ORIGINAL ARTICLE

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Self-referent phenotype matching in a brood parasite: the armpit effect in brown-headed cowbirds (*Molothrus ater*)

Abstract Most birds and mammals learn characteristics of conspecifics from their parents and siblings. In inter-specific brood parasites, however, early social learning could lead to species recognition errors because young are reared among heterospecifics. Conceivably, juvenile parasites might inspect and memorize aspects of their own phenotype, and later match features of encountered individuals to that template. We tested for such self-referent phenotype matching by manipulating feather colors of hand-reared fledglings ($n = 21$) of the parasitic brown-headed cowbird (*Molothrus ater*). In simultaneous choice trials ($n = 6$ trials/subject) between dyed and normal-colored adult females, juvenile cowbirds (< 2 months old) approached more quickly and associated preferentially with individuals that were colored similar to themselves. These preferences remained even when differences between the associative behaviors of juvenile males and females were controlled statistically. Our data imply that cowbirds incorporate their own plumage color into their recognition template. This provides the first evidence of self-referent phenotype matching through experimental manipulation of a recognition cue.

Key words Armpit effect · Brood parasites · Conspecific recognition · Phenotype matching · Self-referencing

Introduction

When people meet, they attempt to recognize each other by comparing physical features, like height, eye color, and

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nose shape, to mental images ("templates") formed during previous social encounters (Sherman et al. 1997). Other primates (Alberts 1999; Parr and de Waal 1999) and numerous other vertebrates (Holmes and Sherman 1982; Heth et al. 1998; Kendrick et al. 1998) and invertebrates (Getz and Smith 1986) also recognize mates, social partners, and relatives via this process which is called "phenotype matching" (Lacy and Sherman 1983; Waldman et al. 1988).

Most birds and mammals learn characteristics of species identity during early development, based on phenotypes of parents and siblings (Irwin and Price 1999; ten Cate and Vos 1999). Later on they recognize conspecific sexual partners by matching their features to the remembered template. A well-studied example of this phenotype matching process is sexual imprinting (e.g., ten Cate et al. 1993; Laland 1994; Grant and Grant 1997; Kendrick et al. 1998; Salzen 1998). Social learning from relatives is a reliable mechanism for species recognition because parental care is obligatory in all mammals and most birds (Clutton-Brock 1991), young typically are reared in groups, and phenotypic similarity correlates with genotypic similarity (Sherman et al. 1997).

However, some birds can recognize conspecifics and respond to them appropriately even though they were not reared with members of their own species (Dooling and Searcy 1982; Marler 1997; but see Lickliter and Lewkovicz 1995). For example, juvenile white-throated sparrows (*Zonotrichia albicollis*) preferentially call in response to songs of conspecifics even in the absence of prior exposure to adult vocalizations (Whaling et al. 1997). Such recognition may develop via either (1) genetic determination, involving restrictive architectural design of perceptual filters in the individual's sensory processing system (Marler 1997), or (2) learning, involving self-referent phenotype matching, where the recognition template is formed by memorizing salient aspects of the individual's own phenotype (Holmes and Sherman 1982; Sherman et al. 1997; Hauber and Sherman 2000). Dawkins (1982) called the latter mechanism the "armpit effect." Self-referencing is a feasible alternative to genetic determination because naïve and cross-fostered juveniles always are exposed to conspe-

cific cues embodied in their own phenotype (Vidal 1975; Graham and Middleton 1989; Petrie et al. 1999; Mateo and Johnston 2000).

Chicks of obligate brood parasitic birds are reared by heterospecifics (Payne 1977; Rothstein 1990; Rothstein and Robinson 1998), so early social learning of host phenotypes predictably would yield misleading recognition templates (Holmes and Sherman 1982; Sherman 1991; Hauber and Sherman 2000). How parasitic chicks come to recognize conspecifics, therefore, is an intriguing question. Parasitic young might use self-referencing (Graham and Middleton 1989; Sherman et al. 1997; Sherman 1999; Hauber and Sherman 2000), or their entire recognition template might be genetically determined (Tinbergen 1951; Hamilton and Orians 1965; Ortega 1998). It also is possible that their recognition mechanism is a combination of both (M.E. Hauber, S.A. Russo, and P.W. Sherman, unpublished work; West and King 1988).

