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A BANANAQUIT-WASP NESTING ASSOCIATION

AND

A GENERAL MODEL FOR THE EVOLUTION OF SUCH ASSOCIATIONS

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ABSTRACT.-Bananaquits nesting in association (≤ 1 m) with Polybia nests had significantly lower nest predation rates than neighbors with nests unassociated with wasp nests. Males mated to females nesting near wasp nests were more likely to retain their mate through the breeding season than males mated to females having nests unassociated with wasp nests. A survey of Bananaquit and Polybia nests indicated that trees containing both Bananaquit and wasp nests were more frequent than expected by chance alone. Within the same tree, the distance between Bananaquit nests and the nearest wasp nest averaged $82.3 \text{ cm} \pm 10.3$ (SE). Females nesting in proximity of wasp nests did not usually nest with wasps again in the following year. Also, removal of Bananaquit nests proximate to wasp nests did not cause the females to re-nest with wasps. Thus female Bananaquits do not always nest with Polybia nests.

A simple probability model is presented that explains how a spatial association between bird and wasp nests may arise. It is

shown that a bird's random choice of a nest site in conjunction with increased nest survival for nests close to wasp nests can (during several breeding attempts) produce a bird-wasp nest spatial association. Many biologists have assumed that the existence of these spatial associations in nature indicate that site selection is nonrandom with respect to wasp nests. This model suggests that other mechanisms are possible and that testing between models which assume random and nonrandom choice of nest site will be difficult.

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Tropical regions are often noted for their many intricate biological interactions such as: mutualism, commensalism, parasitism, and predation. The complexity and diversity of such tropical symbiotic relationships is partly a reflection of the high species richness of the tropics. Possibly the most complex of these tropical biotic interactions is the relationship between colonial nesting icterids and associated hymenopterans, several avian brood parasites, and an array of ectoparasites as studied in detail by Smith (1968, 1980). In his studies, Smith found that those colonial icterid nests associated with colonial hymenopterans are protected from ectoparasitic flies and vertebrate predators. This bird-hymenoptera nesting association appears to be an example of commensalism or possibly mutualism, for the nesting birds obtain a benefit through reduced nest predation and there is also the possibility that some nesting birds might drive off predators which feed on bee or wasp larva.

Historically there has been considerable interest in bird-insect nesting associations as evidenced by the early literature which contains numerous anecdotal observations of such associations. Several reviews of this literature (e.g. Myers 1929, 1935, Moreau 1936, Maclaren 1950, Chisholm 1952, Hindwood 1955) have found that a variety of bird species will nest in proximity to the nests of ants, wasps, or bees. For example, avian species in families as diverse as: Cuculidae, Furnariidae, Tyrannidae, Corvidae, Muscicapidae, Nectariniidae, Dicaeidae, Parulidae, Icteridae, Fringillidae, Estrildidae, and

Ploceidae have been recorded nesting in the immediate neighborhood of hymenopteran nests. Most of these examples of bird-hymenoptera nesting associations are from tropical regions.

It is generally accepted (e.g. Moreau 1936) that nesting birds seek the association of hymenopteran colonies because the stinging or biting behavior of the ants, bees, or wasps deters nest predators. However, except for Smith (1969) no one has compared the fledging success for bird nests associated with hymenopteran nests with those unassociated with insect colonies. In addition, few of the early workers provide the data necessary to statistically determine whether a nesting association actually exists between the birds and colonial hymenopterans (but see Maclaren 1950).

Despite the documentation of birds nesting in the proximity of colonial hymenopterans many questions remain. What predators of avian eggs and nestlings are inhibited by stinging or biting insects? Does nesting in association with hymenopteran nests actually increase fledging success? What are some other implications of nesting in association with insects? How does this nesting association evolve? What is the role of stochastic events in the evolution of this relationship? How do factors such as the nest predation rate, female abandonment of nest site and length of the breeding season affect the evolution of this association? Such questions are important for understanding the evolution of interactions in general, such as commensalism and mutualism. In this paper, we first specifically

examine these questions in a nesting association between Bananaquits (Coereba flaveola) and wasps (Polybia occidentalis) and then we provide a general model to explain the evolution of such nesting associations.

