



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

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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.

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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.

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 indigo-birds (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 basalidis*. 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

studies generally report high annual variation in occurrence (e.g. recorded in 16 of 58 years at Scheyville, NSW, Australia, Egan et al. 1977). Similarly, parasitism rates at particular sites vary annually (e.g. 0–44% of splendid fairy-wren, *Malurus splendens*, nests parasitized at Gooseberry Hill, WA, Australia, Brooker & Brooker 1989a; 0–37% of superb fairy-wren, *Malurus cyaneus*, nests at Campbell Park, ACT, Australia, Langmore et al. 2007). There is some indication that their movements are influenced by rainfall, because a long-term study reported that they were present in good seasons only and usually appeared in an area following heavy rain (Brooker et al. 1979). We aim to isolate some of the factors that predict breeding site selection in Horsfield's bronze-cuckoos, by testing whether rainfall and host density influence annual parasitism rates.

Choice of Host Species

Horsfield's bronze-cuckoos primarily parasitize fairy-wrens (*Malurus* spp.), but also secondarily parasitize several other small passerines (Brooker & Brooker 1989b). At our study site, potential secondary hosts were yellow-rumped thornbills, *Acanthiza chrysorrhoa*, buff-rumped thornbills, *Acanthiza reguloides*, and speckled warblers, *Chthonicola sagittata*, and, at low densities, brown thornbills, *Acanthiza pusilla*, striated thornbills, *Acanthiza lineata*, and white-browed scrubwrens, *Sericornis frontalis*. All these species are suitable hosts in terms of nest characteristics and diet (Brooker & Brooker 1989b). The latter two species were not included in the study, because of their low numbers and the inaccessibility of striated thornbill nests. Features of the habitats and nest sites and structures (see methods) of the remaining potential hosts allowed us to test between the four hypotheses for host choice, and to make predictions about which hosts should be parasitized under each hypothesis (Table 1):

(1) Because of the sympatry of these species, if Horsfield's bronze-cuckoos use natal philopatry or habitat

Table 1. Host species predicted to be parasitized by Horsfield's bronze-cuckoos in Campbell Park under each of four different mechanisms for host choice

	Natal philopatry	Habitat imprinting	Nest site choice	Host preference
Superb fairy-wren	X	X	X	X*
Brown thornbill	X	X	X	
Buff-rumped thornbill (noncavity nests)	X	X	X	
Buff-rumped thornbill (cavity nests)	X	X		
Yellow-rumped thornbill	X	X		
Speckled warbler	X	X		

*The Host Preference Hypothesis predicts parasitism of superb fairy-wrens only, unless there are host-specific races (*gentes*) in Horsfield's bronze-cuckoos.

imprinting to identify suitable hosts, we should see parasitism of all six species in relation to their density, and individual female cuckoos should not be host specific. If natal philopatry plays an important role, we should see some cuckoo fledglings and adults returning to the study site in consecutive years.

(2) If they use nest site choice to identify their hosts, we should see parasitism of superb fairy-wrens and brown thornbills, and of buff-rumped thornbill gully/bush nests, but not buff-rumped thornbill cavity nests (see Methods). Again, individual females should not be host specific.

(3) If cuckoos imprint on their hosts or recognize them innately, there are two possibilities. Either we should see parasitism of superb fairy-wrens only, or, if like common cuckoos they have several, host-specific races (*gentes*), we should see parasitism of two or more hosts, but individual female cuckoos should be host specific.

Use of Host Individuals

If parasitism of host individuals within a population is nonrandom, this could be attributable to (1) strategic choice by the cuckoo of the best hosts; (2) the ease of locating host nests (e.g. proximity to vantage points, host activity levels); or (3) host defences against cuckoo parasitism. Unfortunately, these hypotheses generate many similar predictions. For example, cuckoos might parasitize novice host females (1) as a strategic choice, if they are less likely to reject cuckoo eggs or chicks; (2) because the nests and behaviour of novice females are less cryptic due to lack of nest-building experience; or (3) because novice females are less likely to have helpers that could deflect cuckoos. Rather than attempting to distinguish between these hypotheses directly, we investigate

(1) Whether parasitism is random with respect to female age, group size and female identity, and

(2) Whether cuckoos choose host individuals strategically, by testing experimentally whether they had greater success with the hosts they selected themselves than with hosts that we selected at random. We predicted that if cuckoos targeted the best host individuals, we would see better growth and survival of unmanipulated cuckoo chicks than cuckoo chicks relocated as eggs by us.