Interest in how brood parasitic birds recognize each other has surged recently (e.g., Soler and Soler 1999; Payne et al. 2000), but there are few experimental tests of the alternative mechanisms. Direct confirmation of a mechanism involving learning (and rebuttal of purely genetic determination) requires manipulating a recognition cue and inducing predictable types of discrimination errors as a result (Reeve 1989; Sherman 1999; Payne et al. 2000). We took this approach to investigate the ontogeny of recognition in brown-headed cowbirds (*Molothrus ater*; henceforth simply "cowbirds"), which are common North American brood parasites (Lowther 1993; Ortega 1998).

Individual female cowbirds may parasitize several host species (Fleischer 1985; Alderson et al. 1999), so a chick's social environment is unpredictable. Upon independence from foster parents at about 1 month of age, cowbird fledglings rapidly join conspecific flocks (Woodward 1983; Lowther 1993). This indicates that species recognition mechanisms are present by early in ontogeny (Ortega 1998). In a previous study, Graham and Middleton (1989) found that hand-reared juveniles associated with models of male cowbirds more than models of closely related red-winged blackbirds (*Agelaius phoeniceus*) and common grackles (*Quiscalus quiscula*), suggesting the importance of visual stimuli in conspecific discrimination. We therefore tested effects of manipulating feather colors of nestlings on their subsequent social preferences. If self-referent phenotype matching is involved in conspecific recognition, color-manipulated juveniles should be more attracted to similarly than dissimilarly colored adults.

Methods

Twenty-one cowbird nestlings (≤ 10 days old) were removed from nests of song sparrows (*Melospiza melodia*) and eastern phoebes (*Sayornis phoebe*) near Ithaca, New York state, in 1997–1999. The environs and field techniques were described by Hauber and Russo (2000). Each nestling ($n = 5$ in 1997, $n = 5$ in 1998, and $n = 11$ in 1999) was housed in its own cage. Cages were placed in an unheated room with a light cycle that mirrored natural conditions. Cages were separated by opaque barriers, and nestlings were reared in visual but not auditory isolation from other cowbirds and heterospecifics. Nestlings were hand-fed to satiation (i.e., until begging ceased) hourly between 0500 and 2300 hours, using the artificial diet described by Graham and Middleton (1989). When fledglings were able to feed themselves, they were provided with clean water and millet/game-starter mix ad lib.

Fourteen nestlings (8 females, 6 males) were chosen haphazardly over the 3 years of this study, and each feather that broke sheath was dyed black with a non-toxic, permanent, Sharpie marker. The seven other nestlings (4 females, 3 males) served as "controls." They were dyed only on the undersides of their wing feathers, so their gray-streaked color was unaffected. Feather colors of each chick were retouched weekly until their recognition abilities were tested. Juveniles were not sexed until their first molt (~2–3 months of age), at which point the sexual dimorphism in plumage became evident (Lowther 1993).

In nature and the laboratory, juvenile cowbirds begin to associate with conspecifics when they are 5–6 weeks old (Woodward 1983; Graham and Middleton 1989). When our juveniles were about 2 months old (mean age $\pm$ SE: 63.9 ± 1.3 days), but prior to molting, they were tested for their preference between two adult (> 2 years old) female cowbirds, one that had been dyed black and the other whose wing feathers had been dyed only on their undersides. Stimulus birds ($n = 12$) came from a mixed-sex captive flock; they were dyed ≤ 4 days before testing. We used only females because they are more similar to juvenile cowbirds in body size and coloration than are adult males (Lowther 1993).

Behaviors of each test juvenile toward pairs of stimulus birds were observed in a *c.* $5 \times 5 \times 5$ m³ chamber through a one-way mirror. Two identical, triangular-shaped cages ($0.9 \times 0.6 \times 0.5$ m³), each with a protruding perch, were placed in adjacent corners of the room and used to confine stimulus birds, but they were not isolated visually or acoustically. The test juveniles were not familiar with the chamber prior to testing.