The Bananaquit is an abundant and widespread species found throughout the Caribbean, Central and South America. On many of the Caribbean islands it is the most abundant species found in almost all terrestrial habitats from sea level to the tops of the highest mountains (MacArthur and Wilson 1967). Both males and females build their own woven, globular, domed nests as either individual sleeping dormitories or breeding nests. These nests are placed in almost every conceivable location with heights above the ground ranging from less than one up to several meters as documented by Skutch (1954), Biaggi (1955), and Gross (1958). Bananaquits have been found nesting near the nests of Polistes canadensis and other wasp species in Trinidad, Jamaica, Haiti, and Venezuela as summarized by Myers (1935). Since not all Bananaquits nest in proximity to wasp nests, it is possible to compare the success and implications for those individuals nesting in association versus those nests unassociated with wasp nests.

Methods

This study was conducted on the island of Grenada at the southern end of the Lesser Antilles from 1975 to 1978, and in 1981, as part of a larger study of Bananaquit breeding biology (Wunderle 1980). Data were collected over five breeding seasons as follows:

March-August 1975, March-September 1976, March-September 1977, March-October 1978 and May-August 1981. The study was done in southern Grenada from Point Saline to Grand Anse on the north and the Mt Hartman estate on the east, covering an area of approximately 900 hectares. Although the area has been extensively disturbed for agricultural purposes, remnants of a dry deciduous scrub woodland can be found as described by Beard (1949).

To examine the possibility that there might be an advantage to Bananaquits which nest in proximity of Polybia nests, the first author compared the fledgling success of those nests associated with wasp nests with nearest-neighbor nests not associated with wasp nests. Newly initiated Bananaquit nests associated with Polybia nests were paired with nearby non-associated nests initiated during the same week. Both members of a pair having either a nest associated or non-associated with a wasp nest were captured with mist nets and colorbanded in 1976 to 1978. Pairing of data (associated versus nonassociated nests) was necessary to control for changes in nest predation over time during the breeding season. Because nesting periods are synchronized with periods of rainfall it was possible to pair nests to the exact week of initiation.

To determine if a nesting association occurred between Bananaquits and wasps it was necessary to ask the following question: Are Bananaquit and wasp nests found together within the same tree more frequently than predicted by chance alone? To answer this question Wunderle censused all the trees >2.5 m in three rectangular plots

in three different habitats. All trees with wasp nests only, wasp nests and Bananaquit nests, Bananaquit nests only, and trees with neither wasp nor Bananaquit nests were recorded. It was not possible to discriminate between Bananaquit roosting and breeding nests so all bird nests were pooled. The first habitat surveyed (10 June and 9 November 1981) consisted of a mixed assemblage of Acacia, Coccoloba, Cocos nucifera, and Hippomane macinella located directly behind the beach at Morne Rouge Bay. This first site was approximately 0.25 ha with trees ranging from 5-10 m in height. The second location surveyed on 21 June and 9 November 1981, consisted of ornamental plantings and open lawns of tourist homes between Pinquin and Madame Jardin. This 1.1 ha site contained a wide diversity of trees (4-17 m tall) and shrubs such as Tamarindus indica, Gliricidia sepium, Nerium oleander, Bursera simaruba, and Citharexylum berlandieri. The third sample site (0.87 ha) was located in an open Acacia savanna with trees of 4-8 m in height at True Blue. This acacia dominated site was sampled on 24 June and 1 November 1981.

A tape measure was used to determine the distance between Bananaquit nests and the nearest wasp nest in trees containing both nests. In addition, Wunderle estimated the height of the nest tree and measured the maximum and minimum crown diameter using a tape placed on the ground under the tree. The length and maximum width of the wasp nests associated with Bananaquit nests were also measured.

To determine if females nesting in association (≤ 1 m) with a

wasp nest would subsequently re-build in association in the following year, Wunderle colorbanded females with nests associated with wasps in July and August and returned the following year to find the female's nest in relation to wasp nests. In addition, he removed the active nests of ^{eight} color-banded females and then located the replacement nest to see if females originally nesting in proximity (≤ 1 m) of a wasp nest would re-build a nest in association with a wasp nest in the same breeding season. All females were captured at the nest with mist nets and given a unique color-band combination. Only females in areas with numerous Polybia nests were used. Nests were collected only during the nestling stage and the young hand-reared for other experiments (Wunderle, manuscript).

As part of another study on Bananaquit social behavior (Wunderle 1980) 507 individuals were colorbanded in southern Grenada. Wunderle mapped the locations of all territories and nests in three different study sites and noted if a female's first nest or subsequent replacement nests (i.e. following nest predation) were associated with wasp nests.

