

Beier & Tungbani – Bird-Wasp Nesting Association

NESTING WITH WASPS INCREASES NEST SUCCESS OF THE RED-CHEEKED CORDON-BLEU IN GHANA

PAUL BEIER¹ AND AGBA ISSAHAKU TUNGBANI²

¹ *School of Forestry and Merriam-Powell Center for Environmental Research, Northern Arizona University, Flagstaff AZ 86011-50018 USA; and*

² *Wechiau Community Hippopotamus Sanctuary Box 569, Wechiau, Upper West Region, Ghana*

ABSTRACT.—Associations between birds and social Hymenoptera (ants, wasps, bees) are common in tropical regions and are usually assumed to be commensal relationships benefiting birds, but neither helping nor harming the arthropods. However, benefits to birds have been documented in only 4 such associations, and no previous research rigorously investigated costs or benefits to associated hymenopterans. We followed the nesting cycles of an Estrildid finch, the Red-cheeked Cordon-bleu (*Uraeginthus bengalus*) and a common nesting associate, the wasp *Ropalidia cincta*, during 2002 and 2003 in northern Ghana to compare reproductive success of birds and wasps nesting in association to that of birds and wasps nesting separately. Cordon-bleus and wasps nested together in the same tree 3.7 times as often as expected if nesting decisions were made independently, with 74% of bird nests and 74% of wasp colonies occurring in associations. Bird nesting was initiated about 33 days after founding of an associated wasp colony; bird nests and wasp colonies were 42 cm apart on average. In both years, Red-cheeked Cordon-bleus in nesting associations with wasps were twice as likely to fledge young as birds nesting in trees without wasps. Reduced predation was apparently a major reason for increased fledging success: we documented 4 cases of nest predation on 122 cordon-bleu nests associated with wasps and 11 cases on 90 nests not associated with wasps. Association with birds did not affect the success of wasp colonies. Although our observational study cannot rule out the possibility that both species coincidentally shared a preference for a habitat feature in limited supply, suitable nest sites did not appear to be limiting (74% of potential nest trees had neither bird nor wasp nests). Reproductive success of Red-cheeked Cordon-bleu populations in this region may be limited by the number of available wasp colonies. By designing our study to address 4 working hypotheses (commensalism, mutualism, parasitism, coincidence of habitat preference), we have provided strong evidence that this relationship is commensal.

“...The good witch was grateful and besought the wasp to ask for whatever he desired. He answered that he and his wife wished not to be wasps, whom everyone hated, but to be birds, well-beloved by all. At once they had their wish and became birds. But they soon missed the company of their brothers and sisters, so they started nesting close to their wasp relatives. And because some of the wasp nature was left in them, they did not build nests as other birds do, but made gray pockets to hold their nests, which from afar looked like wasp nests. And as they did, so do their children to this day.”

– adapted from Owen (1893): *Old rabbit, the voodoo, and other sorcerers*, as quoted by Myers (1934).

Accepted for publication in *The Auk* (2006)

NESTING ASSOCIATIONS between birds and social Hymenoptera (ants, wasps, and bees) have long been noted in tropical regions (Gosse 1847, Myers 1929, 1934, 1935; Moreau 1942, Contino 1968, Young et al. 1990, Dejean and Fotso 1995, other citations below). Four studies, all in the Neotropics, have documented benefits to birds from these associations. Smith (1968, 1983) found that hymenopterans nearly eliminated parasitic botflies in nests of Chestnut-

headed Oropendolas (*Psarocolius wagleri*) and Yellow-rumped Caciques (*Cacicus cela*) in Panama, thus increasing nest success of these birds. Apparently the wasps (*Protobolybia* and *Stelopolybia*) and bees (*Trigona*) attacked adult botflies approaching the bird nest, mistaking them for parasitoids or parasites of wasp nests. Yellow-rumped Caciques in Peru (Robinson 1985) and Bananaquits (*Coereba flaveola*; Wunderle and Pollock 1985) in

Beier & Tungbani – Bird-Wasp Nesting Association

Puerto Rico that nested in the same tree as *Polybia* wasp colonies had markedly lower nest predation rates than conspecifics nesting in trees without wasps. Joyce (1993) experimentally placed wasp nests (*Polybia rejecta*) near nests of Rufous-naped Wrens (*Campylorhynchus rufinucha*) in Costa Rica and documented dramatic decreases in nest predation (mostly by monkeys) on the wrens.

These studies documented that birds benefit from nesting in trees with wasps. No study investigated benefits or costs to the wasp (but see Wunderle and Pollock 1985). The assumption seems to be that the relationship is commensal, with the wasps unaffected by proximity to birds and their nests. However, wasps may incur a cost or benefit from having birds nesting nearby. Thus a bird-wasp nesting association could represent commensalism (benefit to birds, no effect on wasps), parasitism (benefits to birds, costs to wasps), mutualism (benefits to both species), or coincidental selection for the same nesting locations. No previous study measured costs or benefits to the wasp to evaluate evidence for these competing interpretations.

In West Africa, a small Estrildid finch, the Red-cheeked Cordon-bleu *Uraeginthus bengalus* usually nests in leguminous trees within 1 m of nests of the vespid wasp *Ropalidia cincta* (McCrae and Walsh 1974; Fig. 1). In northern Ghana, Beier (unpublished data, June-July 2001) found that 71% of 354 leguminous trees lacked bird or wasp nests, but that 91% of 77 cordon-bleu nests were near a wasp colony, 74% of 95 wasp colonies were near a cordon-bleu nest, and no tree had > 1 cordon-bleu nest. These percentages are higher than observed in the previous studies, suggesting either that the cordon-bleu population is limited by the number of wasp colonies, or that the wasps also benefit from the association.

Primitively social wasps like *R. cincta* have small colonies (starting with one to several founders each year and rarely exceeding 60 workers at maximum – Darchen 1976). Their sting is ineffective against predatory ants and the parasites and ichneumonid parasitoids that are the main enemy of the nest, and only mildly painful to humans (Schmidt 1990). Having “no specific defense against parasites” (Gadagkar 1991:166), *Ropalidia* uses simple vigilance and chasing to thwart intruders. Compared to the elaborate stinging attack against vertebrate predators, this line of defense “is surprisingly crude” (Starr 1990:425). Because stinging and direct attack

are also risky, the first line of colony defense is to be inconspicuous (Akre and Reed 1984, Schmidt 1990, Starr 1990, Gadagkar 1991). In these open-crowned leguminous trees, the bulky, conspicuous nests of cordon-bleus might therefore be a liability for an associated *Ropalidia cincta* colony (Fig. 1). Thus wasp tolerance for cordon-bleus may indicate that the wasp cannot repel the bird (parasitism), or receives a benefit that compensates for the cost (mutualism). Although benefits to the wasps seem unlikely, birds might benefit wasp colony success if birds could help the wasps to cope with insect enemies. Although primarily a seed-eater, even during brooding, cordon-bleus are known to eat termites and other flying insects (Goodwin 1982).

We observed the annual nesting cycle of the Red-cheeked Cordon-bleu and *R. cincta* in 399 permanently marked leguminous trees in a wildlife sanctuary in northern Ghana during 2002 and 2003. Our objectives in this observational study were to (a) describe the nesting cycle of both species, (b) describe nest sites selected by both species, and (c) measure how the nesting association affects reproductive success of both birds and wasps. By measuring effects on the wasp, we hoped to more firmly establish whether the association is commensal, parasitic, or mutualistic. Although an observational study cannot conclusively rule out the fourth option (both species coincidentally sharing and benefiting from the same habitat preference), we reasoned that these 3 types of data should rule out one or two hypotheses and provide stronger support for one of the remaining hypotheses.

