PERSPECTIVES IN ORNITHOLOGY

PARENTAGE WITHOUT PARENTAL CARE: WHAT TO LOOK FOR IN GENETIC STUDIES OF OBLIGATE BROOD-PARASITIC MATING SYSTEMS

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As IN PREVIOUS decades (King and West 1977, Payne 1977, Brooke and Davies 1989), avian obligate brood parasitism—a reproductive strategy defined by laying and not caring for eggs in nests of other species—has continued to feature prominently in the general scientific literature (e.g. Lotem 1993, Sherry et al. 1993, Reboreda et al. 1996, Marchetti et al. 1998, Kilner et al. 1999, Gibbs et al. 2000, Tewksbury et al. 2002). Because obligate brood parasitic birds constitute only ~1% of all avian species (Ortega 1998, Davies 2000), why are they clearly over-represented in terms of publication?

This question seems to have three answers. First, the prominence of parasitic Old World cuckoos (e.g. *Cuculus canorus, Clamator glandarius*), cowbirds (*Molothrus* spp.), indigobirds (*Vidua* spp.), and, to a much lesser extent, the parasitic Black-headed Duck (*Heterocephalus atricapillus*), some New World cuckoos, and honeyguides, is partly due to fascination of researchers with the remarkable array of traits that are tied to unusual and successful reproductive habits of those parasites. These adaptations include behavioral strategies (e.g. nest search-

ing, lack of incubation and brooding, increased chick begging intensity, self-referencing in conspecific recognition), life-history components (e.g. timing and speed of egg laying, increased fecundity, shorter incubation periods, faster development), and morphological features (e.g. stronger egg shells, smaller egg-to-body size ratios, mimicry of host eggs or nestlings) that distinguish some or all parasites from other, nonparasitic birds (Friedmann 1929, Rothstein 1990, Hauber et al. 2000, Hauber and Sherman 2001, Dearborn and Lichtenstein 2002).

A second key source of interest concerns interactions between avian brood parasites and their hosts; those interactions have become classic examples and model systems to test predictions of coevolutionary arms race hypotheses (Clayton and Moore 1997, Payne 1997, Rothstein and Robinson 1998, Davies 1999, Stokke et al. 2002). Interspecific comparisons, as well as geographic, seasonal, and long-term intraspecific comparisons of host egg-morphologies, rejection rates of parasitic eggs, and mimicry of host eggs and nestlings (especially by *Cuculus* and *Clamator* cuckoos, *Molothrus* cowbirds, and *Vidua* finches) have provided evidence for adaptations and counter-adaptations in both hosts and parasites (Davies and Brooke 1988, Moksnes and Roskaft 1995, Hosoi and

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Rothstein 2000, Cherry and Bennett 2001, Payne et al. 2001, Hauber 2003).

Third, there are conservation implications of parasitism. Brood parasites by definition exploit the parental care of their host species, and by reducing fitness they may create population sinks, especially in areas with high parasitism rates (Robinson et al. 1995). Those concerns are particularly relevant to the management of endangered host species (e.g. Least Bell's Vireo [*Vireo bellii pusillus*], Griffith and Griffith 2000; Yellow-shouldered Blackbird [*Agelaius xanthomus*], Wiley et al. 1991, Lopez-Ortiz et al. 2002).

Despite much interest in the evolution, behavior, and development of obligate parasitic birds (Ortega 1998, Rothstein and Robinson 1998, Davies 2000), the genetic revolution in studies of avian mating systems (Sherman 1981, Burke and Bruford 1987) has engulfed the brood parasite camp only since the late 1990s, more than a decade after it started sweeping through studies of nonparasitic bird species. That delay occurred despite early advances in molecular nongenetic approaches that complemented field studies of brood parasitic behaviors. For example, Fleischer (1985) used gel electrophoresis to discriminate yolk allozymes sampled from eggs laid by several female cowbirds. Because yolk and albumin are maternally derived and variable between individual females, such protein electromorph fingerprinting data can identify spatial and temporal laying patterns, egg morphologies, relatedness, and realized fitness of female parasites. That approach has been applied recently in conspecific parasitic waterfowl using a newer nondestructive sampling technique (Ahlund and Andersson 2001, Andersson and Ahlund 2001) and likely has much more to offer to the study of the mating systems of interspecific brood parasites (Sorenson and Payne 2002). In light of recent advances in the use of molecular genetic techniques, we synthesize here the new empirical data on the genetic mating systems of obligate brood parasites, examining those findings within theoretical expectations about the mating systems of species that are freed from the evolutionary constraints of parental care.