Results

When undisturbed, Polybia occidentalis is a docile species which will permit a person to approach within several centimeters of the nest. However, during daylight hours a sudden jarring of a branch supporting a Polybia nest causes the wasps to swarm in the air around their nest. On dark nights the wasps swarmed over the surface of their nest and onto the supporting branch while producing

an audible buzzing sound, but rarely flew. Disturbance of the wasp nests on bright, moon-lit nights did cause some wasps to swarm in the air surrounding their nest. These disturbed wasps readily stung humans and presumably would sting other animals which shook the wasp nest or supporting branch. The wasp sting and its swarming behavior might deter the major predators of Bananaquit eggs and nestlings such as snakes (Boa enhydris), grackles (Quiscalus lugubris), and rats (Rattus rattus).

Those Bananaquits nesting within one meter and on the same branch as a wasp nest, have a significantly lower nest predation rate (G-Test, Sokal and Rohlf 1981:696; $G=3.976$, $p<0.05$) than nearby nests initiated within the same week, but not associated with a wasp nest (Table 1). The three nests within one meter of a wasp nest with the contents removed, showed no outward sign of predation as is characteristic of predation by snakes (Wunderle 1982). Of the 8 females which nested within 2 m but further than 1 m from a Polybia nest only 3 (37.5%) successfully fledged young while half of the control nests ($N=8$) unassociated with wasp nests fledged young ($G=0.002$, $p>0.5$).

Wunderle (1980) demonstrated that females will frequently abandon their nest site and mate following nest predation. Therefore females nesting in areas or sites with low nest predation rates should remain with their original mate for a longer time period. Males having nests within 1 m of a Polybia nest usually had the same mate at the end

of the breeding season, while nearby males with nests not associated with wasps lost their mates significantly ($G=4.57$, $p<0.05$) more often by the end of the breeding season as shown in Table 2. Thus nesting in association with a wasp nest reduces nest predation losses and subsequently reduces the probability of female abandonment.

The possible advantage to Bananaquits nesting near Polybia nests suggests that Bananaquit nests might be frequently associated with wasp nests. The following findings are consistent with this possibility. Trees (>2.5 m) containing both Bananaquit nests (either roosting or breeding) and Polybia nests were more frequently encountered than expected by chance alone within the Pinquin study site in June ($X^2=18.108$, $p<0.005$, d.f.=1) as shown in Table 3. At the two other sites the number of trees with both Bananaquit and wasp nests was small (N=2 and N=3) but significant chi-square values (Morne Rouge $X^2=5.735$, $p<0.025$; True Blue $X^2=4.641$, $p<0.05$) may be inaccurate (see Zar 1974:50, for a discussion of the problems using X^2 when one of the cells in a 2x2 table is <5). The distance between the Bananaquit nest and the nearest Polybia nest within the same tree averaged $82.3 \text{ cm} \pm 10.3$ (SE) as shown for 34 individual nests in Figure 1. This distance between the two nests averaged $15.6\% \pm 1.6$ (SE) of the maximum horizontal distance through the tree crown (Figure 2).

The above evidence suggests that there is a nesting association between Bananaquits and wasps, but does not show which animal

initiates the association. The following evidence suggests that some Bananaquits build their nests near established Polybia nests and not that wasps build their nests near Bananaquit nests. Over the five years of field work, Wunderle observed seven different Bananaquit females as they initiated nest building near Polybia nests, but never found wasps building near an existing bird nest. If wasps were building nests near established Bananaquit nests we would expect that wasp nests associated with bird nests might be smaller in size (i.e. younger) than wasp nests unassociated with bird nests. This was not found. The average length ($16.7 \text{ cm} \pm 1.3 \text{ SE}$) and average width ($9.8 \text{ cm} \pm 0.5 \text{ SE}$) of 34 Polybia nests associated with Bananaquit nests did not differ from the average length ($17.9 \text{ cm} \pm 1.1 \text{ SE}$) and width ($10.7 \text{ cm} \pm 0.6 \text{ SE}$) of 54 randomly chosen Polybia nests not associated with bird nests.

To determine if individual Polybia nests tended to survive longer (e.g. remain active) than individual Bananaquit nests during the summer months, I recorded all active Bananaquit nests associated ($\leq 1.0 \text{ m}$) with active Polybia nests in May and June and returned in late September (1981) to determine which nest of the pair was still active. Of the 29 pairs of wasp and bird nests re-examined in September, 3 pairs (10.3%) had both nests active, 17 pairs (58.6%) had an active wasp nest and a missing bird nest, 4 pairs (13.8%) had an abandoned or missing wasp nest with an active bird nest, and in 5 pairs (17.2%) both nests were destroyed or abandoned.