METHODS

Study Area.—The Wechiau Community Hippopotamus Sanctuary, in northwestern Ghana near the border with Burkina Faso, extends for about 40 km along the Black Volta River, with strict protection in a core area extending for about 1 km from the river’s edge, and a buffer zone (including several small villages) extending an additional 4 km. The dominant natural vegetation in the core area is northern Guinea savannah, with riverine gallery forest along the Black Volta River. In the buffer zone, the savannah is grazed by cattle, goats, and sheep, and is intermixed with farms (millet, maize, beans). Daytime temperatures exceed 30 C year-round, with a pronounced dry season (with cool nights) during November through March. In this region Cordon-bleus begin nesting by June and continue until at least

Beier & Tungbani – Bird-Wasp Nesting Association

October (McCrae and Walsh 1974). *R. cincta* starts nesting after the rains return, and wasps aestivate in crevices during most of the dry season.

In the study area, birds and wasps nest exclusively in four species of thorny, leguminous trees, namely drought-deciduous *Acacia gourmaensis*, *A. nilotica*, *A. hookeri*, and evergreen *Balanites aegyptiaca*. Locally, these trees typically occur on sandy soils with large stones or rock outcrops, near streams but outside the gallery forest, and are rare elsewhere. We selected two study areas with many leguminous trees and wasp nests. Each site was dominated by grasses, with scattered *Acacia*, *Balanites*, shea nut trees (*Butryospermum parkii*) and other fire-tolerant trees. One site (about 50 ha, 300 tagged trees) was in the core area near the Black Volta River, and the other (about 20 ha, 99 tagged trees, about 2 km from the first site) was along a small stream within the core area but close to the buffer zone. All cordon-bleu nests were constructed of a single species of grass, *Tricholaema monochnae*. Potential predators on cordon-bleus, cordon-bleu eggs, or wasps included > 200 species of birds, several arboreal lizards and snakes (including the nocturnal common egg-eater, *Dasypeltis scabra*), monkeys (*Cercopithecus*, *Patas*), and ants.

Tagging and measuring trees.—We considered all *Acacia* and *Balanites* trees to be potential nest trees and non-selectively tagged trees as we encountered them until 400 trees were tagged. One tree was cut by humans early in the study and removed from the study, leaving 399. We tagged trees with numbered stainless steel bands about 5 mm wide (manufactured as cable ties) that we attached around the main stem near eye level. The bands survive the annual dry season fires, and can be seen from any side of the tree. Although birds, wasps, and their predators can see them, the bands do not flutter in the wind and we believe they did not influence placement or fate of wasp or bird nests. Because all trees (not just nest trees) were tagged, potential predators could not use tags as a cue to nest locations. We used a GPS receiver to create stem maps to facilitate subsequent surveys. Before tagging each tree, we searched for wasp nests and recorded our observations. After tagging a tree in which no wasps were detected, we shook the tree to provoke attacks by any wasps that escaped our visual inspection. Because shaking the tree may not cause solitary foundresses to leave the nest, we repeated this test 30 days later. The lack of any wasp attacks validated the efficacy of our visual

searches.

We used a clinometer to measure the height of each tree to nearest 0.1m, and a Biltmore stick to measure diameter at breast height to the nearest cm. We recorded tree species only to genus (about 75% of the *Acacias* were *A. gourmaensis*). For *Acacia* trees that had > 1 stem at breast height, we recorded the diameter of the largest stem. Many *Balanites* stems were elliptical in cross section; we calculated the average of the narrowest and largest diameters of these stems.

Nest site selection.—In 2002 we recorded height above ground, aspect (position of the nest relative to the stem, measured to the nearest 5 degrees), and radial distance from the main stem, of every cordon-bleu nest and most wasp colonies in tagged trees. When more than one wasp colony occurred in a tree, we recorded data for the wasp colony closest to a cordon-bleu nest (when present) or the first-established wasp colony (when no cordon-bleu nested in the tree). We recorded distance between each cordon-bleu nest and the nearest wasp colony in the same tree.

We used χ^2 tests of independence to determine if wasps or cordon-bleus preferentially nested in *Acacia* or *Balanites* trees. We used independent samples *t*-tests within tree genus to determine if wasps or birds selected trees of a particular height or diameter. After reclassifying nest aspect into four cardinal directions, we used a χ^2 test to compare the observed distribution to a uniform one (25% in each cardinal direction).

Observations of Red-cheeked Cordon-bleus.—Cordon-bleu nests are ellipsoids about 20-30 cm long and about 15-20 cm in diameter, with a single apical entrance, and thus easy to detect. Females are easily distinguished by the lack of a red cheek patch. We briefly visited each tagged tree weekly starting May 1 until the first cordon-bleu nest was initiated, which occurred in early June each year. We then visited each tree every 2-6 days during 4 June – 5 November 2002, every 10 days from 5 November – 2 December 2002, and every 2-6 days during 4 June – 29 December 2003. We observed each active nest for 30-60 min during each visit. At each visit we recorded evidence of nest building, incubation, brooding, fledging, nest abandonment, and nest predation. We interpreted behavior in light of Goodwin's (1982) detailed descriptions of the behavior of captive Red-cheeked Cordon-bleus and other Estrildid finches. During the nestling phase, we inspected about 15% of

Beier & Tungbani – Bird-Wasp Nesting Association

nests (all of those that were accessible from the ground or relatively transparent) to determine clutch size, and we listened for sounds of older nestlings.

Although it was easy to assign a nest to the “building” stage, adult behavior during a single 30-60-min period of observation provided less reliable estimates of whether adults were incubating or brooding, or had abandoned their nests. Because of prolonged and variable nesting cycles and unexpected parental behavior (see Results), and because we could not see inside most nests, we made inferences about nesting stage based on the entire sequence of observations at a given nest. We inferred incubation if there were at least two observation periods with behavior consistent with incubation (adults alternating periods > 20 minutes each inside the nest) within a 12-day time span (a typical incubation period – Goodwin 1982). We inferred brooding from frequent adult visits of 1-7 minutes each during at least two observation periods, or a white feather or fecal sacs in the nest entrance during at least two visits, or visible or audible nestlings. We inferred fledging if we saw fledglings in or < 5 m from the nest tree (with no other likely nest nearby) within the expected fledging window, or if observations consistent with brooding occurred at least 27 days after the first observation suggesting incubation. This 27-day span encompasses minimum incubation and brooding periods (11-14 and 17-20 days, respectively – Goodwin 1982), minus a 1-day time lag between onset and detection of incubation.

We observed birds near wasp colonies to record any interactions with the wasp nest, wasps, or other invertebrates (ants, moths, ichneumonid wasps) in the tree. We also recorded reaction by cordon-bleus to any vertebrates that approached the nest tree. Although we did not expect brood parasitism on cordon-bleus (Goodwin 1982; Payne 1985, 1997), we recorded observations of any bird approaching or entering a cordon-bleu nest.

Observations of wasps.—We searched for new colonies and monitored known *Ropalidia cincta* colonies in tagged trees about once every 10 days during 4 June – 2 November 2002, then every 2 weeks until 2 December 2002. We monitored wasp colonies associated with cordon-bleu nests every 10 days during 4 June - 29 December 2003, but did not monitor wasps nesting in trees without cordon-bleus in 2003. At each visit, we searched each tree lacking wasps for a new wasp colony and revisited previously

discovered colonies. We did not search for new colonies in trees with known wasp colonies. For each monitored colony, we recorded colony size as the number of wasps on or near the nest. The open crowns of the potential nest trees and the open flat architecture of wasp combs allowed an observer with binoculars to count wasps accurately. Because a wasp colony is founded by a single pregnant female (occasionally 2-5 sisters) that aestivated in crevices through the previous dry season, colony size is a meaningful measure of reproductive success (Darchen 1976). However as colonies mature, some fertile offspring emigrate to found new colonies. In addition, because some workers are away from the colony foraging for food or fiber, counts of wasps at a colony will underestimate colony size. Therefore, as a second measure of colony size, we estimated the number of cells in each colony at each visit by counting the number of cells of length and width of a lobe of the nest, multiplying these numbers, and adding the results for each of the 1-3 lobes of each colony. It took about twice as long to estimate cells as to count wasps.