MATING SYSTEMS THEORY FOR APPARENTLY
NONPARENTAL SPECIES

A mating system describes the behavioral, spatial, and temporal patterns of mating in a population of the same species (Emlen and Oring 1977, Andersson 1994). Quantitatively it includes the order, timing, and number of social and genetic mates and the developmental, morphological, and behavioral traits leading to (or circumventing) mating or fertilization. Postmating behaviors (e.g. mate-guarding, sperm-management, parental care, mate-desertion, divorce) also form an intrinsic component of mating systems because of the potentially causal interaction between alternative postmating strategies and future opportunities for mating (Clutton-Brock 1991, Andersson 1994, Weatherhead et al. 1994, Zuk 2002). As with other population-level traits, the mating system is an epiphenomenon summed across reproductive and social behaviors of the individuals constituting a population. Therefore, in studying sources of variation in mating systems it is necessary to understand mating patterns at the individual level.

Studies of parental bird species throughout the 1980s and 1990s revealed a then-startling incongruence between social mating systems and genetic mating systems (e.g. Westneat 1987a, b). Although subsequent comparative studies have found that genetic mating systems may be correlated with breeding synchrony (Stutchbury and Morton 1995, Chuang-Dobbs et al. 2001), patterns of space use (including density; Westneat and Sherman 1997), social pairbonds (Hasselquist and Sherman 2001), copulation frequency (Villarroel et al. 1998), and plumage and size dimorphism (Webster 1992), the ability of those ecological and social variables to predict (unknown) genetic mating systems is quite weak. Consequently, expansive data sets on the spatial, social, and reproductive behaviors of brood parasitic birds derived from studies of radiotagged, color-banded, and longitudinally observed individuals are only a first informative step in examining the mating system of those species (Elliott 1980, Dufty 1982, Darley 1983, Rothstein et al. 1984, Yokel 1986, Mason 1987, Thompson 1994, Barnard 1998, Hahn et al. 1999, Raim 2000).

As we shift into an era in which genetic data are becoming available for brood parasites (Marchetti et al. 1998; Martinez et al. 1998a; Alderson et al. 1999a,b; Longmire et al. 2001; Sefc et al. 2001), we need to develop a theoretical predictive model that combines potential effects of both ecological (e.g. host availability and spe-

cies richness, predation rates, host vs. parasite breeding season) and social (e.g. conspecific density, competition for host nests) constraints on mating behaviors with the opportunities afforded by a nonparental life history tactic (i.e. facultative brood parasites) or strategy (i.e. obligate brood parasites) (sensu Gross 1996). Because parental care is typically costly (e.g. lost time, lost energy, increased predation risk), it can limit the number of mating opportunities and the reproductive effort and output of each breeding attempt (Clutton-Brock 1991, Martin 1995, Ricklefs and Wikelski 2002). In the absence of social, ecological, and temporal constraints of parental care, we predict a variety of differences between the genetic mating systems of parasitic and nonparasitic species (Table 1).