To begin a trial, the lights in the chamber were turned off and a juvenile was placed in a small box on the wall opposite the cages. After 2 min., the lights were turned on and the bottom of the box was opened by remote control, forcing the cowbird to fly. Where and when it landed and spent the remainder of the trial were recorded. In 1997, trials lasted 15 min ($n = 30$) and in 1998–1999 they lasted 10 min ($n = 30$ and 66). Each juvenile was tested six times; at least four hrs. and no more than 2 days elapsed between sequential trials of the same juvenile. Between trials, stimulus birds were switched randomly between sides of the room; two different adult stimulus pairs were presented to each juvenile ($n = 6$ stimulus pairs total).

"Proximity" was scored when a juvenile entered one of two preassigned areas, marked by lines of colored tape on the floor, comprising the one-quarter of the test chamber nearest to either stimulus bird. We kept track of proximity (i.e., the amount of time spent in either proximity area) using a laptop computer with an event recorder program. Behavior of individual juveniles varied considerably (i.e., the fraction of the total trial duration that individuals spent in proximity ranged from 0 to 0.99, with a mean of 0.77 ± 0.034). Proximity time was influenced by trial order effects: as juveniles became more familiar with the test chamber and adult cowbirds, proximity times increased. Indeed, test juveniles spent significantly more time near either stimulus bird during their second three trials than their first three trials. Differences in proximity times averaged across trials 4–6 and trials 1–3 for each test bird were 0.079 ± 0.026 of total trial duration (paired $t_{20} = 2.9$, $P < 0.0082$). We therefore calculated juveniles' preferences in two ways.

First, overall preference (OP) was the proportion of the proximity time that was spent near a class of adult stimuli (black or control), averaged across all six trials. Trials in which test birds did not approach stimulus birds were omitted. Second, time-dependent preference (TDP) was the difference between the average proportions of the proximity time that was spent near a class of adult stimuli in the first three (1–3) trials and second three (4–6) trials. The latter measure reflected changes in spatial association as juveniles' experience with the choice arena increased; positive values indicated increased time spent with a particular stimulus type.

In addition, we used the time it took each test bird to first come into the "proximity" of each stimulus bird to gauge juveniles' preferences. We calculated relative latencies by dividing the time it took each test bird to come into the proximity of each stimulus bird by the trial duration. A maximum latency of 901 s in 1997 and 601 s in 1998–1999 was assigned to trials in which the test bird did not enter the proximity area of either stimulus bird. We then calculated the difference between these relative latencies for black and control stimuli, and compared the averages for each bird between their first and second three trials. A positive value meant shorter approach times to control stimuli during later trials. All our calculations compress information from the six trials per individual into single data points, thus avoiding pseudoreplication. All statistical tests were two-tailed and data are reported as mean ± SE.

Results

Neither juveniles nor stimulus adult cowbirds vocalized during our trials. Therefore, juvenile cowbirds' responses were based on visual rather than vocal cues.

Combining data across the 3 years of experimentation, a juvenile's own plumage color seemingly had no effect on its overall preference for similar colored stimuli. The OP for the adult whose color matched that of the test juvenile was 0.44 ± 0.042, which is not significantly different from the random expectation of 0.5 (one sample $t_{20} = 1.5$, $P > 0.14$).

