



## **Minireview: On the Rarity of Intraspecific Brood Parasitism**

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# MINIREVIEW

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## ON THE RARITY OF INTRASPECIFIC BROOD PARASITISM<sup>1</sup>

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Brood (or nest) parasitism, wherein a female deposits eggs in the nests of others, is an apparently rare reproductive strategy in birds (documented in <2% of all species; Payne 1977a, Yom-Tov 1980a). Parasites may lay eggs in other females' nests or, less commonly, physically transfer eggs between nests after the eggs are laid (e.g., Trost and Webb 1986, Brown and Brown 1988a). The conventional view has been that these species most often parasitize the reproductive effort of other species (e.g., Payne 1977a, Yom-Tov 1980a). Recently, however, researchers have recognized that in an increasing number of species individuals may also parasitize the broods of conspecifics (see Yom-Tov 1980a, Andersson 1984 for reviews). Because the intraspecific phenomenon is less easily observed (i.e., since host and parasite, and their eggs, are often difficult to distinguish), the actual prevalence of intraspecific brood parasitism may be underestimated. Moreover, despite the difficulties of detecting intraspecific brood parasitism, this alternative female reproductive strategy may be an important aspect of the reproductive biology of many avian species.

The presumed rarity of intraspecific brood parasitism seems surprising given the potential advantages for the parasite and the intuitive notion that parasitic behavior would have more easily evolved among conspecifics than between species. A conspecific would present an ideal host due to the nutritional requirements of the nestling parasite, the compatibility of parental behavior and egg size (Payne 1977a), and the synchrony of egg laying by the host and the parasite (Hamilton and Orians 1965). In fact, it has been suggested that an early stage in the development of interspecific parasitism could well have included intraspecific parasitism (Hamilton and Orians 1965, Yom-Tov et al. 1974, Payne 1977a, Evans 1988).

Intraspecific brood parasitism has most frequently been documented for noncolonial, precocial species, particularly waterfowl (Anseriformes), and is assumed to be rare among altricial and colonial species (e.g., Yom-Tov 1980a, Håland 1986). This apparent dichotomy has led to speculation as to what particular

features have favored the evolution of brood parasitism in waterfowl (Andersson and Eriksson 1982, Andersson 1984), and why this phenomenon is not more prevalent in altricial birds (Yom-Tov 1980a, Lanier 1982, Håland 1986). The importance of these questions is amplified when viewed in light of Hamilton and Orians' (1965) hypothesis that coloniality should favor the occurrence of intraspecific parasitism because a parasite's chances of locating a suitable host improve considerably with increased numbers and proximity of synchronously nesting neighbors.

The aim of this paper is to (1) present additional information from recently published studies on the occurrence, distribution, and prevalence of intraspecific brood parasitism among birds, (2) evaluate methods currently used to identify and quantify intraspecific brood parasitism, and (3) provide impetus and direction for future investigations of this subject. To this end, I first append Yom-Tov's (1980a) list of reported cases of intraspecific brood parasitism with recent accounts from the literature and categorize each species as having either altricial or precocial young, and whether they tend to breed colonially. For those species that may breed either solitarily or colonially, categorization is based upon the spacing pattern of the population from which intraspecific brood parasitism has been reported. A comprehensive list of interspecific brood parasitic species does not appear in the literature, therefore, using published studies, I estimate the number of species known to parasitize other species. For comparison with intraspecific parasitism I list all "new" (post-1980) species for which interspecific parasitism has been documented. Next, I investigate the problematic nature of the various criteria used to detect parasitism and postulate that these limitations may prohibit an unbiased assessment of the occurrence of this behavior among and within bird species. Furthermore, I make explicit those field techniques best suited for detecting and measuring the extent of brood parasitism. Finally, I suggest that researchers who wish to measure intraspecific brood parasitism in avian populations are behooved to verify the efficacy of the methods they employ if their results are to be deemed credible.