EMPIRICAL DATA ON GENETIC MATING SYSTEMS OF OBLIGATE BROOD PARASITES

Testing those predictions requires extensive data on genetic mating systems, and that area of research has seen progress only within the last six years (Jones et al. 1997, Marchetti et al. 1998, Martinez et al. 1998a, Alderson et al. 1999a, Woolfenden et al. 2002, Strausberger and Ashley 2003). Although genetic tools were available before that time, progress has been delayed by the logistic difficulty of obtaining representative measures of breeding success in brood parasites: in the absence of clearly parental behaviors concentrated around a focal point of reproductive activities (i.e. the avian nest), surveys of parasitic breeding behaviors and success rely on intensive sampling of often highly mobile adults and of offspring from many potential (and well-hidden) host nests (Teuschl et al. 1998, Hahn et al. 1999, Woolfenden et al. 2002, Strausberger and Ashley 2003). Also, non-trivial proportions of parasitic eggs are rejected (e.g. ejected or left abandoned) by some host species that recognize heterospecific eggs (Rothstein 1975, Brooke and Davies 1988, Moskat and Honza 2002), thus biasing estimates of parasitic reproductive effort. Another critical obstacle is the ability to know when most or all host nests are found that were available for parasitism by the sampled adult parasites. Failing to find all offspring leads to underestimates of the number of host species used (for generalist parasites), of the extent of realized fitness versus reproductive effort, and, perhaps more

importantly to this review, of the number of mates. Results from studies combining genetic sampling with behavioral observations of individual reproductive strategies using tagging and radiotelemetry are not yet published, but would be informative to evaluate the relevance or extent of those possible methodological and analytical biases.

Data on genetic parentage in brood parasites have been published on at least six populations of three species (Table 2). Here, we briefly summarize those findings in the context of our predictions, followed by a more in-depth description of the most intensively studied species, Brown-headed Cowbird (*Molothrus ater*).

As we saw above, several hypotheses regarding avian mating systems in the absence of parental care predict increased numbers of mates for both females and males. Some predictions indicate simultaneous polygamy, whereas others indicate sequential polygamy. Only one of the currently published data sets that show evidence for polygamy is presented in a way that provides information about simultaneous and sequential multiple-matings by female and male parasites (fig. 3. in Martinez et al. 1998a). The lack of information on simultaneous polygamy versus serial monogamy is due primarily to a lack of detailed behavioral data (especially regarding the temporal and spatial laying patterns of individual females) coupled with genetic parentage data, through the course of a breeding season. More theoretically challenging, however, is the finding that monogamy is prevalent among females in all three parasitic species studied (Table 2).

Great-spotted Cuckoos (*Clamator glandarius*) parasitizing Eurasian Magpie (*Pica pica*) nests in Spain bred primarily monogamously (Martinez et al. 1998a). For 9 of 11 females (median 3 eggs sampled per female, range 2–10), only one mate was detected, though 2 of those 9 females were mated polygynously to the same male; the two remaining females mated polyandrously, with the mates of one of those females also siring eggs laid by an unknown female. Although previous behavioral studies had suggested occupation of territories by breeding pairs in this species (Arias de Reyna et al. 1987), overlap in the egg-laying ranges of females suggests that cuckoos were not strictly territorial (Martinez et al. 1998b). Because concurrent behavioral data were not reported in this study, it is not possible

TABLE 1. Comparative predictions of aspects of the mating systems of obligate brood parasites versus parental species.

Number of mates for parasites of both sexes

A) The lack of (bi)parental care and the uncoupling of breeding and feeding in brood parasites should remove the benefits of pair bonds. Researchers have historically predicted high levels of "promiscuity" (i.e. both polyandry and polygyny) for parasitic species.

B) Parasites may add or change partners at any stage of reproductive cycle without causing clear disruption to the breeding effort. This predicts weaker seasonal pair bonds, more divorce and remating, and hence more sequential monogamy.

C) Cooperative nest searching by female and male parasites may increase access to host nests, especially in specialists with low densities of host nests. If time-intensive nest searching interferes with the opportunities for extra-pair copulations, this predicts greater monogamy in specialist vs. generalist parasites.

Number of mates for female parasites

A) In the absence of parental care, females may choose to mate with the genetically most superior male. This predicts female monogamy, male polygamy, and female mate choice based on sexually selected male traits, displays, dominance hierarchies, or leks.

B) Each female may choose to mate with the most genetically compatible male; if compatibility varies by individual genotype, this predicts monogamy by both sexes.