However, tendencies of juveniles to associate with stimulus birds whose colors matched their own increased significantly across trials. The TDP for the adult whose color matched that of the test juvenile was 0.12 ± 0.055, whereas random expectation was 0 (one sample $t_{20} = 2.2$, $P < 0.039$). Association also was influenced by the test bird's sex: males preferred control (brown) stimulus birds more than females did. The TDP for control adults by juvenile males was 0.079 ± 0.091 versus -0.16 ± 0.068 for juvenile females (two sample $t_{20} = 2.1$, $P < 0.046$). Considering these two factors simultaneously (Fig. 1), discrimination depended significantly and independently on a juvenile cowbird's manipulated plumage color and sex (TDP for control adults: color $F_{1,17} = 5.2$, $P < 0.037$, sex
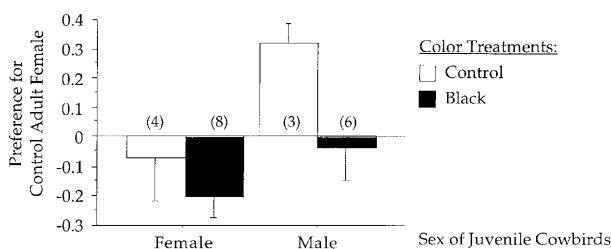
Fig. 2 Relative latency of control (sham-dyed) and black-dyed, hand-reared juvenile brown-headed cowbirds ($n = 21$, n for each condition in parentheses) to approach control (natural-colored) versus black-dyed adult female cowbirds in simultaneous choice trials (6 trials/test bird). *Negative values* represent shorter latencies to approach black-dyed stimuli during trials 4–6 than during trials 1–3. Within each sex, black-dyed juveniles consistently preferred black-dyed stimuli more than did control-colored juveniles

$F_{1,17} = 6.5$, $P < 0.021$, respectively; interaction of color × sex $F_{1,17} = 1.1$, $P > 0.31$).

Over all trials, relative latencies to approach similar-colored adult females did not vary between male and female juveniles or between dyed and control birds ($P > 0.46$ and $P > 0.97$, respectively, unpaired t-tests). However, relative latencies to approach similar-colored stimulus birds increased significantly across trials ($t_{20} = 2.3$, $P < 0.032$). This indicates that juvenile cowbirds approached similar-colored stimuli more quickly than dissimilar-colored stimuli during later trials. Considering sex and color simultaneously (Fig. 2), relative latencies to approach stimuli depended significantly on juveniles' manipulated plumage color ($F_{1,17} = 4.7$, $P < 0.046$), and juveniles' sex had an independent, marginally significant effect ($F_{1,17} = 3.0$, $P < 0.099$; interaction of color × sex $F_{1,17} = 0.097$, $P > 0.75$).

Discussion

We assessed social preferences of naïve brown-headed cowbirds by quantifying two response variables. On the one hand, coloring fledglings' feathers had no effect on the overall proportion of time (OP) juvenile cowbirds subsequently spent near experimentally manipulated and control (natural-colored) adults among all trials. On the other hand, test birds' preferences for adults colored like themselves increased over the course of the experiment both among female and male juveniles (TDP, Fig. 1). In addition, color manipulation affected the relative latencies of juvenile birds to approach color manipulated and control adult stimuli: juveniles approached like-colored stimuli more quickly (Fig. 2).

OP is the conventional method of testing for preferences (Wagner 1998). However our TDP and relative latency measures take into account something that OP misses: inexperience of hand-reared test birds with both the apparatus and adult birds during the initial trials. Also, time-dependent measures of spatial association may better reflect the ontogeny of behavior because the accuracy of cowbird

Fig. 1 Time-dependent preferences (TDP, mean ± SE) of control (sham-dyed) and black-dyed, hand-reared juvenile brown-headed cowbirds ($n = 21$, n for each condition in *parentheses*) for control (natural-colored) versus black-dyed adult female cowbirds in simultaneous choice trials. *Negative values* represent increased preferences of juveniles for black-dyed stimuli. Within each sex, black-dyed juveniles consistently preferred black-dyed stimuli more than did control juveniles
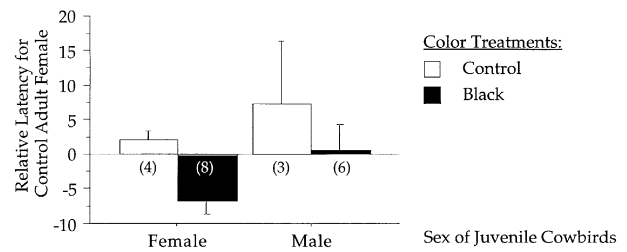
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species recognition improves through social experience with adults (Freeberg et al. 1995; O'Loghlen and Rothstein 1995). Thus we are inclined to accept the results based on TDP over those based on OP.