We looked for any wasp interactions with cordon-bleus, ants, or flying insects in the crown of the tree. At each visit, we looked for potential vertebrate predators, and recorded wasp response to any animal that approached or entered the tree.

Analysis of the influence of nesting associations on reproductive success.—Because all cordon-bleu nests were discovered during the building phase, no correction for time of discovery was needed. We excluded nests that did not meet our criteria for determining stage (above) or any nest where incubation was initiated < 30 days before the end of our monitoring period. Several nests were active for > 50 days, presumably spanning 2 or 3 clutches by a single pair. Because of non-independence of these clutches, we assigned the single “best” outcome to the nest; thus if two clutches failed during incubation and one fledged, the nest was considered to have fledged.

Our analyses probably included a few “second nests” (see Results); we did not exclude them because we could not identify them with certainty. Furthermore, because cordon-bleus explore and sometimes take over nests of other species (see Results), they probably also commandeer other cordon-bleu nests. Thus one pair’s successful nest could have been another pair’s unused second nest. Any second nests included in the analysis would

Beier & Tungbani – Bird-Wasp Nesting Association

appear to be nests that failed before the incubation period.

We used χ^2 tests to compare fledging success of cordon-bleus associated with wasps to those nesting in trees without wasps during each year. We also considered the order in which birds and wasps initiated nesting in each tree as evidence suggesting which species might benefit.

During 2002, we measured success of wasp colonies (number of wasps per nest) both for wasps nesting in association with cordon-bleus and for wasps nesting apart from birds. For statistical analysis, we selected observations of colony size from two time periods. For colonies associated with cordon-bleus, Time 1 was first day cordon-bleu nest building was observed. For wasps nesting apart from birds, Time 1 was the first observation of the wasp nest. Time 2 was the day on which the largest subsequent number of wasps was observed. Because cordon-bleus eventually nested near almost every wasp colony that exceeded 15 wasps, only 3 of 37 non-associated wasp colonies were larger than 15 wasps at first detection. Thus we lacked “control” (non-associated) colonies for cordon-bleu nests initiated adjacent to larger wasp colonies. Therefore we analyzed the influence of nesting associations on wasp reproductive success only for wasp colonies that had 0-15 wasps when cordon-bleu nesting began. We also limited the analysis to wasp colonies founded before 1 October 2002, so that the colonies would have had about 35 days of potential growth before the annual fires and 65 days before the end of monitoring. Our primary test was ANOVA of colony size by time (Time 1 versus Time 2) and nesting association. We also compared wasp growth rates measured as the number of wasps added between the 2 time periods and in terms of percent growth between the 2 time periods.

RESULTS

Red-cheeked Cordon-bleu nesting cycle.—Nesting occurred in 2 pulses and the first pulse occurred during June-July in both years (Fig. 2). The second pulse occurred in September-October during 2002, and was abruptly terminated when the annual dry season fires started during 5-10 November 2002 and burned many active cordon-bleu nests. No tagged trees were destroyed in these fires. In 2003, the second pulse of nesting was more diffuse, and the fires began in late November and burned less severely, destroying only one active cordon-bleu nest.

Although some nests were completed within 24 hours of initiation, Red-cheeked Cordon-bleus typically took 4-10 days to construct a nest. Up to 68 days elapsed between nest completion and the first indication of incubation behavior. The interval between building and the start of incubation decreased as the season progressed (regression of interval on date, $r = -0.326$, $n = 130$ nests, $P < 0.0005$). Nests initiated during June-July started incubation an average of 21.7 days later (SD 19.5, $n = 69$ nests), decreasing to 14.5 days (SD 12.2, $n = 40$) for nests initiated during August-September and to 7.5 days (SD 15.7, $n = 21$) for nests initiated after 1 October. During the period between nest completion and incubation, cordon-bleus usually visited the nest zero to two times during a 60-minute observation period, each visit less than 1 minute long.

On two occasions we observed adults building 2 nests simultaneously in adjacent trees; incubation was observed in only one of these four nests. Adults commonly made brief visits to a completed nest (at which incubation had not been initiated) while building a new nest nearby. In some cases, other adult cordon-bleus visited the older nest during the same observation period, but usually we had no evidence to suggest that the pair building the new nest had not constructed both of them. Sometimes adults would take grasses from an existing nest (built earlier in the same year) to build a new nest in a different tree; over the course of a day or two, the older nest could have most of its material removed. We excluded such pillaged nests from our analyses of nest success.

At several nests, behavior consistent with incubation occurred over periods of 20-44 days, sometimes continuously but more often with 7-20 days of apparent abandonment between incubation periods; in three cases brooding behavior persisted for several days between two incubation periods within a nest. One nest (associated with a large wasp colony) exhibited 3 cycles of incubation and brooding behavior over a 121-day period, and the last 2 clutches apparently fledged. Both males and females incubated eggs and attended young.

Cordon-bleus sometimes gave misleading cues about incubation and brooding. On 13 occasions involving seven nests (1-3 occasions per nest), we observed an adult inside a nest for periods of 30-60 minutes on days when we saw that no eggs or nestlings were present. On nine occasions (five nests with wasps, four without wasps), no adult visited a

Beier & Tungbani – Bird-Wasp Nesting Association

nest in 60 minutes of observation when we could see or hear nestlings in the nest. At each of these nests, adults attended to the clutch or brood during later observation periods, indicating that the nest had not been abandoned during the previous observation.

Ropalidia cincta nesting cycle.—Counts of number of worker wasps at a colony were highly correlated with calculated number of cells per colony at first discovery ($r = +0.898$, $n = 111$ colonies, $P < 0.0005$), and at maximum number of workers ($r = +0.933$, $n = 111$, $P < 0.0005$). The regression was the same for colonies associated and not associated with cordon-bleus (Fig. 3). Hereafter we report wasp colony size only in terms of numbers of wasps.

Colonies were initiated regularly throughout the season; we found 1-3 new colonies (1-4 founders per nest) during each week from June 4 through October 15. Of the colonies discovered during 4 Jun – 14 Aug (long enough to observe their trajectory for 90 days before the fires), 22 colonies had 1-3 wasps at first discovery in 2002, suggesting that they were newly founded, of which 12 colonies became extinct without ever exceeding 5 wasps, and only 6 eventually exceeded 10 wasps. It took an average of 66 days (SD 26, range 35-86) for these 6 colonies to grow from 1-3 wasps to 10 or more wasps. The few colonies that survived this slow founding phase usually went on to persist and grow. The 26 colonies that reached a threshold of 10-16 wasps by 12 Aug 2002 (i.e., either grew above 9 from a lower initial number or were discovered with 10-16 wasps) survived an additional 104 days on average (SD 51, range 1-180), and grew to an average colony size of 49 wasps (SD 32, range 14-117).

We discovered 42 *Ropalidia cincta* colonies at our first systematic visits to tagged trees during 2-5 June 2002; these ranged in size from 1-35 wasps (mean 14.2). Eleven of these colonies had 10-19 wasps, and 14 had 20-35 wasps at first observation. Given the time needed to grow to a threshold of 10 wasps (above), most of these colonies were probably founded between early March and late April.

Only 8 colonies exceeded 100 individuals; the largest had 167 wasps at its peak. Even large colonies occasionally plummeted to zero wasps throughout the season. Most population disappearances were abrupt, with colonies of > 20 wasps appearing to be on a growth trajectory when nests were found abandoned at the next visit. Other large colonies slowly declined to zero over 40-50 days. When a colony of any size

started to decline, it rarely recovered. Only one colony with > 30 wasps declined by 50% and then rebounded to > 30 individuals. Most colonies that reached 20-50 wasps during June-August 2002 continued to grow through October but declined after the fires in early November. Of 54 colonies with > 10 wasps during 18-23 October, only 12 were still active at our last surveys on 2-4 December, 11 of which had declined by 50-90% since the previous visit.