C) Female parasites may have a protracted fertile period over several bouts of egg-laying. This predicts increased opportunity to counteract male mate-guarding. Females could copulate with additional males because there could be no reduction in paternal care for young due to low assurance of paternity.

D) In the presence of a prolonged breeding season, females may be sperm limited. This predicts multiple mating with the same male or, if males are sperm limited, too, multiple matings with different males and increased polygynandry.

E) In the absence of male retaliation against extrapair copulations, fertilization insurance by females predicts increased polyandry.

F) In the absence of paternal care for related young, females may be more likely to engage in genetic bet-hedging. This predicts increased polyandry.

G) Female parasites may gain direct benefits from males (e.g. assistance with nest searching, facilitation of access to key food resources). This predicts multiple matings by females and increased polyandry if a single male's resources are exhaustable.

Number of mates for male parasites

A) The absence of paternal duties may increase males' ability to seek additional mates. This predicts male polygyny because reproductive success is expected to increase with number of mates (sensu Bateman 1948).

B) Male parasites may prevent harassment of individual females by other courting males. If harassment is costly because it disrupts female nest-searching, feeding, or calcium acquisition, this predicts higher incidence of monogamy, particularly in populations with strongly male-biased sex ratios.

C) Male territoriality may not be an economically feasible option to assure paternity if female parasites are highly mobile during the day. This predicts mate following and guarding, and reduced opportunity for polyandry.

Other aspects of mating system

A) The absence of parental costs in brood parasites predicts increased reproductive rates for parasites (i.e. longer breeding season, breeding more often, or having greater clutch sizes than nonparasitic species).

B) The absence of chick-feeding constraints predicts parasites to be more like precocial species in that their decisions about egg-laying should be more based on current rather than future capital.

C) Natural and sexual selection on brood-parasitic birds cannot act on postlaying (i.e. parental) traits. Therefore, pre- and perizygotic reproductive traits (e.g. foraging efficiency to yolk up and calcify eggs, production of viable sperm) should be under stronger natural selection in parasites.

D) If hosts limit the reproductive success of females, females may defend areas of high nest density and good suitability. Territoriality by at least one sex predicts reduced opportunity for polygamy.

E) The removal of the constraint of parental care predicts that there is more temporal plasticity, geographic plasticity, or both, of parasitic mating systems as an adaptive response to variation in host-species composition, parasitic density and sex ratio, and other sociological ecological factors.

F) If host-specificity and mimicry are autosomally encoded in the genome, this predicts that monogamy minimizes the chances of maladaptive "outbreeding" with wrong alleles. In contrast, if host-specificity and mimicry are linked to the W chromosome or the mitochondrial genome, this predicts that polygamy is not constrained.

TABLE 2. Social and genetic mating systems of some obligate brood parasitic birds

Species	Social mating system	Genetic mating system	Sources
Great Spotted Cuckoo	Territorial to nonterritorial, mostly monogamy	Mostly monogamy with some polygamy	Martinez et al. 1998a, b
Common Cuckoo	Territorial, mostly monogamy	Mostly monogamy with some polyandry and, to a greater extent, polygyny	Jones et al. 1997, Marchetti et al. 1998
Brown-headed Cowbird	Territorial to nonterritorial, mostly monogamy to mostly polygamy	Mostly monogamy with some polyandry and, to a greater extent, polygyny	Woolfenden et al. 2002, Strausberger and Ashley 2003

to relate the genetic findings to information on space use, courtship, possibilities of direct benefits supplied by males, parental care provided by adult cuckoos visiting parasitized magpie nests (Soler and Soler 1999, Soler et al. 1999).

