J. Field Ornithol., 69(3):364–375

# ADULT BROOD PARASITES FEEDING NESTLINGS AND FLEDGLINGS OF THEIR OWN SPECIES: A REVIEW

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Abstract.—We summarized 40 reports of nine species of brood parasites feeding young of their own species. These observations suggest that the propensity to provision young has not been lost entirely in brood parasites despite the belief that brood parasitic adults abandon their offspring at the time of laying. The hypothesis that species that participate in courtship feeding are more likely to provision young was not supported: provisioning of young has been observed in two species of brood parasites that do not courtship feed. The function of this provisioning is unknown, but we suggest it may be: (1) a non-adaptive vestigial behavior or (2) an adaptation to ensure adequate care of parasitic young. The former is more likely the case. Further studies are required to determine whether parasitic adults commonly feed their genetic offspring.

**ADULTOS DE AVES PARASÍTICAS ALIMENTANDO PICHONES Y VOLANTONES DE SU PROPIA ESPECIE: UNA REVISIÓN**

Sinopsis.—Resumimos 40 informes de nueve especies de aves parasíticas que alimenaron a pichones de su propia especie. Las observaciones sugieren que la propensividad de alimentar a los pichones no ha sido totalmente perdida en las aves parasíticas, no empece a la creencia de que los parasíticos abandonan su progenie al momento de poner los huevos. La hipótesis de que las especies que participan en cortejo de alimentación, son más propensas a alimentar los pichones no tuvo apoyo. Las observaciones de alimentación a pichones se han hecho en dos especies parasíticas cuyo cortejo no incluye la alimentación de la pareja. La función de proveer alimento se desconoce. No obstante, sugerimos que pueda ser: 1) una conducta vestigial no adaptativa, o 2) una adaptación para asegurar el cuidado adecuado de los pichones parasíticos. El último parece ser la causa más probable. Se necesitan estudios más detallados para determinar si los adultos de especies parasíticas alimentan a sus pichones comúnmente.

Avian brood parasitism is a reproductive strategy that has evolved in 1% of all bird species. Obligate brood parasites lay all of their eggs in nests of other species and are believed to provide no parental care to their offspring. They leave the incubation of their eggs and feeding of their offspring to hosts and do not normally participate in these behaviors (Payne 1977). Interestingly, it has come to our attention that some brood parasites have been observed feeding young of their own species. We reviewed the literature and compiled observations of this behavior (1) to determine which parasitic species have been observed provisioning young; (2) to determine how frequently this behavior has been described in the literature; (3) to describe the nature of the observations (i.e., the sex of the provisioner, whether nestlings or fledglings are involved, and duration of the feeding); and (4) to identify the possible function of this behavior.

## TREATMENT OF RECORDS

Published observations were mainly anecdotal because it was not known in any case whether the provisioning adults were the genetic parents of

the young that were fed. Care must be taken when interpreting the apparent feeding of a young bird because some observers may have mistook it for feeding of an adult female, which occurs during courtship feeding. We determined, therefore, which species also are known to practice courtship feeding because we wanted to determine whether the records of provisioning involved only these species. Species that courtship feed may be more predisposed to feeding young (Benson and Serventy 1957). If the provisioning of young is an extension of courtship feeding, then only males would be expected to perform this behavior because only they feed females. Common names of species were used throughout the paper (scientific names in Appendix); taxonomy follows Sibley and Monroe (1990).

## OBSERVATIONS OF PROVISIONING OF YOUNG BY BROOD PARASITES

Feeding of young brood parasites by individuals of the same species has been reported at least 40 times (Table 1). This behavior has been observed in at least nine parasitic species from the families Cuculidae and Fringillidae (Tribe Icterini), and has been reported most often in Pallid ($n = 9$) and Dideric ($n = 11$) Cuckoos (Table 1). Other authors have made only a general statement that the following parasites feed young of their own species, but did not provide details of the observations: Pied Cuckoo (Ali and Ripley 1969), Fan-tailed Cuckoo (Friedmann 1968), Shining Bronze-cuckoo (Oliver 1955), Dideric Cuckoo (Mackworth-Praed and Grant 1970, Roberts 1958), Channel-billed Cuckoo (Friedmann 1968), and cuckoos in general (Chisholm 1956, Fletcher 1915). Including these observations, provisioning of young by a brood parasite has been recorded in at least 12 parasitic species. Ten of these species also courtship feed. Thus, "parental" feeding has been observed in two species that do not courtship feed: Asian Koel and Brown-headed Cowbird (Table 2). Species that courtship feed are not more likely to provision young (Fisher exact test, one-tailed, $P > 0.05$).