Selection of nest sites by wasps and birds.—*Acacia* trees comprised 58% and *Balanites* 42% of the 399 tagged trees. However, in 2002 (the only year in which wasp colonies unassociated with birds were tallied), 72% of the 81 cordon-bleu nests and 75% of the 80 wasp colonies occurred in *Acacia* indicating a significant preference for that genus by both species ($P < 0.002$ and $P < 0.001$, respectively, χ^2 tests, 1 df). Cordon-bleus nested in 25% and wasps nested in 26% of the tagged *Acacia* trees compared to 13% and 12% (respectively) of the *Balanites* trees. We never found more than one active cordon-bleu nest in a tree.

The average *Acacia* tree was 4.7 m tall (SD 2.0, range 1.6-11.5) and 15 cm in diameter (SD 6.5); the average *Balanites* was 5.6 m tall (SD 2.1, range 1.9-15) and 23 cm dbh (SD 10.4). Within trees of a genus, cordon-bleus and wasps nested in trees that did not differ in height or diameter from congeneric trees lacking nests (each $P > 0.1$, independent sample t -tests).

Wasp colonies occurred in roughly equal numbers (21% to 30%) in each of the 4 cardinal aspects. Cordon-bleu nests were less uniform in aspect, with 11.5% on the west side of the tree, and 26-32% in each of the other 3 cardinal directions ($P = 0.068$, $\chi^2 = 7.1$, 3 df).

On average cordon-bleu nests were located at 60% of the tree's height (SD 22%, range 15-100%) and were 0.9 m from the main tree stem (SD 0.73, range 0-4 m). On average, wasp nests were located at 51% of tree height (SD 21%, range 17-99%) and 0.8 m from the main tree stem (SD 0.44, range 0.1-2.4 m).

There was a strong tendency for wasps and cordon-bleus to nest in the same tree (Table 1). If the probabilities of each species nesting in a tree were independent, they would have nested together in only 16 of the 399 tagged trees (compared to 59 co-occurrences observed). For both birds and wasps, 74% of nests occurred in bird-wasp associations (Table 1). In these associations, the wasp and cordon-

Beier & Tungbani – Bird-Wasp Nesting Association

bleu nests were 42 cm apart on average, but nests abutted in about 16% of associations (Fig. 4). Cordon-bleu nests were located at the same height as the wasp colony (height difference < 10 cm) in 41% of associations, were 10-400 cm higher than the wasp colony in 46% of cases, and were 20-85 cm lower than the wasp colony in 13% of cases.

In nesting associations, the wasp colony was initiated an average of 33 days (SD 33) before cordon-bleus starting building in the same tree, and the bird nest preceded the wasps in only 11% of cases (Fig. 5). We recorded distance between the wasp and bird nest for 4 of the 8 cases in which the bird nested first; these distances were 10, 27, 27, and 200 cm (mean 66 cm). At the time the bird nest was initiated near a wasp colony, there were typically <30 wasps at each wasp colony (Fig. 6).

Effects of nesting association on cordon-bleu reproductive success.—During both 2002 and 2003, Red-cheeked Cordon-bleus in nesting associations with wasps were about twice as likely to fledge young as birds nesting in trees without wasps (Table 2). Five active cordon-bleu nests in 2002, and 25 nests in 2003, were associated with wasp colonies that prematurely and abruptly failed (dropped to 0 wasps) while the birds were still nesting. In 2002, 2 of the 5 affected cordon-bleu nests fledged, 2 failed in the building stage, and 1 failed in the incubation stage. These failures occurred 7, 20, and 31 days after the wasp colony failed. In 2003, eight of the 25 affected cordon-bleu nests (40%) successfully fledged, similar to the 41% success for all birds nesting with wasps that year. Of these, 1, 3, and 4 nests were in the building, incubation, and brooding stages, respectively, at the time the wasp colonies failed. The other 17 cordon-bleu nests failed either at the same time as the wasp colony failure (5 cases), or 6 to 42 days later (12 cases).

In most failures of cordon-bleu nests, we observed cessation of adult activity prior to fledging, with no indication of why the nest failed. As mentioned above, some “failures” doubtless represented second nests. There was strong evidence that predators destroyed 4 nests associated with wasps and 11 nests unassociated with wasps (Table 3). Four cases involved lizards, and three others involved eggs being taken from intact nests, presumably by reptiles. In the other 8 cases, the nest was destroyed, presumably either by monkeys or large birds. In 3 of 4 predation events on wasp-associated nests, and 4 of 11 cases of

predation on bird nests not associated with wasps, eggs or nestlings were taken without destroying the nest.

*Effects on nesting association on reproductive success of *Ropalidia cincta*.*—Because cordon-bleus nested near almost every wasp colony that exceeded 15 wasps, we could assess the influence of nesting associations on wasp reproductive success only for wasp colonies that had 0-15 wasps when cordon-bleu nesting began (Table 4). These comparisons suggest that associating with cordon-bleus did not increase growth of wasp colonies in 2002. This lack of effect was also confirmed by ANOVA ($P = 0.91$ for nesting association, 0.0005 for time, and 0.43 for time x association interaction). We did not monitor wasp colonies in trees lacking cordon-bleus in 2003.

Interactions involving birds or wasps.—Despite intensive attention, we observed no interactions between cordon-bleus and wasps, or between cordon-bleus and any arthropods. One successful cordon-bleu nest, situated 25 cm from a wasp colony with >50 wasps, was blown out of the tree in a windstorm 12 days after fledging, at which time we found a 20-cell wasp nest inside the cordon-bleu nest. We also found a wasp nest inside another storm-tossed cordon-bleu nest a month after that nest failed; in this case we are less certain that the wasps were inside the nest at the same time as the birds.

Cordon-bleus occasionally chased other cordon-bleus that came close to their nest, but generally tolerated both conspecifics and other bird species in the nest tree. Cordon-bleus took over active nests of two Little Weavers (*Ploceus luteolus*), one Heuglin’s Masked Weaver (*Ploceus heuglini*), one Vitelline Masked Weaver (*Ploceus velatus*), and one Spectacle-fronted Weaver (*Sporipipes frontalis*); weaver visits to these nests stopped when the cordon-bleus started using the nests. In each case, the cordon-bleu brought nest material (*Tricholaema monochnae* stems) into the weaver nest and built a nest inside. Of these 5 nests, two were adjacent to wasp nests, and only one nest eventually fledged cordon-bleus. In one of these cases, cordon-bleus had nearly finished building a nest in the same tree as the weaver nest. The cordon-bleu nest was abandoned when cordon-bleus took over the weaver nest, and the birds cannibalized a cordon-bleu nest in a nearby tree (not the adjacent incomplete nest) to line the new nest.

Other birds occasionally took over Red-cheeked Cordon-bleu nests. On three occasions, Bronze

Beier & Tungbani – Bird-Wasp Nesting Association

Mannikins (*Lonchura cucullata*) either took over a nest started by cordon-bleus or started building the nest simultaneously with cordon-bleus. In one of these cases, the two species worked simultaneously on the nest for about 10 minutes during an observation period. In each case, there was a wasp nest near the bird nest, and the cordon-bleus eventually abandoned the nest to the mannikins. Lavender Waxbills (*Estrilda caerulescens*) took over one cordon-bleu nest (with no associated wasp nest) just after it was completed. Lavender Waxbills, Bronze Mannikins, and several species of weavers briefly entered active cordon-bleu nests during the interval between nest-building and the onset of incubation, or during the interval between clutches. Cordon-bleus were usually away from their nest during these visits.