For Common Cuckoos in Japan (Marchetti et al. 1998), within a given year 18 of 21 females mated monogamously, whereas 10 of 19 males mated monogamously (based on all adults for which more than one offspring was sampled). The maximum number of mates detected in a single year was four for one male and three for one female. Those results of pronounced female but not male monogamy were qualitatively in agreement with parentage results from cuckoo eggs sampled in Europe and Japan (Jones et al. 1997). No offspring were detected for over half of all adult cuckoos in Marchetti et al.'s (1998) study; if those individuals truly failed to reproduce, there is large variance in reproductive output for both males and females. In the Common Cuckoo system, host specificity was potentially tied to the mating system, because females showed stronger host preferences than did males (through their matings with females parasitizing particular hosts) (Marchetti et al. 1998). That could cause the observed higher frequency of polygyny relative to polyandry. That some female cuckoo gentes, host races, show distinctive patterns of mitochondrial but not nuclear genome differentiation (Gibbs et al. 2000) is supportive of the relationship between mating system and host specificity. But, viewing that correlation from the opposite causal direction, an alternative is that several ecological factors favor polygyny; and that, in turn, could lead to a statistical bias in observed patterns of host specificity, such that males would appear to be less host-specific than females if males typically have larger absolute numbers of mates. That possibility is supported by the lack of significant mitochondrial differentiation in previous reports on cuckoo populations (Gibbs et al. 1996).

As with the two species of cuckoos, research on Brown-headed Cowbirds at Delta Marsh, Manitoba, revealed an apparent mix of monogamy and other matings. Importantly, that work showed that, as is often the case in ecological research, expanding a project from one (Alderson et al. 1999a) to several years (Woolfenden et al. 2002) proved to be critical in reversing previous conclusions and drawing new ones, because female cowbirds had offspring exclusively from monogamous mating in just one of seven years (1994; Woolfenden et al. 2002). Overall, across seven years the extent of within-year monogamy among the sampled individuals with more than one progeny was $69 \pm 19\%$ (mean $\pm$SD) for females and $42 \pm 26\%$ for males. In a geographic comparison, within-year monogamy characterized 54% of female and 0% of male cowbirds in suburban Chicago, Illinois (Strausberger and Ashley 2003). That apparent geographic variation in the social (Elliott 1980, Dufty 1982, Darley 1983, Yokel 1986, Hahn et al. 1999) or genetic (Woolfenden et al. 2002, Strausberger and Ashley 2003) mating systems of Brown-headed Cowbirds—and perhaps of other brood parasites—could be due to similar proximate factors that also caused the temporal plasticity of cowbird mating systems at Delta Marsh.

Despite the apparent reproductive advantage to multiple mating, the proportion of monogamously mating cowbird females was never <50% at both the Delta Marsh and the Chicago population in any study year. Also, most cowbird offspring were produced by either monogamously mated females or by polygamous females that mated with their own primary mates respectively (females: 75%, males: 51% at Delta Marsh; females: 85%, males: 75% at Chicago).

Because monogamously mated females had lower reproductive success than polyandrously mated females, it remains unclear why not all female cowbirds mated with multiple mates, especially in those populations that have consistently male-biased sex-ratios. This is particularly puzzling because, as expected according to the Bateman principle (Bateman 1948), male cowbirds' reproductive output (i.e. the number of offspring sired) is reported to be positively associated with number of females that laid eggs fertilized by that male (Woolfenden et al. 2002, Strausberger and Ashley 2003). In contrast to predictions of the Bateman principle (Tang-Martinez 2000), the same two studies detected similar positive relationships between numbers of genetic mates and measures of the reproductive output of female cowbirds. The slopes of those relationships (y: offspring vs. x: mates) were >1.0 and not significantly different between sexes, indicating that, typically, multiple (i.e. ≥2) offspring are sired by at least one of the parasites' genetic mate(s). If that is a true reflection of female reproductive behavior, then females could be receiving direct benefits from males (e.g. access to host nests in male territories: Woolfenden et al. 2002, male protection from hosts, and help with nest-searching: Strausberger and Ashley 2003). To date, however, the nature of direct benefits provided by male cowbirds to female conspecifics is unclear and cowbirds are not likely to resemble one of the clearest examples of brood-parasitic, resource-based polygynous mating systems: the Orange-rumped Honeyguide (*Indicator xanthonotus*), in which females trade copulations for access to bee-hives patrolled by male honeyguides (Cronin and Sherman 1976). Unfortunately, in the absence of experimental approaches (or a way to confirm that all parasite offspring are sampled), it also remains possible that non-Bateman-like correlations between female reproductive success and mate numbers are due to spatial and numerical sampling biases in assigning parentage to progeny (Woolfenden et al. 2002, Strausberger and Ashley 2003).