Polybia nests remained active for a significantly ($G=10.29$, $p<0.005$) longer time period than did the associated Bananaquit nest. This suggests that wasp nests remain active long enough to provide predator deterrence during the span of Bananaquit nesting.

No association was found between the placement of the Bananaquit nest relative to the wasp nest and the tree trunk. Eighteen Bananaquit nests were further from the main trunk than the wasp nest, while 16 bird nests were closer to the trunk than the nearby wasp nest in 1981. In addition, in November (nonbreeding period) Wunderle found no trees with both wasp and birds together in the three sites surveyed earlier in June and July (1981) despite the presence of numerous roosting nests. These findings suggest that no association exists between Bananaquit nest placement relative to wasp nests and the tree trunk during the breeding season and in the nonbreeding season there is no association between Bananaquit nest placement and wasp nests.

Female Bananaquits which nested in association with wasps in one breeding season did not usually nest in association in the following year. Of 15 colorbanded females nesting in association with wasps, only one (6.6%) nested near (1.2 m) a wasp nest in the following year. Nest removal experiments were run to determine if some females would always nest near wasp nests during the same breeding season. All females used for this experiment had several Polybia nests available within their territories as shown in

Table 4. After nest removal, one of the females abandoned her territory, while the remaining seven females re-nested on their territories which contained at least 9 Polybia nests. At the time of nest removal, the eight breeding nests were located an average of $0.65 \text{ m} \pm 0.09 \text{ (SE)}$ from the nearest wasp nest while the replacement nest averaged $6.47 \text{ m} \pm 1.27 \text{ (SE)}$ from the nearest wasp nest. This difference was significant (Mann-Whitney U Test, Sokal and Rohlf 1981:432; $U=49$, $p<0.001$). The inverse relationship, a female first nesting without a wasp nest, but re-nesting in association ($\leq 1 \text{ m}$) with a wasp nest in the same territory was observed in four colorbanded females. These females built their original breeding nests in trees without wasp nests (mean distance to nearest wasp nest = $8.43 \text{ m} \pm 2.02 \text{ SE}$), but after their nests were destroyed they subsequently re-nested an average of $0.69 \text{ m} \pm 0.07 \text{ (SE)}$ from a wasp nest.

Discussion

Bananaquit nests within 1 m of a Polybia nest had a lower predation rate than nearby nests which were unassociated with wasp nests. However, those Bananaquit nests which were more distantly associated with wasp nests ($>1 \text{ m}$ but $<2 \text{ m}$) had predation rates equivalent to nearby nests unassociated with wasp nests. These findings are consistent with the hypothesis that stinging insects might deter potential nest predators and thus birds nesting in association with them would benefit by having lower nest predation

rates. The swarming and stinging response of disturbed wasps might serve as an effective deterrent to most predators. For example, on Grenada, grackles and rats might be reluctant to disturb wasp nests. However, some large birds with heavy feather coverings may not be deterred by Polybia stings as illustrated by the observations of Gray-headed Kite (Leptodon cayanensis) predation upon wasp brood in Costa Rica (Windsor 1976). It is also possible that some snakes might be able to thwart the Polybia defenses of associated bird nests by feeding at night and with slow movements which are unlikely to disturb the wasp colony. For example, in this study, three Bananaquit broods in nests less than 1 m from a wasp nest were destroyed by snakes.

The Bananaquit-Polybia nesting association is probably a case of commensalism rather than mutualism. The Polybia wasps do not appear to obtain any benefit from the neighboring Bananaquits. There is no evidence to suggest that Bananaquits might drive-off or deter the predators of wasp larvae, as has been suggested for tyrannids nesting in proximity to wasp nests (Smith 1980). Nor is it likely that the bird nest is the more conspicuous component of this association which might reduce the risk of accidental damage to the fragile wasp nest as discussed by Myers (1935). In this case, the bird nest might advertise the presence of a wasp nest and thus provide a warning to foraging animals.