Wasps tolerated all birds in the nest tree with the exception of 2 incidents in which wasps attacked a Black-crowned Tchagra (*Tchagra senegala*) and a Pied Crow (*Corvus albus*) that landed in the nest tree. In each case, the attacked bird left the tree after about 5-10 seconds. These were the only occasions on which we saw a tchagra or crow in a tree with a wasp colony. Birds of 34 other species, mostly small, but including Green Wood-hoopoes (*Phoenicurus purpureus*), Black Wood-hoopoes (*Rhinopomastus aterrimus*), Laughing Doves (*Streptopelia senegalensis*), and wood doves (*Turtur* species) used wasp trees without provoking an attack. Speckle-fronted Weavers and true weavers (*Ploceus* species) occasionally nested in close proximity to wasp colonies. Several arboreal lizards were active in trees with wasp colonies; one small lizard approached a wasp nest, ate one of 14 adult wasps attending the nest, and left without provoking a reaction from the other wasps. We never observed aggressive response of wasps toward lizards near nests (~ 10 observations total). We never saw a snake in a tagged tree, but encountered them regularly on the ground. We never observed a non-human mammal touching a nest tree. Wasps usually tolerated human observers near their colonies, but occasionally attacked us when we approached within about 3 m of the colony tree, and always promptly attacked and stung us if we touched the tree in a way that sent a vibration through the wood. Wasps focused their attacks on the skin at the edge of our eyes.

DISCUSSION

The relationship between numbers of wasps and

numbers of cells in the colony did not differ between colonies associated versus not associated with cordon-bleus (Fig. 3), suggesting that the birds did not affect the fraction of wasps emigrating from colonies to found new colonies. For this reason, and because *Ropalidia cincta* colonies complete their annual cycle during the avian nesting season, our measure of colony size is a reasonably comprehensive measure of fitness for the wasp. It seems implausible that nesting with birds would affect the quality of wasps produced (their ability to aestivate during the dry season or found new colonies in the current or following year). Therefore, our observation that nesting with the Red-cheeked Cordon-bleu did not decrease the size of wasp colonies suggests that the bird is not a parasite of *Ropalidia cincta*. Similarly, the lack of benefit to the wasp suggests that the association is not mutualism. The two-fold increase in nest success and the one-month time lag between onset of wasp and bird nesting suggest that the association is commensal, with the bird enjoying increased reproductive success and the wasp neither harmed nor helped by the interaction.

However, there is a fourth hypothesis besides commensalism, parasitism, or mutualism, namely that some unmeasured site effect caused the observed benefit. If both cordon-bleus and wasps seek the same particular nest site characteristics that benefit birds, and if such sites were in limited supply such that they had to nest together to obtain them, the benefits could be wrongly credited to wasps. The critical experiment would be to experimentally create or destroy associations, as Joyce (1993) did. The cordon-bleu-*Ropalidia* system is amenable to experimental removal of wasp nests because trees are short, the wasp nests are attached to the tree via a single pedicel, and the wasp stings are relatively mild to humans. If the wasps stay with a translocated comb, it may even be possible to experimentally add wasps to a tree containing a cordon-bleu nest.

Even in the absence of this critical experiment, we think it is unlikely that cordon-bleus and wasps nest together because they coincidentally share the same nest-site preferences. Cordon-bleus and wasps did share a preference for *Acacia* over *Balanites* trees, and a similar indifference to tree size. We suspect that this preference for thorny trees represents common selection for sites inhospitable to climbing predators, and was an early step in evolution of this nesting association. However, one divergence in nest site preferences (an aversion to western aspects by birds

Beier & Tungbani – Bird-Wasp Nesting Association

but not wasps) is inconsistent with the hypothesis. Furthermore, the hypothesis requires preferred nesting sites to be in limited supply, such that both species would be forced to nest together. Although we may have failed to measure some habitat feature that truly was in limited supply, the study area seemed to have no shortage of potential nest sites such that birds and wasps could find appropriate sites without nesting in the same tree, much less in such close proximity.

Wunderle and Pollock (1985) reported no difference in length and width of *Polybia* wasp nests associated versus not associated with Bananaquits, but did not report whether these measurements were standardized for date or nesting stage. No other study reported any data relevant to potential cost or benefits to wasps. Although evidence to support the most plausible hypothesis of commensalism is useful, we agree with Chamberlin (1890) that scientific progress depends on attempts to disprove competing hypotheses rather than attempts to marshal evidence supporting a favored hypothesis. The recent emphasis on model selection (Burnham and Anderson 1999) has revived interest in testing competing models. However, as Guthery et al. (2001) pointed out, all too often scientists claim to use this approach when they are testing among several statistical models (e.g., logistic versus linear) sharing one set of driving variables, rather than (as Chamberlin intended) in attempts to disprove several fundamentally different ideas of how the world works.

Doubling of cordon-bleu nest success, timing of nest initiation, proximity of bird nests to wasps, relatively uniform location of bird nests slightly above the wasp colony, and a cordon-bleu nest near almost every large wasp colony all support the notion that nesting with wasps increased reproductive success of cordon-bleus and that cordon-bleus actively tried to nest with wasps. However, we note one discordant observation. Cordon-bleu nests associated with wasp colonies that prematurely failed had the same fledging success as bird nests associated with enduring wasp colonies. Because this finding was based on a sample of 25 nests in 2003, it does not seem to be a quirk of sample size. Perhaps potential predators had learned to avoid these trees, or perhaps the empty wasp comb continued to provide a visual deterrent after the wasp colony failed.

We also note one observation inconsistent with our conclusion that wasps receive no benefit from nesting near birds. In three of four cases where

cordon-bleu nests preceded wasp colonies in a tree, the wasp colony was located remarkably close to the bird nest. However, small sample size (4 inter-nest distances) and possible non-random selection of pairs to measure (we failed to record this distance in the other 4 cases where the bird nested first) could have given rise to a spurious pattern.

Decreased nest predation was clearly a major reason that cordon-bleus benefited from nesting near wasps. Similarly, Robinson (1985) credited wasps with reducing nest predation on associated Yellow-rumped Caciques, and witnessed wasps attacking and repelling attempts by primates to prey on bird nests. Joyce (1993) demonstrated that predation was the main cause of nest failure for Rufous-naped Wrens, and reported that nesting with wasps more than doubled nest success, an effect size similar to what we observed.

In about half of our documented cases of nest predation, the nest was not destroyed and we suspect that reptiles (including at least 3 species of lizards) were the predators involved. Because we never observed wasp aggression toward lizards near wasp colonies, and because putative predation by reptiles was documented as often at bird nests associated and unassociated with wasps, the wasps may benefit birds mainly by repelling non-reptilian predators, such as monkeys, and perhaps birds such as Black-crowned Tchagras and Pied Crows. However, we probably documented only a small fraction of the predation events that occurred without destroying the nest, and we had only a handful of observations of wasps tolerating lizards. Thus we don't know if wasps can repel lizards or snakes. The tendency of wasps to sting skin at the edge of the human eye may indicate a general strategy for attacking vertebrates in a well-innervated site relatively unprotected by fur, feathers, or scales. Given the paucity of observations of wasps interacting with vertebrates under natural conditions, placing wasps and other species together in experimental arenas will probably be necessary to determine how wasps interact with potential predators, and how vulnerable the potential predators are to wasp stings.

Our data cannot rule out the possibility that other mechanisms might also contribute to increased fledging success. For example, Barnard and Markus (1990) hypothesized that Southern Cordon-bleu (*Uraeginthus angolensis*) and Melba Finches (*Pytilia melba*) nested with wasps (*Polistes* spp.) because the

Beier & Tungbani – Bird-Wasp Nesting Association

wasp nest signals that a particular tree is free of *Pseudomyrmex* ants, which swarm over both wasp and bird nests.

