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Breeding site and host selection by Horsfield's bronze-cuckoos, *Chalcites basalis*

N. E. LANGMORE* & R. M. KILNER†
*School of Botany and Zoology, Australian National University
†Department of Zoology, University of Cambridge

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Cuckoos are faced with a series of reproductive decisions unique to the brood-parasitic lifestyle. Choice of the appropriate host to rear their young requires decision making at three levels. First, selection of a breeding site may take into account host densities in addition to environmental considerations. Second, once they have selected a breeding site, female cuckoos must ensure that they choose the nests of an appropriate host species to rear their young. Third, cuckoos may also choose among individuals of the host species in relation to the likelihood that the host will successfully rear their young. By observation and experiment, we investigated the factors that influenced annual parasitism rates and the mechanisms of host choice in Horsfield's bronze-cuckoos, *Chalcites basalis*. Parasitism rates varied from 0% to 37% annually, and were influenced by host density and spring rainfall. Despite the availability of several suitable hosts with similar nest sites within the same habitat, over 99% of Horsfield's bronze-cuckoo eggs were laid in superb fairy-wren, *Malurus cyaneus*, nests, lending strong support to the Host Preference Hypothesis for host choice. Patterns of parasitism were nonrandom with respect to host female age and identity, but we found no evidence that cuckoos preferentially parasitized those individuals that were most likely to successfully rear their young.

Keywords: avian brood parasitism; *Chalcites basalis*; Horsfield's bronze-cuckoo; maternal effect; habitat imprinting; host density; host partitioning; host preference

Brood parasites lay their eggs in the nests of other species, and are thus spared the challenge of rearing their young. However, their reproductive success depends on the successful choice of a breeding site and suitable hosts. Unlike nonparasitic species, brood parasites must assess not only the suitability of a breeding site for their own requirements, but also the availability of hosts to rear their offspring. Brood parasites lay their eggs during the egg-laying period of their hosts (Davies 2000), so a suitable breeding site should contain sufficient host numbers to ensure a ready supply of host nests at the appropriate stage for parasitism. A second challenge for brood parasites is to identify the appropriate host species. Selection of the appropriate host ensures that parasitic chicks are provided with suitable and sufficient food (Kleven et al. 1999) and, in parasitic cuckoo species with egg or chick mimicry, choosing the right host reduces the probability of egg or chick rejection by hosts (Rothstein 1982; Davies 2000; Langmore et al. 2003). Finally, brood parasites may also choose between host individuals depending on the likelihood that the host will successfully rear their young (e.g. Soler & Møller 2004). The hypotheses relating to each of these reproductive decisions are discussed below.

Correspondence: N. E. Langmore, School of Botany and Zoology, Australian National University, Canberra 0200, Australia (email: naomi.langmore@anu.edu.au). R. M. Kilner is at the Department of Zoology, Downing Street, Cambridge, CB2 3EJ, U.K.

SELECTION OF A BREEDING SITE

Rates of parasitism by brood parasites vary widely over time and between nearby sites (Davies 2000), and many studies report years in which parasitism rates declined to zero (e.g. Brooker & Brooker 1989a; Langmore et al. 2007). Few studies have attempted to identify the factors that influence parasitism rates at a particular site. There is some indication that brood parasites assess host numbers, because parasitism rates were found to increase with host

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density in brown-headed cowbirds, *Molothrus ater* (Smith & Arcese 1994; Barber & Martin 1997; Fauth 2000; but see Clotfelter 1999) and common cuckoos, *Cuculus canorus* (Alvarez 2003), and relative population size of host species was found to effect host choice in the common cuckoo (Soler et al. 1999). However, host species that nest in colonies or in close proximity may experience reduced parasitism with increasing density through corporate vigilance and nest defence (Lawes & Kirkman 1996; Martinez et al. 1996) or through 'swamping' parasites with many synchronous nests (Soler et al. 1998). Brood parasites may also choose between sites in relation to whether they are good feeding grounds. For example, parasitism rates of brown-headed cowbirds increased with forest fragmentation (Brittingham & Temple 1983 cited in Davies 2000). This could reflect a higher food supply in the intervening agricultural land, but could also be related to higher host densities in edge habitat (Robinson et al. 1995b cited in Davies 2000). Some brood parasites are less constrained in their choice of breeding site, because they occupy separate feeding and breeding areas that may be several kilometres apart (Vogl et al. 2002; Nakamura et al. 2005).