### OCCURRENCE OF BROOD PARASITISM

In his review, Yom-Tov (1980a, table 1) tabulated 53 species, from eight orders, for which intraspecific brood parasitism has been recorded. His list contained mainly precocial, noncolonial species, particularly waterfowl (Anseriformes), suggesting that intraspecific brood par-

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asitism is rare among altricial and colonial birds. An additional three waterfowl species known to exhibit "egg dumping" were omitted by Yom-Tov, presumably because documentation was based solely on the occurrence of unusually large clutches. However, I include those species as intraspecific brood parasites because primary sources indicate that egg dumping by one or more females was strongly implicated in the occurrence of clutches that were substantially larger than the range of natural clutch-size variation reported for the species, or there was additional indirect circumstantial evidence. These include the Lesser Scaup *Aythya affinis* (Vermeer 1968, Palmer 1976, Bellrose 1980), Hooded Merganser *Lophodytes cucullatus* (Morse et al. 1969, Johnsgard 1978, Bellrose 1980), and Musk Duck *Biziura lobata* (Frith 1967, Johnsgard 1978).

Subsequent to Yom-Tov's review, intraspecific brood parasitism has been documented for four additional orders, and 26 new species (Table 1). It is noteworthy that of the 26 new species, 19 have altricial young, and 16 breed semi- or fully colonially. Consequently, when all species reported to exhibit intraspecific brood parasitism are considered, 31 (37.8%) of these are classified as altricial species, and at least 37% are semi- or fully colonial. Thus, while intraspecific brood parasitism remains most prevalent among precocial species, an increasing number of altricial and colonial species are being found to exhibit this reproductive strategy. Prior to 1980 interspecific parasitism had been documented for 102 species (Weller 1959; Friedmann 1964; Hamilton and Orians 1965; Palmer 1976; Cronin and Sherman 1977; Payne 1977a, 1977b; Johnsgard 1978; Bellrose 1980; Wyllie 1981; Short and Horne 1985; Eadie et al. 1988). As of 1980 interspecific parasitism was reported for only six new species, including the Australian Blue-billed Duck *Oxyura australis* (Attiwell et al. 1981), Great Egret *Casmerodius albus*, Black-crowned Night Heron *Nycticorax nycticorax* (Cannell and Harrington 1984), Spotted Flycatcher *Muscicapa striata* (Achterberg and Schaefer 1985), Song Thrush *Turdus philomelos* (Erard and Armani 1986), and Verdin *Auriparus flaviceps* (Carter 1987). As a result, while interspecific brood parasitism is apparently more prevalent (approximately 108 vs. 82 species), these additional reports lend support to the notion that the intraspecific phenomenon may be more widespread, particularly among altricial and colonial species, than is currently believed.

#### DETECTING AND QUANTIFYING BROOD PARASITISM

Andersson (1984) and Håland (1986) have questioned the presumed predominance of precocial birds among intraspecific brood parasites, and a number of observers have recognized the problematic nature of many of the criteria used to detect and measure the frequency of intraspecific brood parasitism (e.g., Eriksson and Andersson 1982, Andersson 1984, Emlen and Wrege 1986, Frederick and Shields 1986a, Gibbons 1986, Westneat et al. 1987, Wrege and Emlen 1987). However, no one has questioned whether these problems may hinder our ability to make cross-species generalizations about its distribution among birds and, consequently, an accurate assessment of the factors promoting this behavior. In other words, might the

presumed rarity of intraspecific parasitism among altricial and colonial breeders be, in part, a consequence of biased detectability?