The nesting association between the Red-cheeked Cordon-bleu and *Ropalidia cincta* on our study area was strikingly strong. McCrae and Walsh (1974) investigated a grove in northern Ghana containing 38 *Acacia* trees and noted that the Red-cheeked Cordon-bleu and wasps nested only in thorny *Acacias* (avoiding broadleaved trees), and that all 8 cordon-bleu nests were associated with wasps. Ours is only the third study (after Maclaren 1950 and Wunderle and Pollock 1985) to demonstrate a statistical tendency for bird and wasp nests to occur in the same tree. No previous study has documented such a large fraction of wasp nests associated with birds. For instance only 8 of 18 trees with wasp colonies observed by McCrae and Walsh (1974) were associated with cordon-bleus, only 6 of 25 trees with *Polybia* colonies were used by Bananaquits (Wunderle and Pollock 1985), and only 7 of 19 trees with ant nests were associated with Bronze Mannikins (Maclaren 1950). Myers (1929) also noted that “more [hymenopteran] nests occur alone than in association with birds,” and argued that therefore wasps probably did not benefit from the association. The fact that over 73% of trees with wasp colonies also harbored cordon-bleu nests in our preliminary fieldwork (a level confirmed in the full study, and similar to the fraction of cordon-bleus nesting with wasps) made mutualism a plausible hypothesis at the outset of our study. Because we found that nesting associations do not benefit wasps, the low fraction of wasp colonies not associated with cordon-bleus suggests that wasp colonies are a habitat feature in limited supply for the Red-cheeked Cordon-bleu on our study area. This idea could be tested by experimentally manipulating wasp colonies per unit area in several locales.

Ninety percent of cordon-bleu nests were less than 1 m from associated wasp colonies. McCrae and Walsh (1974) reported similar distances for these same two species, as did Wunderle and Pollock (1985) for Bananaquits nesting with *Polybia* wasps. Hindwood (1955) reported a frequency distribution of distances between nests of Double-barred Finches (*Taeniopygia bichenovii*) and wasps (*Polistes humilis*), and a tendency for bird nests to lie above wasp colonies, similar to the distributions we observed. Dejean and Fotso (1995) reported that five species of small birds in Cameroon nested within 30 cm of wasp colonies but that larger birds nested > 75

cm from wasp colonies. They speculated that smaller animals do not trigger attacks by wasps, but that larger animals would trigger aggressive responses. Robinson (1985) reported that monkeys could sometimes reach into Yellow-rumped Caciques nests > 1 m from a wasp colony without provoking a wasp attack, and that shorter distances were needed for wasps to effectively protect the birds. Wunderle and Pollock (1985) similarly reported that the degree of protection provided by a wasp nest decreases with distance and that beyond 1 m nest predation rates are equivalent to nests not associated with wasps. We agree with Hindwood (1955) that birds probably position their nests above the wasp nest to maximize protection from predators approaching from below, such as mammals and reptiles.

Although McCrae and Walsh (1974) speculated, based on size of wasp colonies in October, that the cordon-bleu nests were initiated second, ours is the first report that cordon-bleus initiate their nests about a month after founding of the wasp colony, at which time wasp colonies usually have about 10-30 workers, although some were much smaller. Contino (1968) reported that Dull-colored Grassquits (*Tiaris obscura*) often started building their nests when a wasp (*Polistes canadensis*) colony had only 1-2 wasps. Smith (1968) reported that Chestnut-headed Oropendolas that nested in association with bees and wasps did not begin to breed until the hymenopteran colonies were established, resulting in a breeding season nearly 2 months shorter than birds at sites lacking bees or wasps. This represents a significant diminution of benefits to birds. Individual oropendolas or cordon-bleus could pursue mixed strategies (nesting apart from wasps early in the season when wasp colonies are small, then nesting again later near wasps). Studies involving banded parents are needed to determine how per-parent reproductive success relates to the strategies of individual birds.

The two peaks in nest initiation dates probably represent two nest attempts per year by individual birds. Although some Estrildid finches build small dummy nests touching the top or side of their nest (Goodwin 1982), this is the first study to report that individual pairs of cordon-bleus may build two complete nests at one time in two different trees. Observations of banded birds would be needed to confirm both of these suggestions. Second nests could be constructed to promote pair bonding, to confuse predators, or as backup nests in case of failed nest

Beier & Tungbani – Bird-Wasp Nesting Association

attempts in one location. Until the degree of renesting and the prevalence of alternate nests are calculated, it would be inappropriate to use our data to represent per-pair nest success of cordon-bleus.

Although multiple nest attempts per season are not uncommon in the tropics, we were surprised that some second clutches were raised in the same physical nest as the first clutch. Although we presume that second clutches within a nest were made by the same parents, our observations of cordon-bleus taking nests from other species, building second nests, and occasionally sharing a nest with other adult cordon-bleus suggest that new parents could have been involved in some of these cases.

Why did cordon-bleus often delay incubation for 10-68 days after nests were constructed? This was an unexpected finding, and we can only speculate that cordon-bleus build nests to occupy favorable sites (such as those near wasp colonies) and then wait until seed production or size of wasp colonies increase to a level more favorable for raising young. This explanation is consistent with our observation that the interval from building to incubation was two weeks longer early in the season than late in the season. We hope that future investigators will develop alternative hypotheses and develop observational or experimental approaches to discriminate among them.

The avoidance of west-facing nest sites by the Red-cheeked Cordon-bleu has not previously been reported, and was of only marginal statistical significance ($P = 0.068$). However, the pattern was identical in both *Acacia* and *Balanites*. We believe that it is real, and that it reflects avoidance either of the hottest microclimate. In the tropics, the sun is almost overhead at noon, but the evening sun (in the west) is much hotter because air temperatures are higher in the afternoon and because fog and clouds are more common during the morning (personal observation). Storms and strong winds typically came from the southeast (personal observation).

Our observations of the wasp nesting cycle are consistent with published descriptions for the genus *Ropalidia* (Gadagkar 1991, 2001) and the single paper on *R. cincta* (Darchen 1976). Our paper provides the first detailed quantitative observations on nest density per tree and the fates and trajectories of *R. cincta* colonies.

ACKNOWLEDGMENTS

Ben Nomann first called our attention to this bird-

wasp system. Rob Longair (University of Calgary) taught us how to identify *Ropalidia cincta*. The Wechiau Community Hippopotamus Sanctuary, Nature Conservation Research Centre, and the people of the villages of Wechiau and Talawona provided hospitality and logistical support. Zachariah Wareh (Ghana Wildlife Department) helped us become familiar with the birds of the region, and Muhammad Ali helped us tag trees. About 50 EarthWatch volunteers assisted in the field, and EarthWatch International provided financial assistance.

LITERATURE CITED

- AKRE, R. D., AND H. C. REED. 1984. Vespine defense. Pages 59-89 in H. R. Hermann, editor, *Defensive Mechanisms in Social Insects*. Praeger, New York.
- BARNARD, P., AND M. B. MARKUS. 1990. Reproductive failure and nest site selection of two Estrildid finches in Acacia woodland. *Ostrich* 61:117-124.
- BURNHAM, K. P. AND D. R. ANDERSON. 1998. *Model Selection and Inference*. Springer, New York.
- CHAMBERLIN, T. C. 1965 (1890). The method of multiple working hypotheses. *Science* 148:754-759. (1890 paper reprinted in 1965).
- CONTINO, F. 1968. Observations on nesting of *Sporophila obscura* in association with wasps. *Auk* 85:137-138.
- DARCHEN, R. 1976. *Ropalidia cincta*: guêpe sociale de savane de Lamto Cotê-d'Ivoire. *Annales Societe Entomologique de France* 12:579-601.
- DEJEAN, A, AND R. C. FOTSO. 1995. Nesting associations of small birds and *Polybioides tabidus* (Vespidae Epiponinae) in southern Cameroon. *Ethology Ecology & Evolution* 7:11-25. requested from Cline
- GADAGKAR, R. 1991. *Belonogaster*, *Mischocyttarus*, *Parapolybia*, and independent-founding *Ropalidia*. Pages 149-350 In K. G. Ross & R. W. Matthews, editors, *The Social Biology of Wasps*. Comstock, Ithaca, New York.
- GADAGKAR, R. 2001. *The social biology of Ropalidia marginata: toward understanding the evolution of eusociality*. Harvard University Press.
- GOODWIN, D. 1982. *Estrildid Finches of the World*. Comstock Publishing, Ithaca, New York.
- GOSSE, P. H. 1847. *Birds of Jamaica*. John Van Voorst, London.
- GUTHERY, F. S., J. J. LUSK, AND M. J. PETERSON. 2001. The fall of the null hypothesis: liabilities and opportunities. *Journal of Wildlife Management* 65:379-384.