SELECTION OF HOST SPECIES

Four hypotheses have been generated to explain the mechanism by which cuckoos select the appropriate host (de Brooke & Davies 1991; Moksnes & Røskaft 1995; Vogl et al. 2002): (1) The Host Preference Hypothesis. The cuckoo either recognizes its host innately or imprints on its host parents and seeks nests of the same species to parasitize (Lack 1968; Brooke & Davies 1991). (2) Habitat imprinting. The young cuckoo imprints on the habitat in which it was reared, and seeks similar habitats in which to breed (Teuschl et al. 1994, 1998). (3) Natal philopatry. Cuckoos return to the site in which they were born and choose nests randomly (Brooke & Davies 1991). (4) Nest site choice. A cuckoo chooses a group of birds with similar egg types and nest sites and searches randomly for nests within that group (Wyllie 1981; Moksnes & Røskaft 1995).

Host imprinting was demonstrated to be the key to host choice in an experimental study of brood-parasitic indigobirds (Payne et al. 2000). However, evidence from other brood parasites is equivocal. A captive study of common cuckoos failed to find evidence of host imprinting, but this was probably due to artificial conditions leading to a failure to breed (Brooke & Davies 1991). Support for the Host Preference Hypothesis came from a study of egg mimicry in common cuckoos, which found that cuckoo eggs matched those of their chosen host more closely than those of other potential hosts within the same habitat (Avilés & Møller 2004). Furthermore support for the Host Preference Hypothesis comes from findings that individual female common cuckoos are consistent in their choice of host (Nakamura & Miyazawa 1997; Marchetti et al. 1998; Honza et al. 2002; Avilés & Møller 2004; Skjelseth et al. 2004; Nakamura et al. 2005). Vogl et al. (2002) demonstrated that individual female common cuckoos consistently laid eggs in a preferred habitat type, although because of the habitat specificity of hosts, their results were compatible with both the Habitat Imprinting and the Host Preference hypotheses. Teuschl et al. (1998) found partial experimental support for the Habitat Imprinting Hypothesis, because hand-reared cuckoos preferred the habitat in which they were reared in 1 of 2 test years. Thus, most evidence to date points to a role for host preference or habitat imprinting. Teuschl et al. (1998, see also Honza et al. 2001) suggest that cuckoos may locate the appropriate host through a combination of these processes; first a young cuckoo would return to the general area in which it was born, then it would seek similar habitat to that in which it was reared, and finally it would seek out birds that shared the characteristics of its foster parents.

SELECTION OF INDIVIDUAL HOSTS

The question of whether cuckoos strategically choose among individual nests of their host species in relation to the likelihood that the host will successfully rear their young has received relatively little attention. In theory, cuckoos might benefit by selecting host individuals that are less likely to reject their eggs or young (e.g. novice breeders, Lotem et al. 1992), individuals that are likely to provide sufficient food for the cuckoo chick (e.g. individuals on the best quality territories, Soler & Møller 2004, experienced breeders, Smith et al. 1984; Soler et al. 1999), or individuals that are more likely to protect their young from predators (e.g. larger groups in cooperative or colonial species, Poiani & Elgar 1994, or those with well-concealed nest sites). Evidence from an experimental study suggests that such choices can take place. Soler & Møller (2004) demonstrated that great spotted cuckoos, *Clamator glandarius*, preferentially parasitized magpie, *Pica pica*, pairs with larger nests, an indicator of territory quality. The probability of survival of cuckoo chicks increased if they were laid in the nests of high quality hosts.

Alternatively, cuckoos may be so constrained by the demands of finding sufficient host nests at the appropriate stage for parasitism (e.g. Strausberger 1998) that further choice between host individuals is not feasible. Cuckoos may be particularly constrained when it comes to finding novice breeders, because they would lack previous knowledge of their nest sites and habits (Brooker & Brooker 1996), and in parasitizing large groups, which are likely to have higher levels of vigilance and nest defence against cuckoos (Payne et al. 1985). Evidence in support of the latter is that larger colonies of red bishops, *Euplectes orix*, suffer lower parasitism rates by Diederik cuckoos, *Chrysococcyx caprius*, perhaps because they are better able to drive cuckoos away (Ferguson 1994; Lawes and Kirkman 1996).

Here we explore the parasitic strategies of a small, Australian cuckoo, Horsfield's bronze-cuckoo, *Chalcites basalis*. We aim to assess its host choice strategies at three levels.

Breeding Site Selection

Horsfield's bronze-cuckoos in southern Australia are described as nomadic or migratory (Higgins 1999), and