In particular, the possibility of sampling bias has the potential to confound two aspects of the results from genetic studies of parasitic mating systems. First, many sampled adults may have been assigned no offspring because either none were sampled or genotype comparisons did not produce sufficient matches between potential parents and young. That problem (and any conclusion about the strength of sexual selection, as inferred from variance in reproductive success) is compounded by difficulties in assigning residence status to birds for whom no offspring are detected; in the absence of radiotelemetry data, researchers are forced to resort to mark–resight or –recapture criteria for determining the inclusion of birds in the pool of potential breeders or residents (e.g. Woolfenden et al. 2002). Second, polygamy in the published studies is assigned to adult parasites to whom at least two eggs or nestlings were successfully assigned. If the probability of multiple mating is random, by chance alone adults with more offspring sampled would be more likely to be detected as having mated polygamously (Woolfenden et al. 2002, Strausberger and Ashley 2003). There were nontrivial proportions both of adult parasites to whom no offspring were assigned and of sampled progeny for whom parentage could not be determined in cowbirds and other parasitic species (Marchetti et al. 1998, Martinez et al. 1998a). Sampling concerns will cloud conclusions about the sexual dimorphism of variance in reproductive outputs, despite much need for statistically sound measures and comparative empirical data of the strength of sexual selection (Lande and Arnold 1983, Webster et al. 1995, Wade and Shuster 2002), especially between parasitic and nonparasitic species (Payne and Payne 1977, Hauber et al. 1999, Woolfenden et al. 2002).

A more informative approach for future studies could be to examine the reproductive history and reproductive potential of individual female cowbirds by repeated scans of their ovaries using noninvasive structural magnetic resonance imaging (MRI) throughout the breeding season (Czisch et al. 2001). Some brood parasites, such as Brown-headed and Bronzed (*M. aeneus*) cowbirds would be amenable study subjects for that approach because they are relatively stationary, territorial, or both during the breeding season (Friedmann 1929, Dufty 1982, Raim 2000) and can be easily captured using conspecific playbacks and baited walk-in traps (Hahn and Fleischer 1995, O'Loghlen and Rothstein 1995, Hahn et al. 1999). Information on the numbers of ovulating and ovulated eggs (Payne 1976) could then be combined with a time-series analysis of the genetic identity of the father of the parasitic progeny versus the identities of males who have

their sperm contained in the female's reproductive tract or trapped in the egg's perivitelline layer (Carter et al. 2000). That female cowbirds copulate throughout their prolonged breeding season (Payne 1976) was already demonstrated by observations of seasonal copulation patterns (Elliott 1980, Yokel 1986) and examinations of female cowbirds' cloacae for presence of fresh sperm (Quay 1989). Future studies of brood parasitic reproductive behaviors should carefully examine temporal and social aspects of variability in female and male reproductive success using these or other methods.

MORE PUZZLING QUESTIONS

Empirical tests of our predictions regarding brood-parasitic mating systems (Table 1) should be more feasible and common as genetic analyses become standard in complementing field research in behavioral and evolutionary ornithology. Already, new genetic techniques (Carter et al. 2000, Andersson and Ahlund 2001) and genomic markers are available or being developed for parasitic taxa (Alderson et al. 1999b, Longmire et al. 2001, Sefc et al. 2001, Strausberger and Ashley 2003). We identify four areas that seem particularly informative for future work.