Beier & Tungbani – Bird-Wasp Nesting Association

HINDWOOD, K. A. 1955. Bird-wasp nesting associations. *Emu* 55: 263-274.

HUNT, J. H. 1991. Nourishment and the evolution of the social vespidae. Pages 426-450 in K. G. Ross & R. W. Matthews, editors, *The Social Biology of Wasps*. Comstock, Ithaca, New York.

JOYCE, F. J. 1993. Nesting success of rufous-naped wrens (*Campylorhynchus rufinucha*) is greater near wasp nests. *Behavioral Ecology and Sociobiology* 32:71-77.

MACLAREN, P. I. R. 1950. Bird-ant nesting associations. *Ibis* 92:564-566.

MCCRAE, A. R. W., AND J. F. WALSH. 1974. Association between nesting birds and polistine wasps in north Ghana. *Ibis* 116:215-217.

MOREAU, R. E. 1942. The nesting of African birds in association with other living things. *Ibis* 84:240-263.

MYERS, J. G. 1929. The nesting-together of birds, wasps and ants. *Proceedings of the Royal Entomological Society of London* 4: 80-88.

MYERS, J. G. 1934. An aboriginal folk-tale based on the bird and wasp nesting association. *Proceedings of the Royal Entomological Society of London* 9: 96-97.

MYERS, J. G. 1935. The nesting associations of birds with social insects. *Transactions Royal Entomological Society of London* 83:11-22.

PAYNE, R. B. 1985. The species of parasitic finches in West Africa. *Malimbus* 7: 103-109.

PAYNE, R. B. 1997. Field identification of the brood-parasitic whydahs *Vidua* and Cuckoo Finch *Anomospiza imberbis*. *Bulletin of the African Bird Club* 4: 18-28.

ROBINSON, S. K. 1985. Coloniality in the yellow-rumped cacique as a defense against nest predators. *Auk* 102:506-519.

SCHMIDT, J. O. 1990. Hymenopteran venoms: striving toward the ultimate defense weapon against vertebrates. Pages 387-419 in D. L. Evans and J. O. Schmidt, editors, *Insect Defenses*. State University of New York Press.

SMITH, N. G. 1968. The advantage of being parasitized. *Nature* 219:690-694.

SMITH, N. G. 1983. Chestnut-headed oropendola *Zarhynchus wagleri*. Pages 614-616 in DH Janzen, ed. *Costa Rican Natural History*. University of Chicago Press.

STARR, C. K. 1990. Holding the fort: colony defense in some primitively social wasps. Pages 421-463 in D. L. Evans and J. O. Schmidt, editors, *Insect Defenses*. State University of New York Press.

WUNDERLE, J. M. JR., AND K. H. POLLOCK. 1985. The bananaquit-wasp nesting association and a random choice model. *Ornithological Monographs* 36:595-603.

YOUNG, B. E, M. KASPARI, AND T. E. MARTIN. 1990. Species-specific nest site selection by birds in ant-acacia trees. *Biotropica* 22:310-315.

Table 1. Red-cheeked Cordon-bleus and the wasp *Ropalidia cincta* nested together much more frequently than expected by chance ($\chi^2 = 177$, 1 df, $P < 0.0005$). Body of table indicates numbers of trees in 2002 that contained birds, wasps, or both; some trees contained more than one nest per species, but no tree had more than one active cordon-bleu nest at the same time.

Wasp nest in tree	Cordon-bleu nest in tree		Total
	No	Yes	
No	297	22	319
Yes	21	59	80
Total	318	81	399

Table 2. Red-cheeked Cordon-bleu nests in trees with wasps were twice as likely to fledge as birds nesting apart from wasps. Body of table gives percentage of bird nests reaching each stage.

Nest Stage	2002		2003	
	Without wasps (36 nests)	With wasps (61 nests)	Without wasps (54 nests)	With wasps (61 nests)
Building	100	100	100	100
Incubation	72	71	48	66
Brooding	36	38	26	48
Fledged	11 ^a	25 ^a	20 ^b	41 ^b

^a $P = 0.095$, $\chi^2 = 2.5$, 1 df, cordon-bleu nest success by wasp association.

^b $P = 0.017$, $\chi^2 = 5.7$, 1 df, cordon-bleu nest success by wasp association.

Beier & Tungbani – Bird-Wasp Nesting Association

Table 3. Predators destroyed eggs or hatchlings in 3% of Red-cheeked Cordon-bleu nests associated with wasps and 12% of nests not associated with wasps. Notes following table entries describe conditions observed on the day we noted nest failure. Except as noted, the nests had been torn apart.

Nest Stage	Number of predator-destroyed nests that were	
	Not associated with wasps	Associated with wasps
Building/laying	3 <i>Agama agama</i> lizard in 1 partially-broken nest	1 At one nest (not destroyed), 2 eggs disappeared during laying; 3 weeks later 2 eggs again disappeared from the same intact nest.
Incubation	5 Eggs disappeared from 1 intact nest. Lizard and egg fragments in 2 intact nests.	2 Broken eggs in 1 intact nest.
Brooding	3	1 Lizard in intact nest.
Total	11 of 90 nests	4 of 122 nests

Table 4. Success of wasp (*Ropalidia cincta*) colonies, as measured by increases in numbers of wasps, was not influenced by association with Red-cheeked Cordon-bleu nests in 2002. Only colonies founded by 5 October 2002 that had 0-15 wasps at first observation of start of cordon-bleu nesting are included because only 3 of 37 potential control nests (wasp nests not associated with cordon-bleu nests) had >15 wasps at first observation.

	Nesting Association		Significance test		
	Without cordon-bleu	With cordon-bleu	<i>t</i>	df	<i>P</i>
Number of wasp colonies	34	21			
Starting number of wasps per colony (SD)	6.2 (4.5)	8.5 (4.8)	1.83	53	0.07
Number of wasps at peak of colony (SD)	24.7 (28.7)	20.9 (15.4)	0.56	53	0.59
Growth expressed as number of additional wasps (SD)	18.5 (25.9)	12.4 (14.3)	1.00	53	0.32
Percent growth (SD)	372% (257%)	354% (446%)	0.19	53	0.85



Fig. 1. Nest of Red-cheeked Cordon-bleu about 35 cm above nest of *Ropalidia cincta* in *Acacia nilotica* tree on the Wechiau Community Hippopotamus Sanctuary.

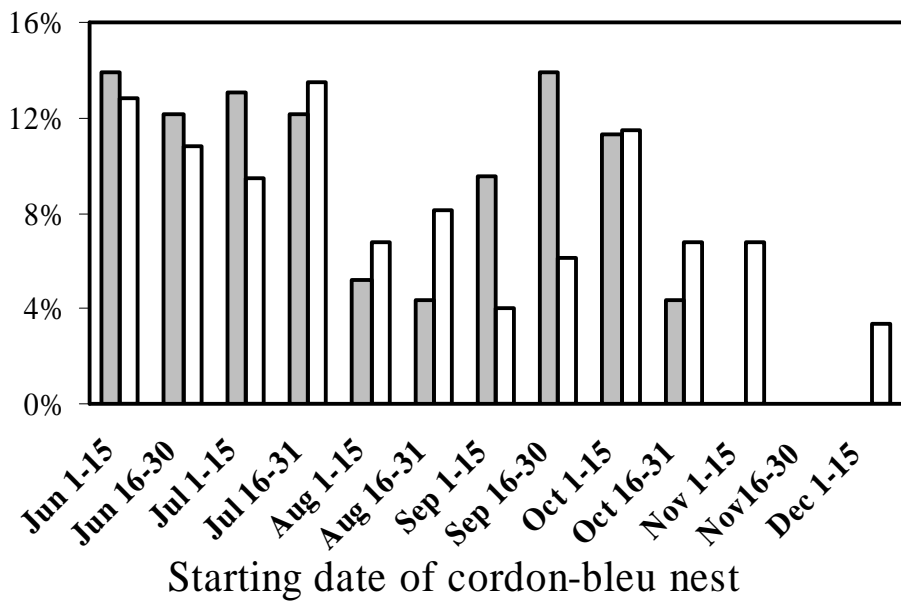


Fig. 2. Red-cheeked Cordon-bleus nested in 2 pulses in 2002 (115 nests, gray bars) but more evenly in 2003 (148 nests, open bars).