The most frequently used method of identifying intraspecific parasitism is the presence of abnormally large clutches (e.g., references in Yom-Tov 1980a, Littlefield 1981, Dhindsa 1983a, Colwell 1986, Håland 1986, Kendra et al. 1988, Picman and Belles-Isles 1988, Savard 1988, Semel et al. 1988, Young and Titman 1988). Abnormally large clutches are particularly common in precocial birds (e.g., waterfowl) and are assumed to be the result of egg dumping by one or more parasitic females. Given that such abnormally large clutches are relatively easy to detect, it seems probable that brood parasitism is less likely to go undetected in egg-dumping species, than in those in which a parasitic female deposits one egg per host nest. Further, such a criterion becomes wholly unreliable for those species that remove the host's egg before depositing their own, as occurs in a variety of altricial species including cuckoos (Cuculidae; Chance 1922), European Starlings (*Sturnus vulgaris*; Feare 1983, Evans 1988), Cliff Swallows (*Hirundo pyrrhonota*; Brown 1984, Brown and Brown 1988b), and White-fronted Bee-eaters (*Merops bullockoides*; Wrege and Emlen 1987), or for parasite-host relationships in which host females treat a parasitic egg(s) as their own and decrease accordingly the number of eggs that they lay (Andersson and Eriksson 1982). In short, this technique is highly insensitive to more "subtle" forms of parasitism that may be characteristic of altricial species.

Given that most birds lay with almost constant time intervals between eggs (Yom-Tov 1980a), and no species is known to lay more than one egg per day (Sturkie 1965, van Tienhoven 1983), a number of studies have cited an irregular sequence in the appearance of eggs in a nest as an indication of parasitism (e.g., Yom-Tov 1980b, Eriksson and Andersson 1982, Dhindsa 1983a, Thomas 1984, Earle 1986a, Håland 1986, Møller 1987, Evans 1988, Picman and Belles-Isles 1988). But, while an increase of two or more eggs per day in a clutch is considered strong presumptive evidence of parasitism (e.g., Brown 1984; Martin 1984; Colwell 1986; Frederick and Shields 1986b; Kendra et al. 1988; Lombardo 1988; Semel et al. 1988; Brown and Brown, in press), a break in egg laying is considerably problematic. It has been demonstrated that interruptions in egg laying may occur in a variety of different bird species (e.g., Wood Duck *Aix sponsa*, Heusmann et al. 1980; tits, *Parus* spp., Dhondt et al. 1983; Willow Ptarmigan *Lagopus lagopus*, Martin 1984; Common Moorhen *Gallinula chloropus*, Gibbons 1986). Interruptions may occur as a response to adverse environmental conditions or, as Eriksson and Andersson (1982) suggest, because of the female's poor physical condition. Furthermore, if parasites lay just before or after the egg-laying period of the host, and eggs are uniformly colored, then brood parasitism will go undetected and its frequency in the population will be underestimated. Frederick and Shields (1986a) have shown that, assuming only one parasitic egg is laid in any clutch, the probability of detecting brood parasitism using daily nest checks is equal to the ratio between the number of days on which a parasitic egg is theoretically detectable and the total number of days on which one parasitic egg could be deposited. If the parasite does

TABLE 1. Additional (post-Yom-Tov 1980a) species reported to exhibit intraspecific brood parasitism.