Previous experiments on self-referent phenotype matching were inconclusive because they did not eliminate the possibility of social learning (Alexander 1990; Sherman et al. 1997). Recently, Mateo and Johnston (2000) reported that female golden hamsters (*Mesocricetus auratus*) use their own odors as a template to recognize relatives. While their results strongly suggest learning via self-referencing the possibility that the hamsters' template is genetically determined was not eliminated, for example by manipulating the odor cue and inducing predictable recognition errors (Hauber and Sherman 2000). Others have attempted to discriminate between genetic and self-referent explanations of species recognition by manipulating the putative recognition cues, but results again were inconclusive (Salzen and Cornell 1966; Vidal 1975).

Our observations that juvenile cowbirds' social preferences were influenced predictably by changes in their own phenotypic cues eliminates the possibility that their recognition template was genetically determined. Any potential effects of experience with conspecifics prior to experimental removal (e.g., prenatal exposure: Lickliter and Lewkovicz 1995; adults returning to parasitized nests or parasitic nestmates: Soler and Soler 1999) seem to have been outweighed by effects of the experimental manipulation. Although it is possible that the behavior of the stimulus birds influenced the association patterns of the test birds, in another set of experiments using the same test chamber we found no differences in the rate at which stimulus adult female cowbirds directed behaviors toward dyed and control juveniles (H.E. Pearson and M.E. Hauber, unpublished work). We are left with the likelihood that a cowbird's own plumage color affected its social preferences.

Our results do not mean that an individual's own color is the only cue young cowbirds use to recognize conspecifics in nature. Additional cues may be learned from mothers if females predictably return to nests they parasitized, or from parasitic nestmates when multiple parasitism is predictable. Recognition of still other species-specific characteristics, such as vocal signals (King and West 1977; West and King 1988; M.E. Hauber et al., unpublished work) or behavioral displays (Rothstein 1977), may develop without social exposure to conspecifics.

Multiple recognition mechanisms may be especially beneficial to juvenile parasites for two reasons (Sherman et al. 1997; West et al. 1998). First, multiple mechanisms and cues can establish a more restrictive (i.e., discriminating) recognition template than would be possible using just one cue. In turn, this reduces errors when conflicting cues are presented simultaneously. For example, a fledgling cowbird may use chatter calls to locate flocks containing cowbirds (Dufty 1982; M.E. Hauber et al., unpublished work), but other species such as red-winged blackbirds often are associated with these flocks (Lowther 1993). Picking out conspecifics may require the use of ad-

ditional cues, such as plumage color or a display, learned via self-referencing.

Second, multiple recognition mechanisms provide a fail-safe if one type of cue is unavailable. For example, female cowbirds may usually return to nests they have parasitized (Hahn and Fleischer 1995) and identify themselves to their offspring via a "password" (e.g., a parasite-specific vocalization, behavior, or physical characteristic: Hauber et al. unpublished data). This induces the young to learn the entire cowbird-specific phenotype (e.g., plumage color, bill morphology) from an unambiguously appropriate model. However, if a female does not return (e.g., if she is killed by a predator), her chick could use its own plumage as a template to identify conspecifics. We are presently unable to discriminate among these possibilities because so little is known about the ontogeny of cowbird species recognition in the field (Woodward 1983) and because most studies of the behavioral ontogeny of conspecific recognition in brood parasitic birds (King and West 1977; Graham and Middleton 1989; Payne et al. 2000), including the present work, have not considered multiple mechanisms and cues simultaneously (but see West and King 1988; Hamilton et al. 1998).