METHODS

Study Species

Horsfield's bronze-cuckoos occur throughout Australia. They generally lay during the egg-laying period of the host, removing one host egg from the nest and replacing it with one of their own. The cuckoo chick usually hatches 1–2 days before the host chicks and ejects the host eggs or chicks from the nest within 2 days of hatching (Brooker & Brooker 1989a). Unlike many cuckoo hosts, fairy-wrens rarely reject cuckoo eggs (Brooker & Brooker 1989a; Langmore et al. 2003). However, at naturally parasitized

nests around 40% of superb fairy-wren females abandoned cuckoo chicks in the first few days after hatching and immediately re-nested (Langmore et al. 2003). The cuckoo chicks died in the nest within the next 48 h.

Host Species

All the thornbill and speckled warbler host species build dome-shaped nests, occupy overlapping territories within the same open eucalypt woodland, and overlap substantially in the timing of breeding (Taylor 1992). Annual densities of superb fairy-wrens were more than double those of other hosts (personal observation). For example, in 2001 our study area contained 51 superb fairy-wren territories, 21 speckled warbler territories (J. L. Gardner, personal observation), 17 buff-rumped thornbill territories, 14 yellow-rumped thornbill territories and four brown thornbill territories. Superb fairy-wrens built grassy dome nests in dense bushes, low clumps of vegetation, or in the vegetation on the banks of gullies. Buff-rumped thornbills built similar nests in the vegetation on the banks of gullies and in dense bushes, but also built in cavities behind the peeling bark of a eucalypt. Yellow-rumped thornbills built nests in the outer foliage of trees, or in dense bushes. Their nests differed substantially from superb fairy-wren nests in both size and structure. Brown thornbills built grassy nests similar to those of superb fairy-wrens in dense bushes. Thus, superb fairy-wrens and all three thornbill species overlapped in the use of dense bushes, and large *Hakea* bushes sometimes contained the nests of two or even three of these species. Speckled warblers built well-concealed, dome-shaped nests in a shallow depression on the ground (Gardner 2002). The egg types of superb fairy-wrens, buff-rumped thornbills and brown thornbills are similar to one another and to those of Horsfield's bronze-cuckoo (white with reddish-brown speckling, Higgins & Peter 2002; Langmore et al. 2003), whereas the eggs of the yellow-rumped thornbill (white) and the speckled warbler (dark brown) differ from those of the other potential hosts and Horsfield's bronze-cuckoo. These features of habitat, nest site, nest structure and egg type allow us to make predictions about which host species should be parasitized under each of the four hypotheses (Table 1).

Field Methods

The study was conducted in Campbell Park, Canberra, in southeastern Australia (149°9'E, 35°16'S) from 1999 to 2006. This is an area of open eucalypt woodland bordered by grazing land to the north and east, suburbs to the south and dry sclerophyll forest on the western side. In this region, Horsfield's bronze-cuckoos are migratory and arrive to breed in late winter or early spring. The shining bronze-cuckoo, *Chalcites lucidus*, also breeds in the study site and primarily parasitizes thornbills, although fairy-wrens are reported to be secondary hosts (Brooker & Brooker 1989b). Because of the potential overlap in host use between Horsfield's bronze-cuckoos and shining bronze-cuckoos,

we also collected data on parasitism by shining bronze-cuckoos to explore the degree of host segregation between these species.

Each breeding season we attempted to locate every superb fairy-wren nest in the study site, and as many thornbill nests as possible, to check for parasitism by Horsfield's bronze-cuckoos or shining bronze-cuckoos. In a concurrent study at the same study site, Gardner (2002) notified us of any parasitism of speckled warblers. Fairy-wrens and thornbills are multibrooded, and will re-nest after nest failure or fledgling independence for the duration of the breeding season. After commencement of incubation, many parasitized nests (52%) and some unparasitized nests were protected with a large, dome-shaped, mesh cage that encompassed the nest bush and reduced depredation rates from 66% to 28%, whilst allowing access by the parents through the large mesh (Langmore et al. 2003).