What is the genetic mating system of unstudied parasitic species?—A rich array of published behavioral studies exist, including taxa from five of the at least five (Hughes 2000) but probably seven (Sorenson and Payne 2002) monophyletic groups of avian obligate parasites (e.g. *Cuculus* and *Clamator* cuckoos, honeyguides, cowbirds, and parasitic finches) (Barnard 1998, Ortega 1998, Davies 2000). As we reviewed, there is also a growing body of genetic studies, including three parasitic lineages that indicate a remarkable variety of social and genetic mating systems among brood parasites (Table 2). A direction for future work is to expand those genetic data sets to encompass other species (e.g. African and Australasian parasitic cuckoos, honeyguides, and cowbirds other than *M. ater*), especially from those lineages for which neither individual-based behavioral nor genetic data are available (i.e. Black-headed Duck, some South American cuckoos) (Barnard 1998). Information from additional brood parasites will facilitate comparative studies that examine quantitative predictions of mating-system hypotheses regarding parasitic and nonparasitic

species. Nonetheless, it must be acknowledged that, short of new discoveries of brood-parasitic taxa, comparative methods will be constrained by the few phylogenetically independent lineages of avian obligate brood parasites (Sorenson and Payne 2002). In light of that limitation, case-by-case analyses of intraspecific variation in mating systems across ecological gradients may represent a complementary and fruitful approach to test predictions of ultimate evolutionary and adaptive hypotheses about parasitic mating systems.

How plastic are parasitic mating systems in response to variation in ecological and social contexts?—A second, related direction is to carry out concurrent behavioral and genetic studies to examine alternative hypotheses about the individual-level plasticity and mating tactics leading to population-level descriptions of mating systems. Such an approach is present in some of the already published genetic studies (Hahn et al. 1999): for example, Marchetti et al. (1998) examined multiple mating by female versus male Common Cuckoos in the context of host usage—progeny of individual female cuckoos were more likely to be found in the nest of a single host species, whereas progeny of individual males were more frequently scattered in nests of two or more host species. However, it is largely unclear what traits female cuckoos use to choose conspecific mates and host nests (Brooke and Davies 1991, Teuschl et al. 1998).

In parasitic finches (*Vidua* spp.), ontogenetic experiments and behavioral trials demonstrated that females chose males that sing songs mimicking songs of these females' own foster parents. In turn, females preferentially approached and parasitized hosts of the same species as the foster parents (Payne 1973, Payne et al. 2000). Although genetic parentage data are available only for a handful of nestlings, as part of an ongoing project Payne et al. (2002) already reported that a female Village Indigobird (*V. chalybeata*) that repeatedly visited and mated with a male mimicking the song of a Brown Firefinch (*Lagonosticta nitidula*) subsequently laid an egg fertilized by the same male in a nest of *L. nitidula* rather than in the nest of a related, locally common and commonly used host species. This is evidence in brood parasitic birds for the concordance between a female's preference for sexually selected displays (as described from behavioral trials) and fertilization of that

female's progeny by a male exhibiting the preferred trait.

Elsewhere, in studying Brown-headed Cowbirds, Woolfenden et al. (2002) showed that body size of trapped, measured, and DNA-sampled male but not female cowbirds was related to their seasonal reproductive success. On one hand, because female cowbirds preferentially mate with older males and use acoustic and visual traits (West et al. 1981, Yokel and Rothstein 1991, O'Loghlen and Rothstein 1995, Hamilton et al. 1997, McGraw et al. 2002), it would be critical to determine, as seen in *Vidua* spp., whether the realized reproductive success of male and female cowbirds is related to the presence of preferred mate-choice traits in mated males. On the other hand, because sex ratios are male biased in most cowbird populations (Ortega 1998), it would be useful to determine—for those female cowbirds that mate with only a single male throughout the breeding season—what their phenotypic traits are and what functional benefits they derive from fertilizing eggs by single rather than multiple males. Experimental studies of individual plasticity in mating tactics in response to variation in conspecific density or sex ratio might be feasible and relevant in many understudied populations of cowbirds where those parasites are managed (i.e. removed) for conservation purposes (Griffiths and Griffiths 2000, Lopez-Ortiz et al. 2002).