Our results also do not indicate if free-living cowbirds use phenotype matching in contexts additional to species identification. For example, self-referencing also might enable young cowbirds to associate with conspecifics of similar age, dominance status, or sex (Freeberg 1999). Nonetheless, it is clear that visual cues do play an important role in recognition by juvenile cowbirds and that an individual's own feather coloration modifies its social preferences (Figs. 1, 2). In general, color is important in avian social and mating interactions, birds' necks are highly mobile, and preening (which would facilitate self-inspection) is common during plumage development. For these reasons, and in view of our results, we suspect that plumage-based self-referent phenotype matching will turn out to be important in species recognition of parasitic birds generally.

References

Alberts SC (1999) Paternal kin discrimination in wild baboons. Proc Roy Soc Lond B 266:1501–1506

Alderson GW, Gibbs HL, Sealy SG (1999) Determining the reproductive behaviour of individual brown-headed cowbirds using microsatellite DNA markers. Anim Behav 58:895–905

Alexander RD (1990) Epigenetic rules and Darwinian algorithms: the adaptive study of learning and development. Ethol Sociobiol 11:241–303

Cate C ten, Vos DR (1999) Sexual imprinting and evolutionary processes in birds: a reassessment. Adv Study Behav 28:1–31

Cate C ten, Vos DR, Mann N (1993) Sexual imprinting and song learning: two of one kind? Neth J Zool 43:34–45

Clutton-Brock TH (1991) The evolution of parental care. Princeton University Press, Princeton

Dawkins R (1982) The extended phenotype. Freeman, San Francisco

Dooling RJ, Searcy MH (1982) Early perceptual selectivity in the swamp sparrow. Dev Psychobiol 13:499–506

Dufty AM (1982) Response of brown-headed cowbirds to simulated conspecific intruders. Anim Behav 30:1043–1052

Fleischer RC (1985) A new technique to identify and assess the dispersion of eggs of individual brood parasites. Behav Ecol Sociobiol 17:91–99

Freeberg TM (1999) Spatial associations provide a context for social learning of courtship patterns in brown-headed cowbirds (*Molothrus ater*). J Comp Psychol 113:327–332

Freeberg TM, King AP, West MJ (1995) Social malleability in cowbirds (*Molothrus ater artemisiae*) – species and mate recognition in the first 2 years of life. J Comp Psychol 109:357–367

Getz WM, Smith KB (1986) Honey bee kin recognition: learning self and nestmate phenotypes. Anim Behav 34:1617–1626

Graham DS, Middleton ALA (1989) Conspecific recognition by juvenile brown-headed cowbirds. Bird Behav 8:14–22

Grant PR, Grant BR (1997) Hybridization, sexual imprinting, and mate choice. Am Nat 149:1–28

Hahn DC, Fleischer RC (1995) DNA fingerprint similarity between female and juvenile brown-headed cowbirds trapped together. Anim Behav 49:1577–1580

Hamilton WJ, Orians GH (1965) Evolution of brood parasitism in altricial birds. Condor 67:361–382

Hamilton KS, King AP, Sengelaub DR, West MJ (1998) Visual and song nuclei correlate with courtship skills in brown-headed cowbirds. Anim Behav 56:973–982

Hauber ME, Russo SA (2000) Perch proximity correlates with higher rates of cowbird parasitism of ground nesting song sparrows. Wilson Bull 112:150–153

Hauber ME, Sherman PW (2000) The armpit effect in hamster kin recognition. Trends Ecol Evol 15: 349–350

Heth G, Todrank J, Johnston RE (1998) Kin recognition in golden hamsters: evidence for phenotype matching. Anim Behav 56: 409–417

Holmes WG, Sherman PW (1982) The ontogeny of kin recognition in two species of ground squirrels. Am Zool 22:491–517

Irwin DE, Price T (1999) Sexual imprinting, learning and speciation. Heredity 82:347–354

Kendrick KM, Hinton MR, Atkins K, Haupt MA, Skinner JD (1998) Mothers determine sexual preferences. Nature 395:229–230

King AP, West MJ (1977) Species identification in the North American cowbird: appropriate responses to abnormal song. Science 195:1002–1004

Lacy RC, Sherman PW (1983) Kin recognition by phenotype matching. Am Nat 121:489–512

Laland KN (1994) On the evolutionary consequences of sexual imprinting. Evolution 48:477–489