Cuckoo chicks were colour banded and weighed 8–9 days after hatching. From 2000 onwards we also obtained a small blood sample from the brachial vein for genetic analysis (Adcock et al. 2005). We mist netted and colour banded most fairy-wren adults and colour banded fairy-wren chicks in the nest. Almost all female fairy-wren offspring dispersed outside the study area, so we had few confirmed novice breeders. However, adult females are philopatric (Mulder 1992), so we can be reasonably confident that unbanded females that arrived each spring were first year dispersers. Therefore, any unbanded female that replaced a banded female was classified as a first year female. Females that were colour banded in the first year of the study were of unknown age and were not included in this analysis. However, in subsequent years, when they were known to be greater than one year, their minimum age was included. For example, females who were known to be two or older were classified as 2 years old. Our study area expanded over the course of the study. To enable comparison of host density between years, we calculated the number of host territories each year within the area that was monitored during the first year of the study (123 ha).

Relocation Experiment

For this experiment, pairs of nests that were at a similar stage of incubation were used; one parasitized and one not parasitized. Twenty-nine cuckoo eggs were removed from the nest in which they were laid and transferred to the matched nonparasitized nest. Twenty of these nests survived to hatching, and the survival of these chicks was compared to survival of chicks in unmanipulated nests. A single host egg was removed from 13 of the host nests when the cuckoo egg was added, to simulate removal of a single host egg by the female cuckoo, and in seven nests the fairy-wren clutch was unmanipulated. Chick survival did not differ significantly between nests where a host egg had been removed (6/13) and nests where no host eggs were removed (2/7, $\chi^2_1 = 0.59$, $P = 0.44$), so the data were pooled for analysis.

Statistical Analysis

We used a generalized linear mixed model (GLMM) with logit link function to test whether the probability of parasitism could be explained by (1) group size and (2) host female age. We also included the year in which the nest was built. To control for repeated measures on host females, we included female identity as a random term in the model. The model was run including all terms and interactions, and then least significant interactions and terms were dropped sequentially until only significant terms remained. All statistics were carried out in GenStat v.8.1 (VSN International Ltd, Hemel Hempstead, U.K.), except the survival analysis, which was performed in JMP v.6.0 (SAS, Cary, NC, U.S.A.). Kaplan–Meier survival estimates were used, as data did not conform to any parametric distribution (e.g. Weibull, exponential).

RESULTS

Parasitism Rates

Although Horsfield's bronze-cuckoos visited Campbell Park in early spring every year, parasitism rates varied between years and declined to zero in some years of the study (Fig. 1). Of 715 superb fairy-wren nests in which eggs were laid in Campbell Park between 1999 and 2006, 114 were parasitized by Horsfield's bronze-cuckoos (16%), and three of those nests received two Horsfield's bronze-cuckoo eggs. Parasitism only occurred during 5 of the 8 years of the study, and the parasitism rate in those years was 22%. Of the 117 Horsfield's bronze-cuckoo eggs laid in fairy-wren nests, 90 chicks hatched and 38 fledged.

The decline in parasitism rates coincided with a period of drought and a decline in superb fairy-wren density. The decline in fairy-wren density was probably related to clearing of exotic sweet briar, *Rosa rubiginosa*, from the study site, which resulted in a substantial reduction of available nest sites for superb fairy-wrens. Nias (1984) found a similar dependence on exotic blackberry brambles, *Rubus* spp., for nest sites in his study of superb fairy-wrens. We explored the effects of drought and the decline in host density using a GLM (with binomial distribution) with the annual proportion of nests parasitized as the dependent variable and rainfall and host density as independent variables. We had no a priori prediction about whether rainfall would be influential in the lead up to breeding or during the breeding season. Therefore, we ran the model twice; once with prebreeding rainfall (June–August) and once with breeding season rainfall (September–December. Source: Australian Bureau of Meteorology). There were no significant effects of either prebreeding rainfall ($\chi^2_1 = 0.24$, $P = 0.63$) or breeding season rainfall ($\chi^2_1 = 1.1$, $P = 0.29$). However, despite our small sample size of only eight years, there was significant effect of host density ($\chi^2_1 = 27.5$, $P < 0.0001$, Fig. 1). There was also a significant interaction between host density and breeding season rainfall ($\chi^2_1 = 4.0$, $P = 0.045$), indicating that cuckoo parasitism rates were positively related to breeding season rainfall, but only while host density remained high (Fig. 1).