Ciconiiformes			
<i>Ciconia maguari</i>	Maguari Stork	altricial, colonial	Thomas 1984
<i>Eudocimus albus</i>	White Ibis	altricial, colonial	Frederick and Shields 1986b
Galliformes			
<i>Lagopus lagopus</i>	Willow Ptarmigan	precocial, noncolonial	Martin 1984
Gruiformes			
<i>Gallinula chloropus</i>	Common Moorhen	semi-precocial, noncolonial	Gibbons 1986
<i>Grus canadensis</i>	Sandhill Crane	precocial, noncolonial	Littlefield 1981
<i>Fulica americana</i>	American Coot	precocial, noncolonial	Arnold 1987
Charadriiformes			
<i>Limosa fedoa</i>	Marbled Godwit	precocial, semi-colonial	Colwell 1986
<i>Phalaropus tricolor</i>	Wilson's Phalarope	precocial, semi-colonial	Colwell 1986
<i>Catoptrophorus semipalmatus</i>	Western Willet	precocial, semi-colonial	Colwell 1986
Coraciiformes			
<i>Merops bullockoides</i>	White-fronted Bee-eater	altricial, colonial	Emlen and Wrege 1986
Passeriformes			
<i>Ficedula hypoleuca</i>	Pied Flycatcher	altricial, noncolonial	G. Hogstedt unpubl., cited in Håland 1986
<i>Hirundo rustica</i>	Barn Swallow	altricial, semi-colonial	Møller 1987
<i>H. pyrrhonota</i>	Cliff Swallow	altricial, colonial	Brown 1984
<i>H. spilodera</i>	South African Cliff Swallow	altricial, colonial	Earlé 1986a
<i>Riparia riparia</i>	Bank Swallow	altricial, colonial	A. P. Møller unpubl., (pers. comm.)
<i>Tachycineta bicolor</i>	Tree Swallow	altricial, colonial	Lombardo 1988
<i>Gymnorhinus cyanocephalus</i>	Pinyon Jay	altricial, colonial	Trost and Webb 1986
<i>Pica pica</i>	Black-billed Magpie	altricial, colonial	Trost and Webb 1986
<i>Troglodytes aedon</i>	House Wren	altricial, noncolonial	Picman and Belles-Isles 1988
<i>Turdus migratorius</i>	American Robin	altricial, noncolonial	Gowaty and Davies 1986
<i>Turdus pilaris</i>	Fieldfare	altricial, noncolonial	Håland 1986
<i>Sialia sialis</i>	Eastern Bluebird	altricial, noncolonial	Gowaty and Karlin 1984
<i>Ploceus manyar</i>	Striated Weaver	altricial, colonial	Dhindsa 1983a
<i>P. benghalensis</i>	Black-throated Weaver	altricial, colonial	Dhindsa 1983a
<i>Lonchura malabarica</i>	White-throated Munia	altricial, colonial	Dhindsa 1983b
<i>Passer melanurus</i>	Cape Sparrow	altricial, noncolonial	Earlé 1986b

not remove a host egg, the probability of detection decreases with decreasing clutch size (Frederick and Shields 1986a). For those species in which parasitic females remove a host egg prior to depositing their own, the probability of detecting parasitism is reduced dramatically and, if the host species lays eggs daily, is reduced to zero (Frederick and Shields 1986a). Frederick and Shields (1986a) have devised a computational formula that conservatively corrects for the underestimation of the frequency of brood parasitism due to reduced detection probabilities. Their method is most robust when the laying interval of host females is constant, only one parasitic egg is deposited per nest, parasites do not remove host eggs, and when parasitism

is equally likely to occur on any given day of a host's egg-laying schedule. In studies where these assumptions are violated detection probabilities must be adjusted, if possible, otherwise the actual frequency of intraspecific brood parasitism will be greatly underestimated.

Odd egg dimensions, markings, and/or color have frequently been used to infer intraspecific parasitism (references in Yom-Tov 1980a, Littlefield 1981, Feterolf and Blokpoel 1984, Colwell 1986, Earlé 1986a, Gibbons 1986, Møller 1987, Evans 1988, Kendra et al. 1988). The use of this criterion requires that egg patterns vary among individuals and are constant for each female. However, in Herring Gulls *Larus argen-*

tatus (Baerends and Hogan-Warburg 1982) and House Sparrows *Passer domesticus* (Lowther 1988), for example, odd-colored eggs may result from pigment depletion in a single female laying in a nest. Also, in some species, eggs within clutches become paler with increased exposure to sunlight (Eriksson and Andersson 1982). If egg appearance is used to estimate the frequency of intraspecific brood parasitism investigators must quantify the degree of individual variation within and between clutches. Furthermore, egg variation must be sufficiently low within, and high between, clutches that parasitic eggs can be unequivocally distinguished within a clutch.