Lickliter R, Lewkowicz DJ (1995) Intersensory experience and early perceptual development: attenuated prenatal sensory stimulation affects postnatal auditory and visual responsiveness in bobwhite quail chicks (*Colinus virginianus*). Dev Psychol 31: 609–618

Lowther PE (1993) Brown-headed cowbird (*Molothrus ater*) (The birds of North America, 47). The Academy of Natural Sciences, Philadelphia

Marler P (1997) Three models of song learning: evidence from behaviour. J Neurobiol 33:501–516

Mateo JM, Johnston RE (2000) Kin recognition and the "armpit effect:" evidence of self-referent phenotype matching. Proc R Soc Lond B 267:695–700

O'Loghlen AL, Rothstein SI (1995) Culturally correct song dialects are correlated with male age and female song preferences in wild populations of brown-headed cowbirds. Behav Ecol Sociobiol 36:251–259

Ortega CP (1998) Cowbirds and other brood parasites. The University of Arizona Press, Tucson

Parr LA, Waal FBM de (1999) Visual kin recognition in chimpanzees. Nature 399:647–648

Payne RB (1977) The ecology of brood parasitism in birds. Annu Rev Ecol Syst 8:1–28

Payne RB, Payne LL, Woods JL, Sorenson MD (2000) Imprinting and the origin of parasite-host species associations in brood-parasitic indigobirds, *Vidua chalybeata*. Anim Behav 59:69–81

Petrie M, Krupa A, Burke T (1999) Peacocks lek with relatives even in the absence of social and environmental cues. Nature 401: 155–157

Reeve HK (1989) The evolution of conspecific acceptance thresholds. Am Nat 133:407–435

Rothstein SI (1977) The preening invitation or head-down display of parasitic cowbirds. I. Evidence for intraspecific occurrence. Condor 79:13–23

Rothstein SI (1990) A model system for coevolution – avian brood parasitism. Annu Rev Ecol Syst 21:481–508

Rothstein SI, Robinson SK (eds) (1998) Parasitic birds and their hosts: studies in coevolution. Oxford University Press, New York

Salzen EA (1998) Imprinting. In: Greenberg G, Haraway MM (eds) Comparative psychology. Garland, New York, pp 566–575

Salzen, EA, Cornell JM (1966) Self-perception and species recognition in birds. Behaviour 30:44–65

Sherman PW (1991) Multiple mating and kin recognition by self-inspection. Ethol Sociobiol 12:377–386

Sherman PW (1999) Birds of a feather lek together. Nature 401: 119–120

Sherman PW, Reeve HK, Pfennig DW (1997) Recognition systems. In: Krebs JR, Davies NB (eds) Behavioural ecology. 4th edition. Blackwell, Oxford, pp 69–98

Soler M, Soler JJ (1999) Innate versus learned recognition of conspecifics in great spotted cuckoos *Clamator glandarius*. Anim Cogn 2:97–102

Tinbergen N (1951) The study of instinct. Clarendon, Oxford

Vidal JM (1975) The effect of social deprivation and self perception on sexual behavior in the domestic cock. Behaviour 52:57–83

Wagner WE Jr (1998) Measuring female mating preferences. Anim Behav 55:1029–1042

Waldman B, Frumhoff PC, Sherman PW (1988) Problems of kin recognition. Trends Ecol Evol 3:8–13

West MJ, King AP (1988) Vocalizations of juvenile cowbirds (*Molothrus ater ater*) evoke copulatory responses from females. Dev Psychobiol 21:543–552

West MJ, King AP, Freeberg TM (1998) Dual signaling during mating in brown-headed cowbirds (*Molothrus ater*, family Emberizidae/Icterinae). Ethology 104:250–267

Whaling CS, Solis MM, Doupe AJ, Soha JA, Marler P (1997) Acoustic and neural bases for innate recognition of song. Proc Natl Acad Sci USA 94:12694–12698

Woodward PW (1983) Behavioral ecology of fledgling brown-headed cowbirds and their hosts. Condor 85:151–163