The Polybia wasps showed only a mild response (e.g. swarmed

over the surface of their nest, few flew in the air) to female Bananaquits as they began nest building near their colony. With time the wasps habituated to the activity of the Bananaquits at their nests. A similar instance of habituation was found by Janzen (1969) in ants that habituated to the activities of birds nesting in ant acacias. While the light, regular movements of the nesting Bananaquits were ignored by wasps, a sudden jarring of the wasp nest or its associated branch produced an immediate swarming response by the wasps. Presumably the domed Bananaquit nest provides protection to the nestlings from the swarming stinging wasps. Domed or tightly woven pendulent nests protect the nestlings from the stinging or biting insects and may be a pre-adaptation necessary for the evolution of this association since such nests are characteristic of birds associated with aggressive insects (Myers 1929, 1935, Moreau 1936, Maclaren 1950).

Male Bananaquits with females nesting in proximity to Polybia nests within their territory are more likely to retain their original mate through the breeding season than those males with nests unassociated with wasp nests. As discussed elsewhere (Wunderle 1980), female disappearance following nest predation is a result of abandonment of nest site and mate and not a result of mortality due to the nest predator. Abandoning females will leave the territory of their original mate and re-nest with a nearby male at a new location. The original male, following mate desertion, may be without a mate

for several weeks or even for the remainder of the breeding season. This could result in the loss of valuable breeding time for both sexes. In addition, a delay in breeding could also result in reduced fledging success because nest predation rates increase as the breeding season proceeds (Wunderle 1982). Thus Bananaquits nesting in proximity of a Polybia nest will have a higher fledging success per each clutch and possibly more successive clutches per breeding season with the same mate.

Female Bananaquits appear to choose the actual nest site (Wunderle, unpublished observations) and hence females, rather than males, are responsible for the selection of a site in proximity of a Polybia nest. On Grenada, females do not always nest in association with Polybia nests even when several "appear" to be available within the territory. The results of the nest removal experiments are ambiguous and suggest only that females may not always choose to nest in association with wasps or the nest removal (e.g. an act of predation) served as a negative conditioning agent which encouraged females to nest away from wasp nests. The findings that females with nests associated with Polybia nests at the end of the season did not always nest in association with wasps in the following season (even though Polybia appeared to be available) suggest that other factors might be important in female nest site selection. At present, many of those factors are unknown.

It is unlikely that the Bananaquit-Polybia nesting association

occurs because both species are attracted to a particular species of tree for their nests. In southern Grenada, Bananaquits were found nesting in 34 species of trees and shrubs while Polybia nests were found in 22 species. The Bananaquits were found nesting in more different species possibly reflecting their greater flexibility of nest site selection. No Polybia nests were found in tree or shrub species not used by Bananaquits. Both Bananaquits and Polybia wasps appear to attach their nests to a variety of structures. The wasps require at least a horizontal, or nearly horizontal branch from which to suspend their nest. As is well documented by Skutch (1954), Biaggi (1955), and Gross (1958), Bananaquits will accept a tremendous variety of structures for nesting as long as there is at least a fork on to which they can weave their nest. Neither species will nest on the vertical trunk of a tree. However, both species can probably find numerous acceptable sites for nest attachment often within close proximity to each other.

Female Bananaquits will always abandon their nest and often their territories following nest predation and will attempt to re-nest elsewhere. They will make as many as six re-nesting attempts in a breeding season. If they are successful at one nest location they will remain there and produce up to four successful clutches or until the nest is destroyed (Wunderle 1980). This pattern of abandonment following predation or remaining in the same locale to re-nest after successful fledging is a common pattern (e.g. Haartman

1949, Nolan 1978) and might increase the likelihood of finding a safe nesting site. It may be this abandonment behavior which eventually brings some breeding females within close proximity to a wasp nest. Once closely associated with the wasp nest, a safe site, the female might remain and produce a sequence of several successful clutches until her nest finally deteriorates.

The observed statistical association between Bananaquit nests and wasp nests might actually represent only the nest distribution resulting from the female abandonment and relocation behavior. For example, if a female always abandons and relocates after a nest predation she will eventually locate a predation "free" site where she may remain for several successive clutches. If most of these safe sites are in proximity of a wasp nest and the surroundings of the wasp nest contains suitable sites for Bananaquit nests, we might expect to find more females nesting in association with wasps than predicted by chance alone. In this instance, a nesting association would not be dependent upon a female's having to cue-in on a wasp nest as part of her nest site selection behavior. Thus as nest predation rates increase the proportion of females nesting near wasp nests might increase.