Host Specificity in Horsfield's Bronze-cuckoos and Shining Bronze-cuckoos

Despite the overlapping territories and similar nest sites and structures of several host species, Horsfield's

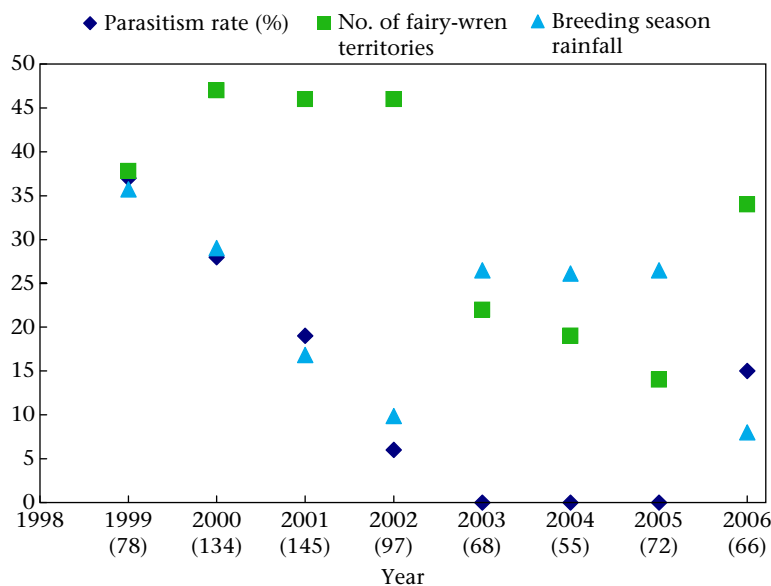


Figure 1. Parasitism rate (% superb fairy-wren nests in which eggs were laid that were parasitized by a Horsfield's bronze-cuckoo. Number of superb fairy-wren nests in which eggs were laid in each year is given in parentheses below the x axis), host density (no. of superb fairy-wren groups in the study area) and rainfall (cm) during the breeding season from 1999 to 2006. Our study area expanded over the course of the study. To enable comparison of host density between years, we included only those superb fairy-wren territories each year that were within the area monitored during the first year of the study.

bronze-cuckoos were almost entirely host specific; over 99% of eggs were laid in superb fairy-wren nests (Table 2). Similarly, shining bronze-cuckoos parasitized thornbills exclusively (Table 2), indicating a high degree of host segregation between these two sympatric cuckoo species. One buff-rumped thornbill nest was parasitized by a Horsfield's bronze-cuckoo. This nest was in a cavity behind peeling eucalypt bark, and genotyping revealed that the chick was a full sibling of two cuckoo chicks reared by fairy-wrens (Langmore et al. 2007).

Use of Individual Hosts

Parasitism of host individuals by Horsfield's bronze-cuckoos did not appear to be random. From 324 nests laid in during the period when cuckoos were breeding in the study site, and for which the superb fairy-wren female's minimum age and group size were known, the probability of a particular nest being parasitized was significantly related to the age of the host female (GLMM, Wald statistic, $\chi^2_1 = 10.41$, $P = 0.001$, Fig. 2), but not to group size or year. Younger birds were more likely to be parasitized than older ones. The random term 'female identity' indicated that there was a high intrabird correlation ($r = 0.6$), suggesting that particular host females or their breeding territories were targeted repeatedly. However, this does not appear to reflect strategic choice on the part of the cuckoos, because the mortality rate of cuckoo chicks (due either to predation or desertion by the host) that were transferred as eggs to new nests ($N = 20$) was not significantly different from that of chicks that hatched from unmanipulated eggs ($N = 57$, Fig. 3; Wilcoxon test, $\chi^2_1 = 2.6$, $P = 0.1$). From our subset of nests that were not caged and excluding those in which the cuckoo chick was deserted or the breeding female died ($N = 206$), there was no evidence that cuckoos targeted those nests that were less likely to suffer predation; 83% (24/29) of parasitized nests suffered predation, compared with 78% (138/177) of unparasitized nests ($\chi^2_1 = 0.34$, $P = 0.56$). Nor could we find any evidence that cuckoos targeted nests of hosts that were less likely to desert their young. Survival

Table 2. Parasitism by Horsfield's and shining bronze-cuckoos of five potential host species in Campbell Park, Canberra, 1999–2006