Five reports involved nestlings and 38 involved fledglings (three reports involved both nestlings and fledglings). Most authors did not report the sex of the individual that fed the young, but in those cases where birds were sexed, provisioners included males ($n = 7$), females ($n = 6$), a pair of adults ($n = 3$), and one group of adults of both sexes. A pair was not assumed to be male and female. Some adult parasites were observed feeding more than one parasitic young (Baird 1945, Merritt 1956). Some observations were made over several days (J. A. Fletcher 1915, L. R. Fletcher 1925, Hanscombe 1915, Hare 1915, Hume *in* Fulton 1904, Kikkawa and Dwyer 1962, Van Someren 1956, Walton 1903); however, because the individuals were not banded, their identities were not known.

McCracken (1984) "believed" a male Bronzed Cowbird fed one of three cowbird fledglings that was in its company, but the evidence was insufficient to include in Table 1. The following records were also excluded from our review because they were criticized: (1) Cheeseman (1890) and (2) Fulton (1910) were criticized by Friedmann (1949), (3) Graham (1940) by Watson and Bull (1950), (4) Hartlaub (*in* Friedmann

TABLE 1. Feeding of parasitic nestlings or fledglings by an adult of the same species.

| Parasite species | Known or suspected host species[a] | Comments | Reference |
|---|---|---|---|
| Great Spotted Cuckoo | *Artamus* sp. (s) | adult fed fledgling | North 1912 |
| Great Spotted Cuckoo | U | adult fed "juvenile" | Mundy and Cook 1977 |
| Common Cuckoo | U | ♀ fed recent fledgling | Browne 1886 |
| Common Cuckoo | U | adult fed fledgling | Kelin 1911 |
| Common Cuckoo | Meadow-pipit (k) | more than one observation of adult feeding cuckoo during nestling and fledgling stages | Bannerman and Lodge 1955:132 |
| Common Cuckoo | U | adult fed young | Palmer *in* Bannerman and Lodge 1955: 132 |
| Pallid Cuckoo | U | adult fed young (2 reports) | Campbell 1900 |
| Pallid Cuckoo | *Artamus* sp. (s) | adult fed fledgling | North 1912 |
| Pallid Cuckoo | U | pair of cuckoos assisted host daily in feeding fledgling | Hanscombe 1915 |
| Pallid Cuckoo | U | adult fed "well-grown young" | Jackson 1949 |
| Pallid Cuckoo | U | adult twice fed young | Learmonth 1949 |
| Pallid Cuckoo | U | adult cuckoo fed fledgling | Cooper 1958 |
| Pallid Cuckoo | U | adult fed fledgling; another adult fed a different fledgling repeatedly during one period of observation | Kikkawa and Dwyer 1962 |
| Pallid Cuckoo | U | feeding young or courtship feeding of immature ♀ | Fleming 1979 |
| Pallid Cuckoo | White-browed Scrubwren (k) | ♀ fed fledgling | Ambrose 1987 |
| Pallid Cuckoo or Shining Bronze-cuckoo | Yellow-rumped Thornbill (k) | adult fed nestling | Howe 1905 |
| Shining Bronze-cuckoo | Grey Gerygone (s) | adult fed nearly full grown cuckoo | Hursthouse 1944 |
| Klaas's Cuckoo | U | adult fed young (4 reports), one young not able to fly | Moreau and Moreau 1939 |
| Klaas's Cuckoo | U | adult fed young (3 reports) | Van Someren 1939 |
| Klaas's Cuckoo | U | adult fed fledgling | Moreau 1944 |
| Klaas's Cuckoo | U | observations of ♂s feeding nestlings and fledglings on separate occasions | Van Someren 1956 |
| Klaas's Cuckoo | U | ♂ fed 2 young repeatedly for 15 min | Baird 1945 |
| African Emerald Cuckoo | U | ♂ fed young | Millar 1943 |
| Dideric Cuckoo | sparrow (*Passer* sp.) (k) | pair fed fledgling daily for a week or more | Hare 1915 |
| Dideric Cuckoo | Village Weaver (s) | captive ♀ fed captive fledgling; ♂ fed same fledgling through cage bars | Millar 1926 |
| Dideric Cuckoo | U | ♂ fed young or courtship feeding | Moreau 1944 |