This simple nest predation response of female site abandonment and relocation until a safe site is found could explain the evolution of some other bird-hymenopteran nesting associations. Many biologists have previously assumed that the existence of bird-hymenopteran

nest spatial associations indicates that site selection by the birds is nonrandom. For example, Myers (1935) suggests that nestlings reared within close proximity to a hymenopteran nest might later prefer such an association for their own nest site. We would like to offer an alternative explanation as a null hypothesis, a random choice model to explain the evolution of nesting associations.

The Random Choice Model

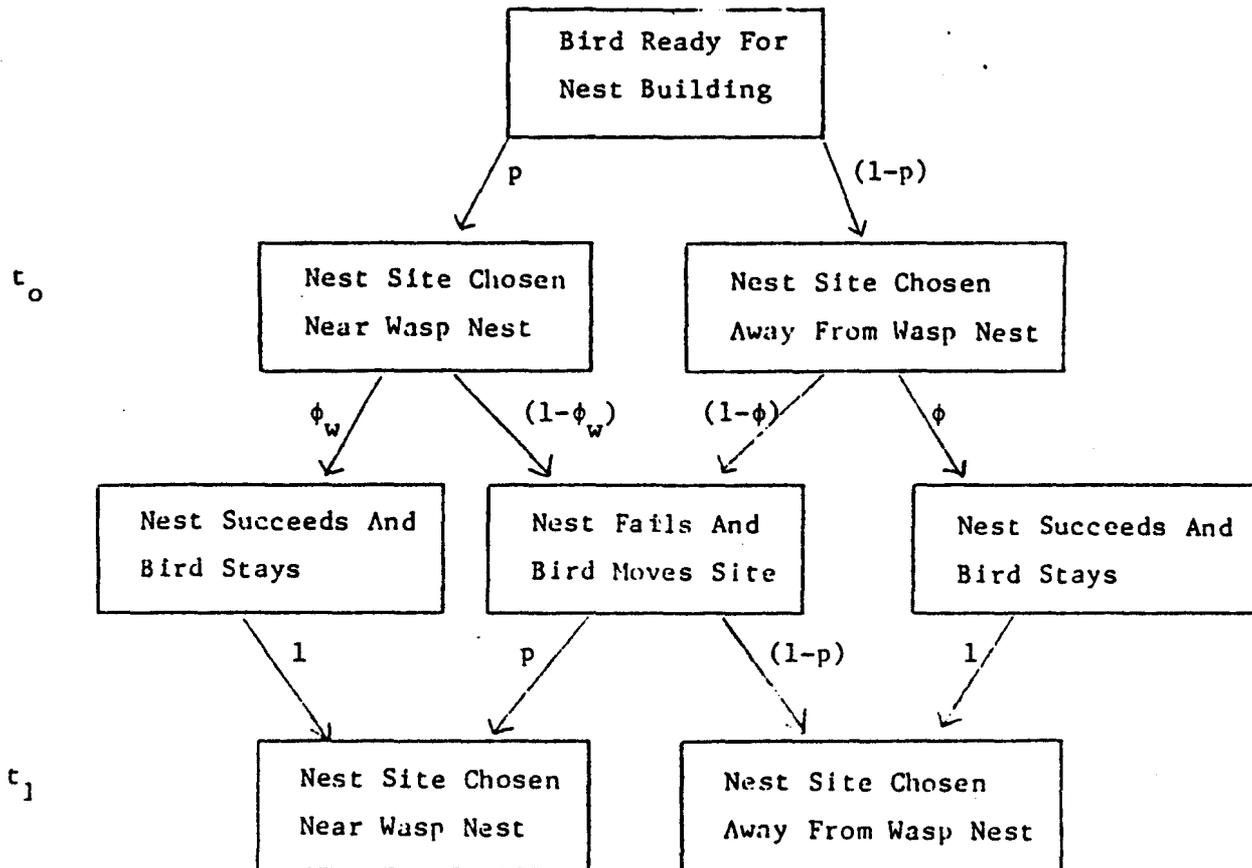
Model Structure and Assumptions

We assume that a bird has a large number of potential nest sites with and without "close" wasp nests so that we can ignore the problems of sampling without replacement. We further denote the proportion of potential safe sites which are "close to" a wasp nest by the parameter p . Assuming that any bird makes a random choice of nest site from those available the probability that the bird chooses a site close to a wasp nest is also given by p .