Host	No. of nests in which eggs were laid	Nests parasitized by Horsfield's bronze-cuckoo		Nests parasitized by shining bronze-cuckoo	
		<i>N</i>	%	<i>N</i>	%
Superb fairy-wren	715	114	16	0	0
Buff-rumped thornbill	97	1	1	12	12
Yellow-rumped thornbill	78	0	0	13	17
Brown thornbill	17	0	0	0	0
Speckled warbler (Gardner 2002)	84	0	0	0	0

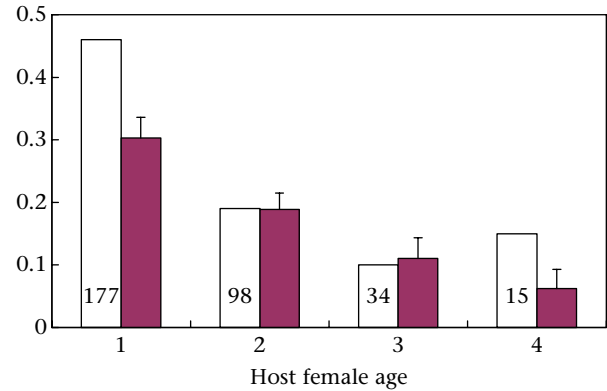


Figure 2. Actual proportion (white bars) and predicted probabilities (+SE, dark bars) of particular nests being parasitized by Horsfield's bronze-cuckoos in relation to the age of the host female (predictions obtained from a General Linear Model). Number of nests in each age class is given in the bars.

analysis of the same data set, considering only the rate of desertion by hosts (predation events censored) again showed no significant difference in the desertion rate of relocated versus unmanipulated chicks (Wilcoxon test, $\chi^2_1 = 1.8$, $P = 0.18$). However, a nonsignificant trend indicated that relocated chicks suffered higher mortality than unmanipulated chicks, which, when combined with the low P value, suggests that a larger sample size would be desirable to confirm our results. There was no significant difference in the growth rate of relocated chicks (mean \pm SE mass at nine days old = 17.25 ± 0.86 g, $N = 5$) and unmanipulated chicks (17.77 ± 0.28 g, $N = 13$; unpaired t test, $t = 0.57$, $P = 0.59$).

DISCUSSION

Horsfield's bronze-cuckoos are migratory in southern Australia, but little is known about their movements, or about how they select a breeding site on arrival in their

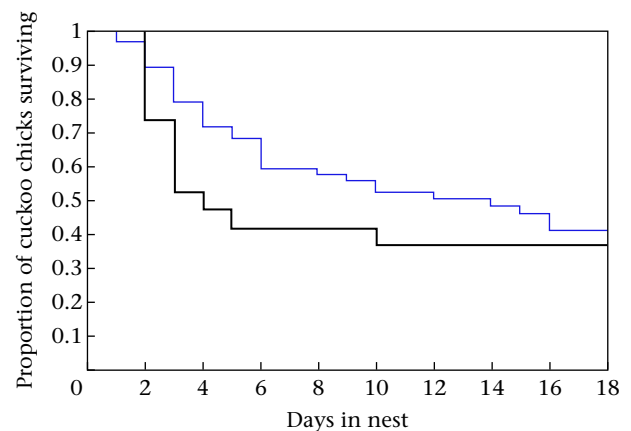


Figure 3. Kaplan-Meier estimate of the survival functions of Horsfield's bronze-cuckoo chicks reared in the superb fairy-wren nests in which they were laid (fine line) and in superb fairy-wren nests selected by us at random (heavy line).

southern breeding grounds. We had no recoveries of colour-banded cuckoos, and genetic analysis indicated that none of 16 adults or 20 fledglings returned to the study site to breed in subsequent years (Langmore et al. 2007; N. E. Langmore et al., unpublished data). Thus, we have no evidence to suggest that Horsfield's bronze-cuckoos return to their natal or breeding territories in consecutive years. A more transitory and nomadic pattern of movements is suggested by the discovery that early in the season females occupied their breeding territories for less than 6 weeks, before being replaced by a second round of females that then continued to breed for a further 2–3 months (Langmore et al. 2007).