TABLE 1. Continued.

| Parasite species | Known or suspected host species[a] | Comments | Reference |
|---|---|---|---|
| Dideric Cuckoo | U | feeding young or courtship feeding | Bannerman *in* Moreau 1944 |
| Dideric Cuckoo | U | ♂ fed "well-grown" young or courtship feeding | Friedmann 1948 |
| Dideric Cuckoo | U | ♂ fed young or courtship feeding observed 10 times in 6 min | Maclaren 1952 |
| Dideric Cuckoo | U | on several separate occasions, different adults fed different young recently able to fly | Maclaren 1953 |
| Dideric Cuckoo | U | ♂ fed fully fledged young | Symons *in* Friedmann 1956 |
| Dideric Cuckoo | U | adults fed fledglings on several occasions | Smith 1957 |
| Dideric Cuckoo | U | ♂ fed young | Thomas 1960 |
| Dideric Cuckoo | U | adult fed fledgling | Ottow and Duve 1965 |
| Asian Koel | U | on several separate occasions, different adults fed different young | Hume *in* Fulton 1904 |
| Brown-headed Cowbird | Rose-breasted Grosbeak (k) | ♀ fed nestling daily | Bonwell 1895 |
| Brown-headed Cowbird | Common Yellowthroat (k) | ♀ fed cowbird at nestling and fledgling stage | Walton 1903:219 |
| Brown-headed Cowbird | U | ♀ fed juvenile repeatedly during one day of observations | Fletcher 1925 |
| Brown-headed Cowbird | U | within a flock, ♂♂ and ♀♀ fed many young | Merritt 1956 |
| Brown-headed Cowbird | Northern Cardinal (s) | ♂ and ♀ cowbird and ♀ cardinal fed young cowbird | Hernandez 1986 |

[a] Known host species (k), suspected host species (s) provided by the author, unknown host species (U).

1955) by Friedmann (1955), (5) Walton (1892) by Fletcher (1925), and (6) Worman (1930) by the editor of the *Oologists' Record.* Graham (1950) addressed Watson and Bull's (1950) criticisms.

## COURTSHIP FEEDING AND PROVISIONING OF YOUNG

Observations of provisioning of young by brood parasites provide strong evidence that the propensity to provision young has not been lost by at least some individuals of some species of brood parasites. This behavior is either vestigial or a new development (Kikkawa and Dwyer 1962). If the latter, this behavior may have developed as an extension of courtship feeding (Benson and Serventy 1957). Courtship feeding and "parental" feeding have similar elements, although the motives for these behaviors differ. Courtship feeding allows females to assess the food-gath-

TABLE 2. Parasitic species that have been observed provisioning young and/or courtship feeding.

