nesting attempts) than near those parasitized nests where I never located the fledged parasitic young (1 of 7 nesting attempts, $p = 0.041$, Fisher's exact test).

In these analyses, each playback session, that was conducted during each of the four developmental stages at each site, was considered an independent data point. Therefore, I also tested the robustness of these trends using non-parametric analyses of detectability scores that took into consideration the number of repeated sampling (playback) sessions at each nesting attempt. The outcomes were similar: female detectability scores were dependent on developmental stages at parasitized nests: developmental stage III consistently had the highest levels of female cowbird detectability at these sites ($\chi^2 = 8.9$, $p < 0.012$, $n = 11$ sites, Friedman test between stages II, III, and IV; there were too few trials for stage I to be included, for data and sample sizes *see* Fig. 2). During stage III, female detectability was also higher than either male detectability at parasitized nests ($Z = 2.2$, $p < 0.027$, $n = 12$ sites, Wilcoxon signed rank test) or female detectability at the equivalent stage at non-parasitized nests ($U = 82$, $p < 0.015$, $n = 12$ and 22 parasitized and non-parasitized sites, Mann-Whitney test) (Fig. 2). In the case of detecting female vs. male responses during the same playbacks the probability value of the comparisons at parasitized nests during the same developmental stages was not judged against a corrected α level because, by definition, this statistical test assumes independence between the responses of the different sexes while the remainder of comparisons were also carried out with independent data sets.

In 2001, detectability of female cowbirds at parasitized phoebe nests was also different

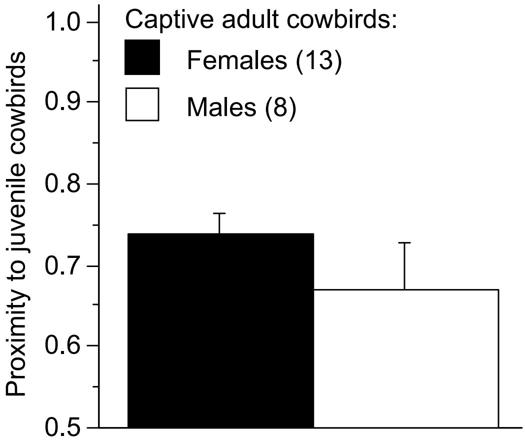

Fig. 3. Spatial proximity of adult cowbirds to a juvenile conspecific in the presence of a heterospecific stimulus (averaged over 12 ten-minute trials for each subject). Means + SE are shown, the *x*-axis is set at the random expectation (from a possible range of 0–1), and sample sizes are indicated in brackets for each sex.

during single chatter playbacks at the nestling (developmental stage II) vs. early fledgling stages (developmental stage III *sensu* 2000): female cowbirds were detected only during the fledgling stage (5 of 15) but not during the nestling stage (0 of 18, $p = 0.013$, Fisher's exact test) at parasitized phoebe nests. These detection levels of female cowbirds during the fledgling stage (III) at parasitized phoebe nests were also greater ($p = 0.045$, Fisher's exact test) on average (33%) than previously recorded average detection measures (12%) during 5 min. chatter playbacks at haphazardly chosen (non-nest based) sites ($n = 108$) at the same study site during the cowbird breeding season (data from Hauber *et al.* 2001).

Laboratory trials with adults

In the laboratory choice test, both female and male adult cowbirds associated with juvenile conspecifics above chance levels ($Z = 3.1$, $p < 0.0016$ and $Z = 2.2$, $p < 0.025$, respectively, Wilcoxon tests, random expectation: 0.5) (Fig. 3). Females spent more time than males in the close proximity of juveniles but not significantly so ($U = 33$, $p < 0.17$, Mann-Whitney test). There were no vocal interactions between cowbirds in the test chamber during test trials (personal observations). On average, adult cowbirds ($n = 21$) received similar peck rates from juvenile conspecifics (mean ± standard error: 3.2 ± 1.1 pecks 10^{-4} s) and adult heterospecifics (1.8 ± 1.2 pecks 10^{-4} s, $Z = 1.3$, $p > 0.18$, Wilcoxon test).