Two other indirect criteria that have occasionally been used to identify parasitism are (1) the appearance of new eggs after completion of the clutch (e.g., Colwell 1986, Frederick and Shields 1986b, Picman and Belles-Isles 1988, Semel et al. 1988), and (2), in species with synchronous incubation, late hatchlings (e.g., Yom-Tov 1980b; Earlé 1986a, 1986b). However, in colonial species, where breeding is typically highly synchronous, such cues may rarely be manifested. For example, in White-fronted Bee-eaters, where egg laying is "moderately" synchronous, most (85%) parasitic females are capable of selecting hosts at the appropriate stage of their cycle; consequently, late eggs and hatchlings are unlikely to occur (Emlen and Wrege 1986). This is in marked contrast to the egg-laying habits of ducks, where eggs are frequently laid in a host's nest well after incubation has begun (e.g., Semel et al. 1988). Even in species with synchronous incubation, hatching may be delayed naturally (e.g., up to 2 days in Dead Sea Sparrow *Passer moabiticus*, Yom-Tov 1980b), and caution is urged in the interpretation of this criterion. For synchronous incubators, if new eggs appear after completion of the clutch and still hatch at the same time as the rest of the clutch, that may be presumptive evidence for egg transfers between nests (cf. Brown and Brown 1988a, 1988b).

Clearly, the criteria considered provide only indirect, circumstantial evidence for the occurrence of intraspecific brood parasitism and, consequently, results obtained from them must be interpreted with caution. Further, I would suggest that there is reasonable cause to believe that some of these criteria favor the detection of more "overt" instances of parasitism, such as waterfowl egg dumping, and that more sensitive methods, such as biochemical analyses (discussed below) are required to detect more subtle forms of the behavior.

The use of noninvasive markers such as fat-soluble dyes (Appleby and McRae 1983), tetracycline (Haramis et al. 1983), and radioisotopes (Dickman et al. 1983) have been advocated, but rarely employed as a means of ascertaining genetic relatedness in birds. The marker is fed or injected into an individual, and subsequently detected in the eggs or offspring. In general, the widespread applicability of such markers appears limited by the number of individuals that can be reliably distinguished with a given marker. More importantly, Eadie et al. (1987) have demonstrated that tetracycline may inhibit egg laying in birds and, consequently, is of limited value in obtaining an accurate assessment of the reproductive success of individual females. As Eadie et al. (1987) have cautioned, more study is required to examine the potential deleterious

effects of egg markers before widespread use of these techniques can be advocated.

The biochemical analysis of egg albumen and yolk protein polymorphisms using starch gel electrophoresis has been of limited use in detecting and measuring the frequency of brood parasitism (e.g., Manwell and Baker 1975, Fleischer 1985, Fleischer et al. 1985, Kendra et al. 1988). This method lacks widespread applicability because egg albumen and yolk proteins are only suitable if the embryo is unincubated (Manwell and Baker 1975). Furthermore, as a destructive technique it prohibits an evaluation of the host or parasite's reproductive success.