| Parasitic species | Observations of feeding: Young | Observations of feeding: Courtship | Courtship feeding references |
|---|---|---|---|
| INDICATORIDAE | | | |
| Greater Honeyguide | N[a] | N | not mentioned in Friedmann 1955[d] |
| CUCULIDAE | | | |
| Pied Cuckoo | Y | Y | Godfrey 1939, Liversidge 1971 |
| Great Spotted Cuckoo | Y | Y | Channer 1976 |
| Thick-billed Cuckoo | N | Y | Rowan 1983 |
| Red-chested Cuckoo | N | Y | Rowan 1983 |
| Black Cuckoo | N | Y | Young 1946 |
| Common Cuckoo | Y | Y | Wyllie 1981 |
| Pallid Cuckoo | Y | Y | Klapste 1981, Lord 1956, Noske 1978, Robinson 1950, White 1950 |
| Brush Cuckoo | N | Y | Noske 1978 |
| Fan-tailed Cuckoo | Y | Y | Chisholm 1940, Smithers 1977, Noske 1978 |
| Shining Bronze-cuckoo | Y | Y | Falla et al. 1978, Serventy 1958, Watson and Bull 1950 |
| Horsfield's Bronze-cuckoo | N | Y | McCulloch 1967, Moffat 1978, Wall 1978, Watson 1955 |
| Klaas's Cuckoo | Y | Y | Winterbottom 1939 |
| African Emerald Cuckoo | Y | Y | Haydock 1950 |
| Asian Koel | Y | N | n/a |
| Long-tailed Koel | N[b] | N | n/a |
| Channel-billed Cuckoo | Y | Y | Goddard and Marchant 1983 |
| FRINGILLIDAE | | | |
| Bay-winged Cowbird | N | N | not mentioned in Friedmann 1929[d] |
| Screaming Cowbird | N | N | not mentioned in Friedmann 1929[d] |
| Shiny Cowbird | N | N | not mentioned in Friedmann 1929[d] |
| Bronzed Cowbird | N[c] | N | not mentioned in Friedmann 1929[d] |
| Brown-headed Cowbird | Y | N | not mentioned in Friedmann 1929[d] |

[a] Possible observation by Hartlaub *in* Friedmann (1955:162).
[b] Possible observation by Cheeseman (1890).
[c] Possible observation by McCracken (1984).
[d] Courtship feeding was not mentioned to occur in these species although there was a section on courtship behavior in Friedmann (1929, 1955).

ering ability of males, increases the female's nutritional reserves, and facilitates pair formation (Nisbet 1973, Smith 1980). "Parental" feeding, on the other hand, contributes primarily to the growth and development of the parasite. Courtship feeding, which also occurs in nonparasitic cuckoos (e.g., Dwarf Cuckoo, Ralph 1975; Black Coucal, Rowan 1983; Black-billed Cuckoo, Spencer 1943) and many other nonparasitic taxa, has been reported in 11 avian orders and in almost three-quarters of passerine families (Smith 1980). Although provisioning of young occurs in many of

the same parasitic species that also courtship feed, there is not enough evidence to suggest that the provisioning of young developed from courtship feeding. First, both male and female brood parasites have been observed provisioning young, whereas only males feed adult females. Second, the provisioning of young has been observed in two parasitic species that do not courtship feed (Asian Koels and Brown-headed Cowbirds). Third, there is no significant association between courtship feeding and provisioning of young.

It is not surprising that female brood parasites have been observed feeding nestlings or fledglings because they probably are the ones that find a nest and determine when it is suitable for laying and, in the case of many species, visit it to remove or pierce a host egg (e.g., Brooker and Brooker 1989, Carter 1986, Gill 1983, Jensen and Jensen 1969, Livesey 1936, Mason 1980, Sealy 1992). Males are not commonly involved in any of these activities, although there are a few observations of activity by parasitic males around nests (e.g., Sealy 1994). In light of the fact that parasitic males are seldom observed around host nests, it is interesting that males of the following species have been observed feeding nestlings and fledglings: Klaas's Cuckoo, African Emerald Cuckoo, Dideric Cuckoo, and Brown-headed Cowbird.

## PARENT-YOUNG ASSOCIATION

Use of molecular genetic techniques would determine whether the adults are the genetic parents of the parasitic young they are feeding. Hahn and Fleischer (1995) found that female and juvenile Brown-headed Cowbirds trapped together had higher band similarities based on restriction fragments than would be expected by chance. This finding, however, was based on only 11 pairs of adult female and juvenile cowbirds, and individuals trapped at the same time may not have arrived at the trap together. Also, baited traps possibly affect the distribution of birds and may unnaturally attract many birds to a small area. Nonetheless, Hahn and Fleischer's finding is interesting because young cowbirds appeared to associate with their mothers. Fletcher (1925) observed an adult female cowbird that repeatedly fed the same juvenile although there were other young cowbirds feeding in the same area. The relationship between these individuals, however, was not known.