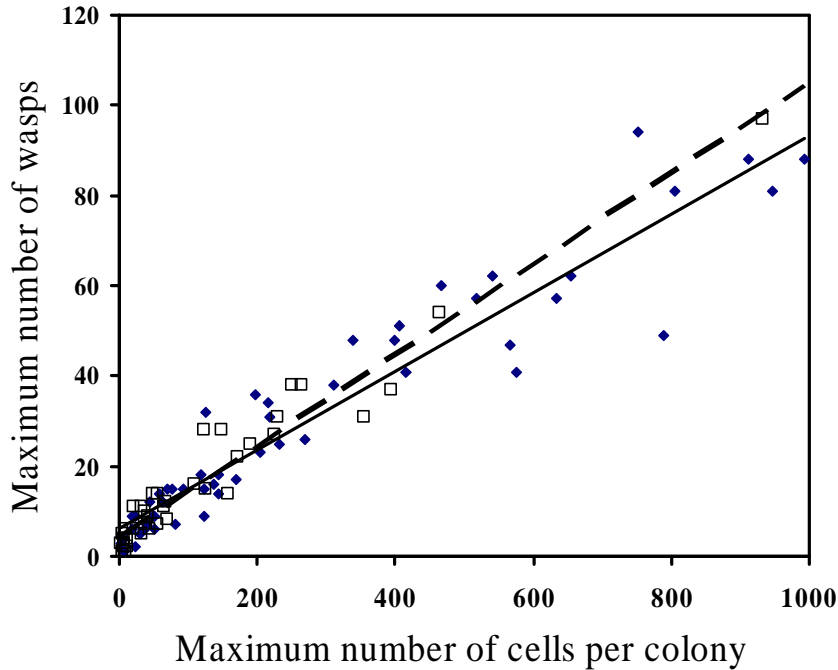


Fig. 3. The number of wasps at maximum colony size was highly correlated with the number of cells in the colony, and the relationship did not differ between colonies associated (solid line, diamonds) versus not associated (dashed line, open squares) with Red-cheeked Cordon-bleu nests. Regressions restricted to colonies with < 1000 cells because cordon-bleus nested in association with all larger colonies. Regression equation for associated colonies: $Y = 6.3 + 0.087 X$, $r^2 = 0.91$. Regression for non-associated colonies: $Y = 4.5 + 0.100 X$, $r^2 = 0.95$.

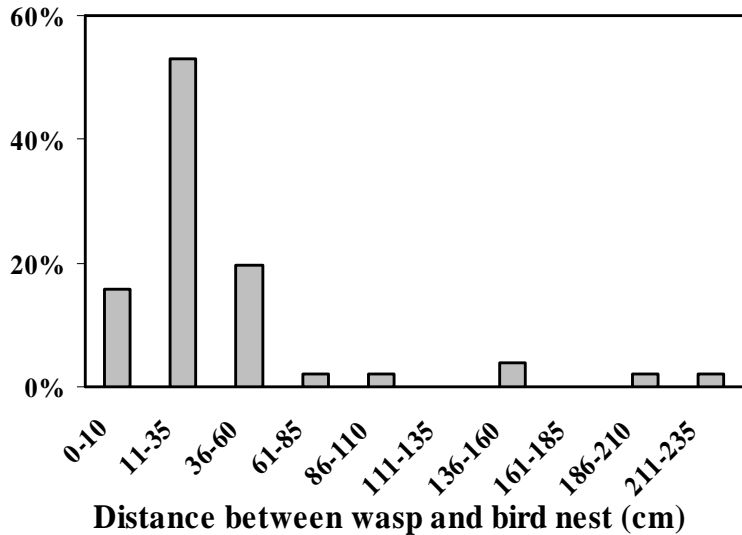


Fig. 4. In 51 bird-wasp nesting associations in 2002, about 16% of Red-cheeked Cordon-bleu nests touched wasp (*Ropalidia cincta*) nests, and the modal distance between nests was 11-35 cm.

Beier & Tungbani – Bird-Wasp Nesting Association

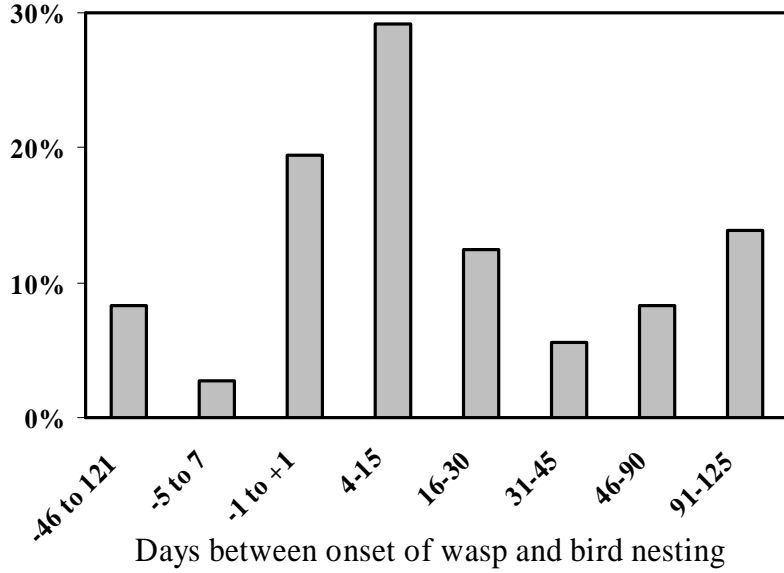


Fig. 5. In 72 bird-wasp nesting associations in 2002, the Red-cheeked Cordon-bleu nest was initiated first in 11% of cases (negative part of x-axis), bird and wasp nests were initiated within 1 day of each other in 19% of cases, and wasps nested first in 70% of cases.

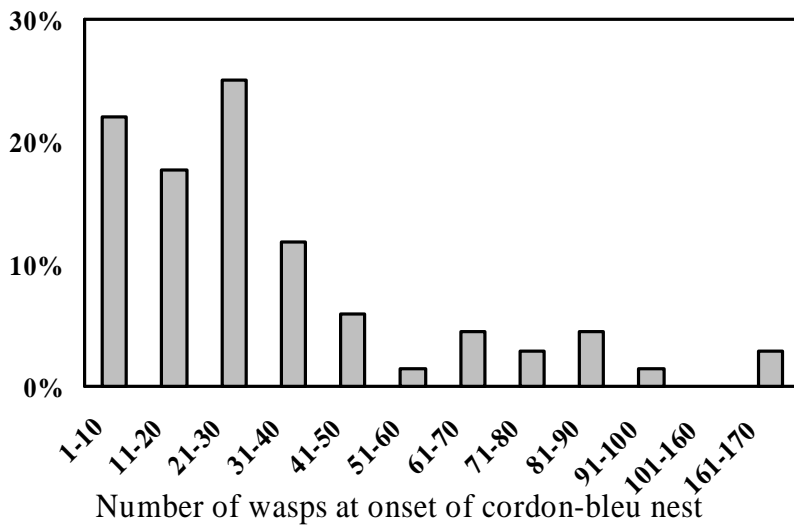


Fig. 6. In 68 bird-wasp nesting associations in 2002, there were an average of 33 *Ropalidia cincta* wasps at the wasp colony on the first day of nest-building by Red-cheeked Cordon-bleus.