The identification of brood parasitism based upon biochemical analysis of potential parent and offspring genotypes (e.g., Gowaty and Karlin 1984, Wrege and Emlen 1987, Evans 1988) is much less problematic than those based on the criteria discussed above, but it too has limitations. Although the electrophoretic analysis of isozyme variation of tissue (e.g., blood, muscle) proteins is a reliable method for separating putative and genetic kinship (Sherman 1981), it is based on parental exclusion, and as such, provides a minimum estimate only (Gowaty and Karlin 1984). The probability of detecting parasitic offspring is limited by the degree of protein polymorphism within a population and the extent to which putative and actual (parasitic female and mate) parents possess different genotypes. The detection of genotypic heterogeneity among individuals using gel electrophoresis is favored when a large number of independently segregating, polymorphic loci can be resolved, and allele frequencies at those loci are not strongly skewed (Westneat et al. 1987, Wrege and Emlen 1987). If, however, hosts and parasites are close kin the likelihood of detecting brood parasitism is diminished because of the increased probability that the parasitic female shares a common genotype with the putative parents (e.g., White-fronted Bee-eaters, Wrege and Emlen 1987). Wrege and Emlen (1987) and Westneat et al. (1987) have developed similar genetic models that incorporate an estimate of the probability of detecting parasitic offspring to generate more accurate estimates of the frequency of successful brood parasitism. If there are additional sources of parental uncertainty (e.g., extra-pair copulations) in a population, the use of these models to estimate the frequency of brood parasitism becomes more complex mathematically, but is theoretically possible (Westneat et al. 1987, Wrege and Emlen 1987). However, even if these models are employed, gel electrophoresis will not permit identification of the parasitic females (Gibbons 1986). Further, although it is theoretically possible, this biochemical method has not to my knowledge been applied to unhatched eggs (i.e., dead embryos). If mortality affects parasitic eggs disproportionately, estimates based on the genotypes of hatched offspring will underestimate the frequency of brood parasitism.

A recent advance in genetic analysis, the use of "minisatellite" DNA probes (DNA "fingerprinting" sensu Jeffreys et al. 1985), appears to be a potentially powerful method of establishing biological relationships. Originally isolated from human DNA, each probe consists of a DNA segment which detects and hybridizes with many hypervariable minisatellites in DNA,

to produce a DNA fingerprint that is completely individual-specific. Minisatellite probes have been applied successfully to wild populations of both birds and mammals (Burke and Bruford 1987, Hill 1987, Quinn et al. 1987, Wetton et al. 1987), and although still in its infancy, the technique is capable of detecting multiple paternity and brood parasitism where conventional biochemical analyses have failed (e.g., Wetton et al. 1987). Because DNA fingerprints are individual-specific (except for monozygotic twins), the probability of detecting parasitism and correctly identifying individual parasites is great. At present, the widespread use of this technique is hampered because it is relatively expensive (particularly when commercial laboratories are employed) and there are often long delays in the development of probes and reaction conditions that produce sufficient resolution for the identification of individuals within a given study species. Unfortunately, this technique shares, with those already discussed, the drawback of being unable to detect those instances of attempted brood parasitism in which host females discriminate against and dispose of parasitic eggs (e.g., African Village Weaverbird *Ploceus cucullatus*, Victoria 1972; White-fronted Bee-eater, Emlen and Wrege 1986; American Coot *Fulica americana*, Arnold 1987; Barn Swallow *Hirundo rustica*, Møller 1987; European Starling, Stouffer et al. 1987; Cliff Swallow, Brown and Brown, in press). The propensity for females of certain species to desert their nests as an adaptive countermeasure to being parasitized will necessarily limit the probability of detecting intraspecific brood parasitism. When a nest is deserted it may not always be clear whether this is a host's response to being parasitized, human interference, or some other factor. Indirect methods essentially detect only "successful" parasitism, and an accurate indication of the prevalence of intraspecific brood parasitism will be difficult to obtain.

Although time-consuming, behavioral observations may prove invaluable in studying and more fully understanding avian parasitic behavior (e.g., Heusmann et al. 1980; Brown 1984; Emlen and Wrege 1986; Brown and Brown 1988b, in press). Not only is it the only reliable method of detecting attempted parasitism, but given a marked population with known genealogies, information can potentially be garnered on the identity and characteristics of the perpetrator (e.g., age, social status, kinship), behavior of host and parasite before, during, and after egg deposition, and, if followed through the nestling period, the subsequent survival and reproductive success of individuals employing the various reproductive strategies. That said, the inherent low frequency of intraspecific parasitism within most populations may limit the efficiency of direct observations. The applicability of direct observations may be further restricted if the behavioral act of parasitism is highly secretive and the females involved are inconspicuous in their actions (e.g., White-fronted Bee-eaters, Emlen and Wrege 1986; Cliff Swallows, Brown 1984, Brown and Brown, in press; European Starlings, Evans 1988). The limitation of direct observations is illustrated by Frederick and Shields' (1986b) study of White Ibis (*Eudocimus albus*). In one of the colonies studied, several lines of indirect, circumstantial evidence suggested that a low level of intraspecific para-