Mother-offspring associations could result from female cowbirds recruiting their young, or from young cowbirds seeking out their mothers (McCracken 1984, Hahn and Fleischer 1995). The only way that young cowbirds could become visually familiar with their mothers is if females visited the nest during the nestling stage. Female cowbirds are known to visit nests after parasitism to remove host eggs (e.g., Mayfield 1961, Sealy 1992), however, mother-offspring associations cannot develop when nests are visited during the egg stage. Young cowbirds could become acoustically familiar with their mothers if the latter vocalize near the nest (Hahn and Fleischer 1995). Females frequently are in the area of a nest they have parasitized because there is evidence that they have home ranges

(e.g., Alderson 1996, Darley 1983, Rothstein et al. 1984, Teather and Robertson 1985).

Hahn and Fleischer (1995) suggested that by associating with adult brood parasites, juveniles can better learn species-specific behavior. However, species-specific behavior of brood parasites, such as singing in males and song recognition in females, has been found to be innate (King and West 1977), and Friedmann (1929) reported that large flocks of Brown-headed Cowbirds formed during the fall are frequently composed entirely of juveniles. Therefore, juvenile parasites likely seek out individuals of their own species rather than being recruited by adults.

There is evidence that Great Spotted Cuckoos monitor nests after laying. Soler et al. (1995) suggested that females of this species monitor nests they have parasitized to ensure that their egg remains in the nest. Nest predation, presumably by female cuckoos, is more likely to occur if the parasitic egg has been ejected. This forces hosts to renest and provides the cuckoos with another chance to lay an egg (see also Zahavi 1979). Similarly, Arcese et al. (1996) suggested that cowbirds depredate nests that are discovered too late in the host's nesting cycle for parasitism to succeed.

Nest protection, another type of parental behavior, has been observed in Brown-headed Cowbirds and Great Spotted Cuckoos. Balda and Carothers (1968) twice observed a female Brown-headed Cowbird alarm call and display at the approach of a potential predator to a parasitized nest, and Gabrielson (1921) described another instance of this behavior. Females should benefit by monitoring the progress of a nest and protecting the nest from the approach of predators, but the costs of spending so much time in this activity, however, likely outweigh the benefits. The scarcity of reports of nest protection by female cowbirds suggests that this behavior is rare. The female cowbirds probably were not at the nest specifically to defend it, but rather defended the nest opportunistically. On the other hand, nest protection by Great Spotted Cuckoos appears to be more common. Soler et al. (unpubl. data *in* Soler et al. 1995) were scolded by cuckoos on 25% of 56 visits to 30 parasitized Black-billed Magpie nests, whereas they were scolded by magpies on only 5% of the visits.

## STRATEGY OR OPPORTUNISM?

About 90% of the records of provisioning in brood parasites involved cuckoos. This may reflect the fact that courtship feeding is found only among the cuckoos. Evidence for this, however, is weak because we did not find a significant association between courtship feeding and provisioning behavior. More likely, it is because there are more species of parasitic cuckoos than cowbirds and honeyguides.

The question remains whether the provisioning of young by brood parasites is common enough to be considered a strategy or whether it is simply trivial behavior. Like other species of birds, brood parasites may possess an innate response to feed begging young (see Craig and Jamieson 1990). If parasitic adults respond to the stimulus of begging young,

then there should also be observations of adult parasites feeding begging young of other species. We did not find observations of this behavior, although there are many cases reported of nonparasitic species feeding other nonparasitic species (Shy 1982), and individuals other than the original foster parents of parasitic species feeding parasitic young (Sealy and Lorenzana 1997). The lack of such observations suggests that it is the adult brood parasite's intention to feed an individual of its own species. Implicitly, the adults recognize young of their own species.