We assume that there is a fixed "generation" time during which either a bird succeeds in raising a brood or fails. If it is successful the bird attempts to raise another brood in the same nest in the next generation. If it fails the bird moves to a new site and builds another nest for the next generation. We assume that there is a probability (ϕ_w) for success if the nest is close to a wasp nest and another lower probability (ϕ) for success if the nest is not close to a wasp nest.

Derivation

We now derive the probability of a bird having a nest site close to a wasp nest after i generations in terms of the three parameters of the model (p, ϕ_w, ϕ) . To aid us in this derivation consider the following flow chart for the first two generations.



Following the flow chart and using conditional probability arguments we can easily show that the probability of a nest site being chosen close to a wasp nest at time t_1 is given by

$$p_1 = p [\phi_w + (1-\phi_w) p] + (1-p) [(1-\phi) p]$$

As each generation flows to the next in the same manner we have for the next generation

$$p_2 = p_1 [\phi_w + (1-\phi_w) p] + (1-p_1) [(1-\phi) p].$$

Using inductive reasoning we have established the recurrence relation

$$p_i = p_{i-1} [\phi_w + (1-\phi_w) p] + (1-p_{i-1}) [(1-\phi) p] \quad (1)$$

Numerical Results and General Implications

In this section we present computations based on equation (1) for a range of model parameter values (Table 5). We consider wasp nests to be sparse ($p=0.2$), abundant ($p=0.5$) or super abundant ($p=0.8$). We allow the degree of protection of wasp nests to range from small ($\phi_w = 0.8, \phi_w = 0.7$) to very large ($\phi_w = 0.8, \phi_w = 0$).

If the wasp nests are abundant and offer substantial protection then it is clear that a bird-hymenopteran nest spatial association can develop very quickly. The rapid evolution of this nesting association would be encouraged by factors such as learning or nonrandom choice, a shortage of nest sites, restriction of wasp and bird nests to very similar nesting sites, and the possibility that unsuccessful birds have a shorter generation time than successful individuals.

Biologists who observe a nonrandom distribution of nests (or organisms in general) should not assume that the spatial distribution results only from nonrandom factors. Our model suggests that other mechanisms are possible and that discriminating between models which assume random and nonrandom choice of nest site will be difficult. Careful quantitative documentation of the association will be necessary possibly in conjunction with experimental manipulation.

In our model we have deliberately ignored the role of learning or nonrandom choice in an effort to illustrate the effects of random choice. It is apparent that random choice of nest sites alone

can have an appreciable effect upon the evolution of this nesting association and might be an important factor in the initial stages of its development. With the addition of learning (e.g. a female associates a wasp nest with previous nesting success and hence seeks wasp nests for future nest sites) we have no doubt that this nesting association will develop at a faster rate. The final stage (should it occur) might be the genetic incorporation of a "mental image" of a wasp nest which serves as a cue for nest site selection. Thus the random choice model could start and initially maintain the nesting association until the more powerful mechanism of behavioral choice (e.g. cue-in on wasp nests for nest sites) finally controls nest site selection.

What factors might explain the prevalence of bird-hymenopteran nesting associations in the tropics relative to temperate regions? The obvious factors are the higher nest predation rates on tropical birds (Ricklefs 1969) and possibly more colonial hymenopterans available to provide protection. In addition, nests which provide protection to nestlings from insect attacks are an essential pre-adaptation for this association and such nests may be more characteristic of tropical bird nests. Less obvious factors are the longer life spans of tropical birds (e.g. Lack 1966) and possibly a longer season available for re-nesting. As shown in our model, an increase in the number of nesting generations increases the probability that an individual will nest in association with a

hymenopteran colony. A tropical species (e.g. Bananaquits) might build more replacement nests (because of higher nest predation rates) in a life-time than similar temperate zone species. Eventually some of these re-nesting attempts would bring the tropical species within close proximity of a protective hymenopteran nest.

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Table 1. Effect of proximity (≤ 1 m) to Polybia wasp nests on nest predation in Bananaquits. Data pooled for 1975-1978, and 1981 breeding season.

	Number of successful nests	Number of unsuccessful nests due to predation
Bananaquit nests associated with (≤ 1 m) with active <u>Polybia</u> nest	20	3
Bananaquit nests not associated with active <u>Polybia</u> nest	13	10

G=3.976, $p < 0.05$

Table 2. Mate fidelity and association with Polybia wasp nests.