sitism had occurred, yet, brood parasitism was never witnessed during more than 15,500 hr of intensive observation. Often it may be advantageous to supplement direct observations with mounted still or motion cameras. For example, time-lapse photography has been used to monitor promiscuous behavior of shags (*Phalacrocorax aristotelis*, Harris 1982), and nest attendance by Pied-billed Grebes (*Podilymbus podiceps*, Forbes and Ankney 1988). For those species that readily accept artificial nest structures (e.g., cavity-nesters), pressure sensitive exposure-release mechanisms at nest boxes may be employed to monitor the nesting activities of individually marked birds (e.g., Tree Swallows, Quinney 1986). In assessing natural levels of brood parasitism it is imperative, however, that the density and distribution of nest boxes faithfully reflect conditions within natural populations (discussed by Semel et al. 1988). For example, Semel and Sherman (1986) observed abnormally high levels of intraspecific brood parasitism in a Wood Duck population when artificial nesting structures were spatially clumped and provided at unnaturally high densities. Indeed, the occurrence of intraspecific brood parasitism in some cavity-nesting species' populations (e.g., European Starling, Evans 1988; Eastern Bluebird, Gowaty and Karlin 1984; Tree Swallow, Lombardo 1988) may have been facilitated by the placement of boxes in highly visible sites and in proximity to other boxes (Semel et al. 1988). The use of photography or video, while costly, may help to circumvent problems imposed by surreptitious brood parasites. For many studies it may be impractical to monitor all nests in a population; however, it may be possible to intensively monitor an unbiased sample that is representative of the entire study population (e.g., Brown and Brown 1988b).

Bearing the above points in mind, a more complete understanding of the extent of intraspecific brood parasitism across taxonomic groups and its importance as an alternative female reproductive strategy within bird populations will best be achieved using a combination of the criteria and research methods discussed above. I suggest that the most fruitful studies will be those that employ DNA "fingerprinting" to clarify biological relationships in conjunction with detailed, long-term behavioral observations (both direct and indirect) of individually marked birds. This approach permits a comparison of the estimates of brood parasitism based on biochemical and observational data which may reveal biases in either method (Wrege and Emlen 1987). Furthermore, for many studies such a synergistic approach will be essential for an analysis of the adaptive value of brood parasitism.

In summary, I suggest that the presumed rarity of intraspecific brood parasitism, particularly among altricial species, may be, in part, a consequence of methodological constraints. Most reports are based upon indirect, circumstantial criteria that are biased toward detecting "overt" expressions of this behavior, as typified by waterfowl; consequently more "subtle" forms, likely to be exhibited by altricial species, may go undetected. Furthermore, intraspecific brood parasitism may be an important aspect of the reproductive biology of many avian species, despite the difficulties of detecting its occurrence. At present, an unbiased assessment of the distribution of intraspecific brood para-

sitism among birds seems improbable. Problems in evaluating parasitism may be circumvented by employing a direct (and/or indirect) observational approach in conjunction with biochemical pedigree analyses. Regardless of the methods employed it is important that investigators justify their use, especially for those studies that extend beyond the anecdotal and attempt to interpret intraspecific brood parasitism in a theoretical or evolutionary framework.

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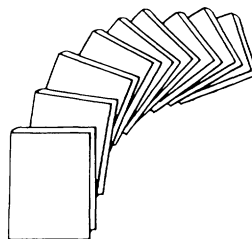
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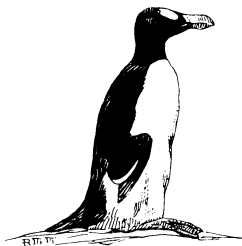
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