Evolution of brood parasitism in birds: constraints related to prey type

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Summary
Few birds are obligate brood parasites and one explanation is that the young will not thrive with the food and parental care provided by another species. We addressed this problem by cross-fostering between two passerine birds with similar breeding ecology, viz., the pied flycatcher (Ficedula hypoleuca), and the great tit (Parus major). A previous study showed that pied flycatchers are readily raised by great tit foster parents, but that cross-fostering of great tits to pied flycatcher nests fails. In the present study, great tit nestlings were temporarily placed in pied flycatcher nests and video filmed when three and 10 days old. The parents did not seem to discriminate between the nestlings of the two species but the great tits had more problems handling the prey. Apparently, the offspring of the two species have adapted to different diets, pied flycatchers providing more adult and winged insects to their young than do great tits. We suggest that species with nestlings feeding on prey items that are difficult to swallow are more likely candidates to become interspecific brood parasites than species feeding on soft prey easily ingested.

Keywords: brood parasitism, prey, parental care, Ficedula hypoleuca, Parus major.

Introduction
In birds, only about 100 species are obligate interspecific brood parasites, and these species are found in only four orders (Yom-Tov & Geffen, 2006). This is surprising because there are apparently some advantages of parasitism, like reducing the costs of reproduction (Davies, 2000). However,
a number of constraints may prevent brood parasitism from evolving: inadequate parental care related to amount and type of food provided by the host (Hamilton & Orians, 1965; Payne, 1977; Kozlovic et al., 1996) and to failure of the parasitic nestlings to display adequate begging stimuli (Davies et al., 1998; Kilner et al., 2004; Madden et al., 2005), competition from host nestlings (Slagsvold, 1998; Hauber & Moskát, 2008), low access to host nests (Hamilton & Orians, 1965), discrepancy between timing and duration of egg laying and incubation periods between parasite and host (Hamilton & Orians, 1965; Slagsvold, 1998; Davies, 2000), rejection behaviour caused by a pre-existing tendency of host parents to clean unfamiliar objects from the nest (Moskát et al., 2003), previously evolved defensive mechanisms against conspecific and heterospecific brood parasitism (Rothstein, 1990; Davies, 2000), and problems with species recognition of juveniles reared as parasites when subsequently trying to mate and breed (Slagsvold & Hansen, 2001; Slagsvold et al., 2002).

In the present study, we focus on the importance of inadequate parental care and food in a model system using two common hole-nesting passerines, the pied flycatcher (*Ficedula hypoleuca*), and the great tit (*Parus major*). The two species compete for nest sites and sometimes eggs of one species are found in the nest of the other species (Slagsvold, 1975). A recent cross-fostering experiment showed that pied flycatcher nestlings can be readily fostered by great tit and blue tit (*Cyanistes caeruleus*) hosts, and that the juveniles have similar local recruitment rate and breeding success as controls reared by their own pied flycatcher parents (Slagsvold et al., 2002; Slagsvold, 2004). In contrast, a pilot test of cross-fostering of a few great nestlings to pied flycatcher nests showed that all the young died (T. Slagsvold, unpublished data). The reason for this discrepancy is not known, but a possibility is that pied flycatcher parents feed great tit nestlings at an insufficient rate because of some particular traits of the young (like inadequate begging calls; cf., Davies et al., 1998), or that they provide prey that the great tit nestlings are unable to swallow or digest. The latter may well be the case because in the breeding season great tits feed predominantly on soft prey, such as spiders and caterpillars (Perrins, 1979), whereas pied flycatchers include more adult insects, such as flies, beetles and butterflies (Lundberg & Alatalo, 1992). The pied flycatcher may have adapted to this by an improved swallowing ability compared to great tit nestlings. Alternatively, the parents provide prey that are small enough to be swallowed despite protruding appendages.