Our analysis of parasitism rates suggests that Horsfield's bronze-cuckoos assess host density when selecting a site to breed. Parasitism rates were strongly related to host density, and no parasitism occurred in years where host density dropped to less than 23 breeding groups in our 123 ha study area. Horsfield's bronze-cuckoos at our site occupied breeding territories of up to 27 ha, encompassing up to 20 fairy-wren breeding territories, with an average of 1.46 ± 0.25 fairy-wren groups/ha (Langmore et al. 2007; N. E. Langmore, unpublished data from 2006). Territory size was inversely related to host density ($R^2 = 0.67$, $F_{1,6} = 12.2$, $P = 0.013$, Fig. 4), suggesting that cuckoos expand their territory size to compensate for low density of hosts. However, the absence of parasitism in the years of lowest host density suggests that it becomes uneconomical to do so when hosts are too sparsely distributed. Our results concur with those of Brooker & Brooker (2003), who demonstrated that Horsfield's bronze-cuckoos preferentially parasitized fairy-wrens in larger patches of remnant habitat, which supported at least 12 or maybe as many as 20 fairy-wren groups. This study contributes to a growing body of evidence that many brood-parasitic species assess host density in selection of a breeding site (Smith & Arcese 1994; Barber & Martin 1997; Soler et al. 1999; Alvarez 2003).

In those years where host density was sufficiently high to support a cuckoo pair, parasitism rates were also associated with breeding season rainfall. This supports the observation of Brooker et al. (1979) that Horsfield's bronze-cuckoos

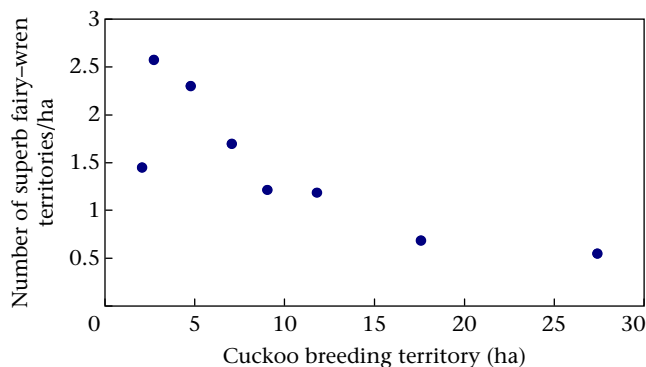


Figure 4. Territory size (ha) of eight breeding pairs of Horsfield's bronze-cuckoo in relation to host density on the territory (number of superb fairy-wren territories/ha). Data from Langmore et al. (2007).

appeared in areas following periods of heavy rainfall. A higher parasitism rate and longer breeding season by Horsfield's bronze-cuckoos was also observed in the year with the highest spring rainfall in a 6-year study in Western Australia (Brooker & Brooker 2003). Selecting a breeding site that receives high spring rainfall may be adaptive in terms of food supply for the cuckoos, but may also increase the number of host nests available for parasitism, or the survival of offspring. High spring rainfall is associated with higher productivity in superb fairy-wrens (A. Cockburn, personal communication) and a longer duration of breeding in blue-breasted fairy-wrens, *Malurus pulcherrimus* (Brooker & Brooker 2001).

Host Choice

Our results strongly support the Host Preference Hypothesis. Despite extensive overlap in habitat, nest sites, nest structures and egg types between potential host species, Horsfield's bronze-cuckoos parasitized fairy-wrens almost exclusively. This suggests that Horsfield's bronze-cuckoos recognize the hosts themselves, rather than features of their habitat or nest sites, when selecting hosts. Our failure to detect Horsfield's bronze-cuckoo eggs or chicks in the nests of the other potential host species is unlikely to be due to high rates of cuckoo egg rejection by hosts, because experiments with model eggs (Brooker & Brooker 1989a; Langmore et al. 2005) and experimental transfer of Horsfield's bronze-cuckoo eggs from fairy-wren to thornbill nests (N. E. Langmore et al., unpublished data) showed that thornbills rarely rejected odd eggs from their nests. Further evidence of poor egg discrimination in thornbills is that they are primary hosts of the shining bronze-cuckoo, which lays an olive-green egg quite unlike their own (Brooker & Brooker 1989b).

Host partitioning between Horsfield's and shining bronze-cuckoos was almost 100% (Table 2). Shining bronze-cuckoos parasitized yellow-rumped thornbills and buff-rumped thornbills, but never parasitized superb fairy-wrens. One case of host overlap occurred, when a Horsfield's bronze-cuckoo chick was reared by a buff-rumped thornbill. Similar evidence of host partitioning was found in Western Australia (Brooker & Brooker 1992), where Horsfield's bronze-cuckoos parasitized splendid fairy-wrens and shining bronze-cuckoos parasitized yellow-rumped thornbills. However, a greater degree of overlap in secondary host use was observed in their study than in ours, because western thornbills, *Acanthiza inornata*, were parasitized by both Horsfield's bronze-cuckoos (8% of western thornbill nests) and shining bronze-cuckoos (5.2%).