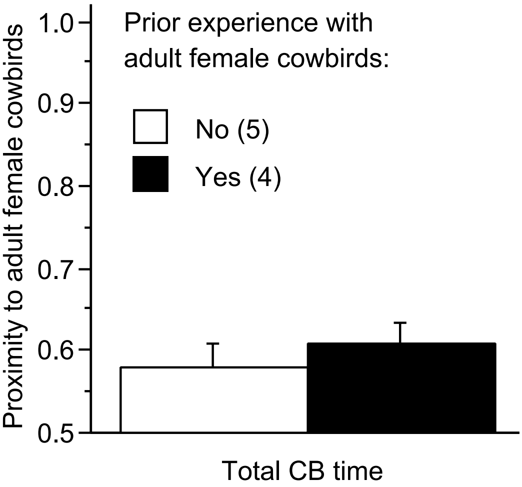

Fig. 4. Spatial proximity of hand-reared juvenile cowbirds to an adult female conspecific in the presence of a heterospecific stimulus (averaged over 6 ten-minute trials for each subject). Means + SE are shown, the *x*-axis is set at the random expectation (from a possible range of 0–1), and sample sizes are indicated in brackets for each group with different, limited, prior social experiences.

Laboratory trials with juveniles

Juvenile cowbirds spent consistently greater proportions of their choice times in the proximity of the conspecific adult female stimuli than expected by chance ($Z = 2.7$, $p < 0.0077$, one-sample Wilcoxon test, random expecation: 0.5) (Fig. 4). When considering only those cowbirds that were socially naïve to conspecifics ($n = 5$), the preference for adult females remained consistent ($Z = 2.0$, $p < 0.043$, Wilcoxon test). Juvenile cowbirds ($n = 10$) received lower rates of pecks from conspecific (30 ± 10 pecks 10^{-4} s) than heterospecific stimuli (70 ± 20 pecks 10^{-4} s, $Z = 2.4$, $p < 0.017$, $n = 10$, Wilcoxon test). There was a non-significant trend of a positive relationship between peck-rates of female cowbird stimuli and subjects ($r_s = 0.55$, $p < 0.099$, $n = 10$), but not between phoebe stimuli and juvenile cowbirds ($r_s = 0.37$, $p > 0.26$, $n = 10$). None of these behavioral rates were statistically related to proximity to either stimulus types (all $p > 0.2$, Spearman rank correlations).

Discussion

During the ontogeny of most birds and mammals the first social partners are predictably close relatives: parents and siblings (Sherman *et al.* 1997). Because obligate brood parasitic birds lay their eggs in nests of other species, the young parasite has been thought to face the task of seeking out conspecifics without experience with relatives (i.e., parents or sibs: Sherman 1999, Hauber & Sherman 2000). In my experiments juvenile cowbirds with and without prior exposure to conspecific adult stimuli associated preferentially with adult female cowbirds. These findings are in agreement with the conclusions of previous studies and conventional wisdom (King & West 1977, Graham & Middleton 1989, Ortega 1998, Hauber *et al.* 2000, Hauber *et al.* 2001).

However, adult parasites too may sometimes initiate conspecific contact with young conspecifics (Hahn & Fleischer 1995, Hahn *et al.* 1999, Soler & Soler 1999). In support of this second possibility, my data showed that, in laboratory choice tests, adult brown-headed cowbirds preferentially associated with conspecific juveniles in the presence of heterospecific stimuli. Overall the preference of adult cowbirds for conspecific juveniles (Fig. 2) was greater than the preference of juvenile cowbirds for conspecific adults (Fig. 3). Mechanistically this is not surprising because adult cowbirds (both in the wild and in this laboratory population) have lived in flocks containing many other cowbirds while juvenile parasites (both in the wild and in the hand-reared laboratory population) have had limited social experience with conspecifics other than themselves.