What is the lifetime reproductive success of alternative reproductive behaviors among brood parasites?—Little is known about the realized seasonal and annual reproductive success of brood parasitic birds and how fitness is related to alternative or sequential (seasonally or annually variable) reproductive behaviors (Payne 1976, Scott and Ankney 1979, Fleischer 1985, Fleischer et al. 1987, Hahn et al. 1999). In light of high nest-predation rates and the potential for increased predation pressure associated with parasitized broods (Dearborn 1999), several genetic studies used extensive nest searching to locate most parasitized clutches which then were sampled destructively for DNA (i.e. eggs were incubated artificially to obtain embryonic DNA, or nestlings were collected; Alderson et al. 1999a, Woolfenden et al. 2002, Strausberger and Ashley 2003). Although this approach may be useful in estimating overall reproductive output, it is unsuitable for testing specific hypotheses about the function of individual

mating tactics. For example, key predictions of both good genes and Fisherian hypotheses of sexual selection require monitoring offspring well beyond the nestling stage to measure their subsequent survival and mating success. In that respect, studies of obligate brood parasites echo much-needed research efforts about fledgling, juvenile, and recruited offspring in many nonparasitic species as well (Woodward 1983, Anders et al. 1997). Accordingly, even if patterns of genetic fertilization are well known, the long-term fitness consequences of within or extrapair paternity or pseudoparasitism in the offspring often remain unclear (Blomqvist et al. 2002, Lyon et al. 2002).

Do brood parasites provide parental care?—The practical definition of obligate brood parasitism in birds concerns the exclusive laying of eggs into nests of other species. Yet, that definition is silent about aspects of parental care other than nest building, incubation, and brood care. For example, adult Great Spotted Cuckoos appear to defend parasitized host nests (Soler et al. 1999) or to interact with parasitic young to cue species recognition (Soler and Soler 1999). Also, female Brown-headed Cowbirds are more likely to be near parasitized nests during the fledging versus the nestling stage of cowbird chicks, preferentially approach fledgling conspecifics versus heterospecifics, and associate with genetically related fledglings on breeding territories and on feeding grounds (Hahn and Fleischer 1995, Hahn et al. 1999, Hauber 2002). Importantly, these behaviors of cuckoos and cowbirds can be classified as parental care rather than mating and, as required by a definition of parental care (Clutton-Brock 1991), because those traits are also likely to carry costs (e.g. Great Spotted Cuckoos may be hurt by attacking magpies during nest visits and female Brown-headed Cowbirds may trade off time from nest searching and foraging to seek out their own young [Soler and Soler 1999, Hauber 2002]). Nontrivial amounts of parental care, in turn, will have important implications on predictions of mating system hypotheses, and researchers should not overlook such possibilities in obligate brood parasites (Hahn and Fleischer 1995, Hauber et al. 2001, Hauber 2002, Strausberger and Ashley 2003). Finally, an exciting, and so far empirically and theoretically unexplored possibility of parasite–host coevolutionary dynamics is that behaviors relating

to the mating systems of brood parasitic species (e.g. whether or not male parasites are involved in nest searching or distraction displays) influences the behavioral and morphological antiparasitic strategies of hosts (e.g. desertion of parasitized nests vs. direct defense against nest-searching and laying parasites). If, for example, cooperative nest defense by female and male hosts together is successful at deterring parasitism but reduces the opportunity for extra-pair matings, this predicts increased monogamy in defending host species.

OUTLOOK ON PARASITIC MATING SYSTEMS

Studies of obligate brood parasitic birds have already provided and continue to generate many insights into the evolution and maintenance of avian behavioral, morphological, and developmental diversity. Yet most brood-parasitic species remain little studied, especially in tropical regions where parasitic species and ecologies are the most diverse (Brooker and Brooker 1992, Rothstein and Robinson 1998, Davies 2000, Kuiper and Cherry 2002, Sorenson and Payne 2002). In addition, even for extensively studied species such as Common Cuckoo, Great Spotted Cuckoo, Brown-headed Cowbird, and Village Indigobird, concurrent data are sparse from both individual-based observations, field experiments, and genetic analyses of mating behaviors and reproductive tactics. What we are missing is likely to change our views about avian brood parasitism just as much as the image of a cuckoo or cowbird chick begging for food from a foster parent continues to challenge our views about behavioral evolution and adaptive decision rules.

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