There are two possible explanations for the use of secondary hosts by Horsfield's bronze-cuckoos; (1) there are several host-specific races (gentes) of Horsfield's bronze-cuckoo, each specializing on a different host species, and/or (2) they use a combination of mechanisms to identify their host, such that if no nests of the favoured host species are available they resort to a more general search for hosts that build similar nest structures and lay similar eggs in the appropriate habitat or vegetation types. Brooker & Brooker (1992) suggested that a plausible explanation for the

pattern of parasitism observed in their study was the existence of two Horsfield's bronze-cuckoo genets which each imprinted on a different host. While it is possible that Horsfield's bronze-cuckoos do have genets, this is an unlikely explanation for the single case of parasitism of buff-rumped thornbills by a Horsfield's bronze-cuckoo in our study, because genotyping revealed that the cuckoo chick was a full sibling of two cuckoo chicks reared by fairy-wrens (Langmore et al. 2007). The second possibility, that cuckoos use a combination of mechanisms to identify hosts, could explain the use of thornbills as secondary hosts. Two mechanisms, natal philopatry and nest site choice, were not supported by our data. We found no evidence of natal philopatry, because none of our genotyped or colour-banded adult or fledgling cuckoos were sighted or resampled on the study site in subsequent years (Langmore et al. 2007). However, cuckoos may have returned to the general vicinity of the Park. Nest site choice at first appears to be the logical explanation for the use of buff-rumped thornbills as secondary hosts, because buff-rumped thornbills use many of the same nest sites as fairy-wrens, build structurally similar nests and lay similar eggs. However, the buff-rumped thornbill nest that was parasitized by a Horsfield's bronze-cuckoo was a cavity nest, quite unlike the nest sites of fairy-wrens. A more likely explanation, as proposed by Teuschl et al. (1998) is that cuckoos use a combination of habitat and host imprinting when selecting a host, and when no nests of the favoured host are available, they may resort to a more general search image of hosts that occupy the appropriate habitat. This process could explain the use by Horsfield's bronze-cuckoos of such a large number of secondary hosts throughout their range (28 biological hosts recorded, although fairy-wrens appear to be the primary hosts in all regions, Brooker & Brooker 1989b).

Use of Host Individuals

Parasitism of individual hosts was nonrandom with respect to host female age and identity, with younger females suffering higher parasitism rates than older ones. However, this does not appear to reflect strategic choice of the best host females by Horsfield's bronze-cuckoos, because the growth and survival of cuckoo chicks was not significantly better in the nests of hosts selected by the cuckoo than in the nests of hosts that we selected at random. A more plausible explanation is simply that with increasing breeding experience, host females are better able to conceal their nests and themselves from both predators and parasites (Brooker & Brooker 1996). Evidence in support of this argument is that novice female superb fairy-wrens are significantly more likely to suffer nest predation (Sims 2002), perhaps because they build nests with more conspicuous entrances than older females, and also tend to be less vigilant when visiting the nest (Sims 2002). The lack of evidence that Horsfield's bronze-cuckoos target particular host individuals suggests that either (1) larger sample sizes are needed to detect an effect, (2) the cues necessary to make such choices between host individuals are not available, or (3) cuckoo reproductive success is maximized by

satürating all available host nests in their breeding territory (Langmore et al. 2007) rather than by being choosy.

Overall, our results contribute to evidence from both longitudinal studies (e.g. Smith & Arcese 1994) and comparative studies across several sites (e.g. Barber & Martin 1997; Fauth 2000; Brooker & Brooker 2003) that brood parasites assess host density in selection of a breeding site. Our findings of almost 100% parasitism of a single host species and host segregation between the two sympatric bronze-cuckoos lend most support to the Host Preference Hypothesis for host choice, although there is some indication that a combination of processes may be used, as suggested by Teuschl et al. (1998). Finally, the lack of evidence of choice between individual hosts by Horsfield's bronze-cuckoos contrasted with findings of another experimental study, which found preferential parasitism of host nests on the best quality territories (Soler & Møller 2004).

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