Using video recordings and playbacks of cowbird chatters at nests of Eastern phoebes (which are some of the earliest nesting and, hence, the earliest parasitized cowbird host species in my study site) I also examined whether wild adult cowbirds returned to parasitized nests. Patterns of cowbird detectability were consistent with the hypothesis that territorial adult female cowbirds (i.e. the putative mothers) predictably associate with and represent first conspecific contact for fledged parasitic young (Hahn *et al.* 1999). From a fitness-level perspective, early association with conspecifics may be beneficial to young cowbirds, and perhaps to other brood parasites in general, through cueing juveniles' species recognition templates and facilitating their joining of conspecific flocks (Hahn & Fleischer 1995, Soler & Soler 1999, Hauber *et al.* 2001).

In the field during extended periods of video-taping I recorded no adult cowbirds visiting host nests with parasitic nestlings. These data, taken together with a similar lack of published observations on non-aggressive behaviors by adult cowbirds at parasitized nests in other extensive video-taping and direct-observational studies (e.g., Sheppard 1996, Lorenzana & Sealy 1998, Dearborn *et al.* 1998, Lichtenstein & Sealy 1998) do not support one specific version of the first contact hypothesis (i.e., that female cowbirds return to nests containing their parasitic young to cue species recognition: Hauber *et al.* 2000, Hauber *et al.* 2001). This, however, is not surprising because (i) typical cowbird hosts recognize and defend their nests from parasitic intruders, and (ii) for almost half of the nestling period (~ 5 days) juvenile cowbirds are blind (Lowther 1993) and, thus, would not be able to learn visual cues from their mothers. Mother cowbirds may instead return to their young during the early fledgling stages, before juvenile cowbirds become independent of their territorial hosts. In agreement with this possibility, I found that female but not male cowbirds were more likely to be detected during the early fledgling stages of juvenile cowbirds. That the presence of female cowbirds is a predictable source of interaction between juvenile and adult parasites is suggested strongly by these data because they relied on very short, 5 min. playback observations compared to the total of 10-day long duration of the juvenile cowbirds' developmental stages (as defined in the Methods). In addition, although my methodology did not include extended behavioral observations on the detected adult cowbirds, in three instances I did observe female cowbirds flying toward the resident juvenile cowbird and in on of these instances the adult female chattered at the juvenile (personal observations). In several other occasions of watching cowbird flocks, others (e.g., Raim 2000) and I also observed female adults chattering at juveniles.

Importantly, these latter incidents were sharply different from the observed, non-vocal interactions between captive adult and juvenile cowbirds, highlighting a potential confounding effect of laboratory studies. Therefore, future research efforts should focus on examining whether these initial interactions in the field facilitate subsequent social preference of juvenile cowbirds for conspecifics as well as other aspects of their species-specific social behaviors and through which sensory modalities they might do so (e.g., visual, acoustic, olfactory: Jones *et al.* 2002, White *et al.* 2002). This is likely to be the case because prior studies showed that species recognition and species-specific social behaviors in juvenile cowbirds were malleable and could be predictably modified by extended (i.e., months: Freeberg *et al.* 1995, West *et al.* 1996) or short term (i.e., days: Hauber *et al.* 2000, Hauber *et al.* 2001, White *et al.* 2002) exposure to different social partners and phenotypic (e.g., visual, acoustic) stimuli.

Adult female cowbirds may benefit from returning to parasitized nests for several possible reasons other than association with their own young. The possibilities include (i) assessment of whether the parasitic egg and young are accepted (Zahavi 1979, Soler *et al.* 1995, Hahn *et al.* 1999) (‘mafia’) and (ii) monitoring the host for potential parasitism of its subsequent nesting attempt (Arcese *et al.* 1996, Hauber 2000) (‘farming’). Naturally, these explanations are not mutually exclusive alternatives to the first contact hypothesis and several functions may be served by the return visits of mother cowbirds. There is conflicting evidence whether cowbirds return to host territories to monitor parasitized nesting attempts (Hauber 2000, McLaren & Sealy 2000) and overall it is more likely that cowbirds generally follow a “farming” rather than a retaliatory “mafia” strategy of selectively destroying host nests that do not contain their own progeny (Arcese *et al.* 1996, Elliott 1999, pers. obs.). The farming strategy, in turn, does not require repeated visits to previously parasitized nests. It is also unlikely that female cowbirds return to parasitized phoebe nests to lay their eggs second nestling attempts or to defend these potential egg-laying resources from territorial intruders because cowbirds typically do not parasitize later clutches of this host (Klaas 1975, Murphy 1994, Hauber 2001). Associating with their own young to cue species recognition and/or to facilitate flock membership, therefore, may be a primary benefit for returning mother cowbirds if flock membership for immature cowbirds confers fitness advantages through safer foraging and access to cultural information carried by adult cowbirds (West & King 1988, O’Loghlen & Rothstein 1993, Freeberg 1999).