	Same female at end of breeding season	Different female at end of breeding season
Bananaquit nests associated with active <u>Polybia</u> nest	9	1
Bananaquit nests not associated with active <u>Polybia</u> nest	4	7

G=4.57, $p < 0.05$

Table 3. Distribution of Bananaquit and Polybia wasp nests in ornamental trees and shrubs at Pinquin.

	Trees without Bananaquit nests	Trees with Bananaquit nests
Trees without <u>Polybia</u> nests	294* (289.36) [†]	12 (16.64)
Trees with 1 or more <u>Polybia</u> nests	19 (23.64)	6 (1.36)

$$\chi^2=18.108, p < 0.005$$

*Observed

[†] Expected

Table 4. Response of female Bananaquits to nest removal on territories with Polybia nests. All females nested less than 1 m from a wasp nest before the nest was removed.

Individual	Distance to Nearest <u>Polybia</u> Nest In Meters		Number of <u>Polybia</u> Nests On Territory
	Original Nest	Replacement Nest	
RW-RW	0.65	1.8	9
BW-YB	0.52	8.1	25
W-R	0.84	7.5	16
B-W	0.96	12.3	17
WB-RY	0.67	5.5	19
YY-YB	0.15	2.5	18
Y-RW	0.78	7.6	17
Mean and SE	0.65±0.09	6.47±1.27	

Mann Whitney U = 49, $p < 0.001$

Table 5. The probability of a bird nest being close to a wasp nest after 1 to 7 generations.

Trial	Model Parameters			Generation Probabilities						
	P	ϕ_w	ϕ	P ₁	P ₂	P ₃	P ₄	P ₅	P ₆	P ₇
1	0.2	0.8	0.7	0.216	0.228	0.238	0.246	0.252	0.256	0.260
2	0.2	0.8	0.6	0.232	0.256	0.275	0.289	0.300	0.308	0.314
3	0.2	0.8	0.5	0.248	0.284	0.310	0.329	0.344	0.354	0.362
4	0.2	0.8	0.4	0.264	0.310	0.343	0.367	0.384	0.397	0.406
5	0.2	0.8	0.3	0.280	0.336	0.375	0.403	0.422	0.435	0.445
6	0.2	0.8	0.2	0.296	0.361	0.406	0.436	0.456	0.470	0.480
7	0.2	0.8	0.1	0.312	0.385	0.435	0.467	0.488	0.502	0.511
8	0.2	0.8	0.0	0.328	0.410	0.462	0.496	0.517	0.531	0.540
9	0.5	0.8	0.7	0.525	0.544	0.558	0.568	0.576	0.582	0.587
10	0.5	0.8	0.6	0.550	0.585	0.610	0.627	0.639	0.647	0.653
11	0.5	0.8	0.5	0.575	0.624	0.655	0.676	0.689	0.698	0.704
12	0.5	0.8	0.4	0.600	0.660	0.696	0.718	0.731	0.738	0.743
13	0.5	0.8	0.3	0.625	0.694	0.732	0.752	0.764	0.770	0.774
14	0.5	0.8	0.2	0.650	0.725	0.763	0.731	0.791	0.795	0.798
15	0.5	0.8	0.1	0.675	0.754	0.789	0.805	0.812	0.816	0.817
16	0.5	0.8	0.0	0.700	0.780	0.812	0.824	0.830	0.832	0.833
17	0.8	0.8	0.7	0.816	0.828	0.836	0.842	0.846	0.849	0.851
18	0.8	0.8	0.6	0.832	0.852	0.866	0.874	0.879	0.883	0.885
19	0.8	0.8	0.5	0.848	0.875	0.890	0.898	0.903	0.906	0.907
20	0.8	0.8	0.4	0.864	0.895	0.909	0.917	0.920	0.922	0.922
21	0.8	0.8	0.3	0.880	0.912	0.925	0.930	0.932	0.933	0.933
22	0.8	0.8	0.2	0.896	0.927	0.937	0.940	0.941	0.941	0.941
23	0.8	0.8	0.1	0.912	0.939	0.945	0.947	0.947	0.947	0.947
24	0.8	0.8	0.0	0.928	0.948	0.952	0.952	0.952	0.952	0.952

Figure Legends

Figure 1. The distance between Bananaquit and Polybia wasp nests in the same tree. (N=34).

Figure 2. The distance between Bananaquit and wasp nests as a percentage of the maximum horizontal distance through the tree crown. (N=34).