Provisioning of young by brood parasites may be important if hosts cannot provide the young parasite with enough or the right kind of food. In such cases, limited parental care by brood parasites could be an adaptation to poor-quality hosts. Benson and Serventy (1957) suggested that provisioning by brood parasites may be necessary in cases where insectivorous brood parasites lay eggs in nests of herbivorous species. There is, however, no evidence for this because parasitic nestlings raised by herbivorous species usually do not survive to fledging (Eastzer et al. 1980, Kozlovic et al. 1996, Middleton 1991; but see Seel and Davis 1981). Furthermore, most observations involve brood parasites feeding fledglings, not nestlings. Brood parasitic species should be strongly selected to avoid herbivorous hosts altogether (Kozlovic et al. 1996), rather than to compensate for herbivorous hosts by feeding the young at the nest.

## ACKNOWLEDGMENTS

This review was initiated during a sabbatical leave granted to SGS by the University of Manitoba. N. L. Sealy provided invaluable help with the early stages of the literature search. Comments from J. V. Briskie and C. R. Chandler greatly improved the manuscript. Financial support was provided by a NSERC research grant to SGS and NSERC and (University of Manitoba) Faculty of Science Undergraduate Summer Research awards to JCL.

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Received 29 Jan. 1997; accepted 30 May 1997.

APPENDIX. Common and scientific names of avian species mentioned in the paper.[a]

| FAMILY<br>Common name | Scientific name |
|---|---|
| INDICATORIDAE | |
| Greater Honeyguide | *Indicator indicator* |
| CUCULIDAE | |
| Pied Cuckoo | *Oxylophus jacobinus* |
| Great Spotted Cuckoo | *Clamator glandarius* |
| Thick-billed Cuckoo | *Pachycoccyx audeberti* |
| Red-chested Cuckoo | *Cuculus solitarius* |
| Common Cuckoo | *Cu. canorus* |
| Pallid Cuckoo | *Cu. pallidus* |
| Brush Cuckoo | *Cacomantis variolosus* |
| Fan-tailed Cuckoo | *Ca. flabelliformis* |
| Shining Bronze-cuckoo | *Chrysococcyx lucidus* |
| Klaas's Cuckoo | *Ch. klaas* |
| African Emerald Cuckoo | *Ch. cupreus* |
| Dideric Cuckoo | *Ch. caprius* |
| Asian Koel | *Eudynamys scolopacea* |
| Long-tailed Koel | *E. taitensis* |
| Channel-billed Cuckoo | *Scythrops novaehollandiae* |
| CENTROPODIDAE | |
| Black Cuckoo | *Centropus grillii* |
| COCCYZIDAE | |
| Dwarf Cuckoo | *Coccyzus pumilus* |
| Black-billed Cuckoo | *Co. erythropthalmus* |
| CORVIDAE | |
| Black-billed Magpie | *Pica pica* |
| MELIPHAGIDAE | |
| White-plumed Honeyeater | *Lichenostomus penicillata* |
| PARDALOTIDAE | |
| White-browed Scrubwren | *Sericornis frontalis* |
| Striated Calamanthus | *Calamanthus fuliginosus* |
| Yellow-rumped Thornbill | *Acanthiza chrysorrhoa* |
| Grey Gerygone | *Gerygone igata* |
| VIREONIDAE | |
| Red-eyed Vireo | *Vireo olivaceus* |
| PASSERIDAE | |
| House Sparrow | *Passer domesticus* |
| Meadow pipit | *Anthus pratensis* |
| Village Weaver | *Ploceus cucullatus* |
| FRINGILLIDAE | |
| Yellow Warbler | *Dendroica petechia* |
| Common Yellowthroat | *Geothlypis trichas* |
| Rose-breasted Grosbeak | *Pheucticus ludovicianus* |
| Northern Cardinal | *Cardinalis cardinalis* |
| Bay-winged Cowbird | *Molothrus badius* |
| Screaming Cowbird | *M. rufoaxillaris* |
| Shiny Cowbird | *M. bonariensis* |
| Bronzed Cowbird | *M. aeneus* |
| Brown-headed Cowbird | *M. ater* |

[a] Order and nomenclature follow Sibley and Monroe (1990).