Although captive male cowbirds showed somewhat less spatial preference for juvenile cowbirds than did females, nonetheless they associated with cowbird young at well above chance levels (Fig. 3). This suggests that preference for conspecific young is characteristic of adult cowbirds of both sexes. However, detection of male cowbirds at parasitized nests showed a dramatically different pattern from females: detectability scores were neither associated with the developmental stage nor with the parasitism of the host nest per se (Fig. 2). In addition, in 33% of the playbacks when any male cowbirds were detected, 2 or more males were seen to have approached simultaneously the chatter source. Because male cowbirds do not defend territories and frequently do not obtain social and/or genetic mates (Dufty 1982b, Darley 1983), perhaps their responses to chatter playbacks were influenced primarily by searching for females as potential mates rather than by territorial defense or association with their genetic offspring.

My observations suggest that the early fledgling stage is the period of potential initial interaction between young cowbirds and female conspecifics. However, neither the nature (vocal, visual) of the behavioral interactions between female adults and juvenile cowbirds, nor the genetic relation of females to the fledgling cowbirds (i.e., mother–offspring) could be inferred quantitatively from these data. Nonetheless, genetic mothers are the most likely candidates to respond to chatter playbacks because female cowbirds in much of North America, especially in the Northeastern populations, defend their breeding territory from conspecific females (Dufty 1982b, Darley 1983, personal observations), and have exclusive access to the majority (> 50%) of host nests within their territories (Alderson *et al*. 1999, Hahn *et al*. 1999). Accordingly, during all the playbacks of chatter calls near host nests around Ithaca, NY, for this study only once did I detect approaches by more than one female cowbird (two females on one occasion). Above-chance genetic relatedness between returning females and encountered juveniles has been already shown to exist in an other NY population of cowbirds by Hahn *et al*. 1999, and this relatedness would assure probabilistically that any benefit conferred upon juveniles through these early interactions with adult female cowbirds be a fitness advantage under natural selection. This putative close relatedness between returning females and encountered juveniles would also argue for the consideration of early association with juveniles as a form of delayed or partial parental care by female parasites (Hahn & Fleischer 1995).

Nonetheless, even if adult cowbirds are not (i) closely related to the juvenile cowbirds that they encounter and interact with, these adults may nonetheless benefit from "first contact" through socializing with and leading juveniles to conspecific flocks for at least two additional theoretical reasons: (ii) selfish herd effects — cowbirds typically forage on the ground in open areas, and foraging in the presence of more juveniles could reduce the probability of per-individual predator attacks (Lowther 1993), and (iii) cooperation without reciprocity — adult cowbirds may interact with unrelated juvenile conspecifics for the immediate benefit of the latter even if these interactions are costly to the adults because their own offspring may benefit from interacting with other adult conspecifics (Riolo *et al*. 2001). Future studies should examine the relevance and the relative benefits derived by adult cowbirds from any of these (i)–(iii) possibilities.

Overall it appears the first contact hypothesis represents a feasible mechanism to cue juveniles' conspecific recognition by adult parasites in some populations of brown-headed cowbirds. This first contact is likely to be involved in mediating social partner preference, contributing to kin-recognition, facilitating conspecific-flock membership, and cueing species recognition in this and perhaps in other brood parasitic species.

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