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RESPONSES OF BARN SWALLOWS TO EGGS, YOUNG, NESTS, AND NEST SITES

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Aspects of egg, young, nest and nest site recognition have been investigated or observed in several species of birds (e.g., Cullen 1957, Davies and Carrick 1962, Beer 1969, Peek et al. 1972). In general, selection appears to favor recognition of as few characteristics as necessary to insure a high probability of caring for the correct eggs or young. Birds that build nests respond to their nest sites, and later their young (usually when mobile), but show little evidence of specifically recognizing their own nests or eggs (Nice 1943, Tinbergen 1953, Beer 1970). Common Murres (*Uria aalge*; Johnson 1941, Tschanz 1959), which do not build nests, and Royal Terns (*Sterna maxima*; Buckley and Buckley 1972), which nest in dense colonies where their eggs may be displaced, recognize both their eggs and laying sites.

Among passerines, Rothstein (1975) found that some species ("rejector species") can recognize foreign eggs placed in their nests, while others ("acceptor species") do not. Bank Swallows (*Riparia riparia*; Hoogland and Sherman 1976), Red-winged Blackbirds (*Agelaius phoeniceus*; Peek et al. 1972), and Carrion Crows (*Corvus corone*; Yom-Tov 1976) do not discern their eggs, or their young until near fledging, at an age when an "error" in progeny care is possible. Tricolored Blackbirds (*Agelaius tricolor*), which nest in dense colonies, accept eggs or young placed in their nests (Emlen 1941). Many non-passerines are similar in their varied ability to recognize their eggs or young (Tinbergen 1953, Davies and Carrick 1962, Beer 1970).

Red-winged Blackbirds recognize their nest sites specifically, but accept substitute nests (Peek et al. 1972). Nero and Emlen (1951) found that female Red-winged Blackbirds would follow displaced nests even across territorial boundaries of males. Meise (1933) moved the nest of a House Sparrow (*Passer domesticus*) 1.5 m and observed no response to it by the adults. Among non-passerines, a Cooper's Hawk (*Accipiter cooperii*) nest moved in small increments from its original location in the crotch of a tall tree to a bushel basket, and then to the ground, was accepted at each step by the adults (Allen 1951). Herring Gull (*Larus argentatus*) nests moved about 30 cm were accepted if they contained eggs and the original nest site was covered with sand (Tinbergen 1953). In experiments with Sooty Terns (*Sterna fuscata*), birds returned to their nest sites rather than to nests displaced short distances (Lashley 1915). From these studies, it appears that selection favors more rigid responses to changes in nest and nest site for colonial than for non-colonial species.

In the present study, I evaluated responses of Barn Swallows (*Hirundo rustica*) to their eggs, young, nests, and nest sites. Barn Swallows are facultative colonial nesters and unique among the above species in that their colonies are passive aggregations of birds (Snapp 1976). Barn Swallows have recently used man-made structures for nesting (Bent 1942), and such behavior may influence the size of their aggregations. Do swallows respond to aspects of the nesting situation in the same way as colonial or non-colonial species?

METHODS

This study was conducted in southern and central Oklahoma during June and July of 1974, 1975 and 1977. Swallow colonies were located in rectangular cement culverts under heavy-duty roads. In 1974, two culverts were used for the behavioral part of the study; one about 2.5 km southwest of Madill, Marshall County (left culvert in Fig. 1), and one under State Highway 99 adjacent to Lake Texoma, Marshall County. The inside culvert dimensions were 183 cm (height) × 244 cm × 25.2 m (excluding triangular corner; see Fig. 1) and 213 cm × 152 cm × 48.0 m, respectively. In 1975 and 1977, a culvert under State Highway 9 near Lake Thunderbird, Cleveland County, was used. It measured 183 cm × 183 cm × 49.6 m. Nests in culverts were numbered sequentially, whether in use or not, and their locations described in relation to: (1) distance from the entrance of culvert and/or nearest nest(s); and (2) shortest distance from outer lip of nest to ceiling of culvert.

Mist nets were placed on the ends of the culverts, opened at night, and checked at sunrise. Captured birds were banded and adults were marked with paint. All males were marked conspicuously on the back with light blue. Females were painted so as to be individually recognizable by using a variety of colors (other than light blue) on various parts of the body including left wing, right wing, back of neck, throat and rump. The paint did not appear to impair any individual, and paint-marked birds were captured in successive years. Sex was determined by measuring tail and wing chord lengths (Wood 1969), and by the presence or absence of a brood patch.

FIGURE 1. Nesting site of Barn Swallows in culverts under heavy-duty road near Madill, Marshall County, Oklahoma. There were 17 active nests in culvert on left and 4 active nests in culvert on right. Note closed mist-nets at entrance of culvert.

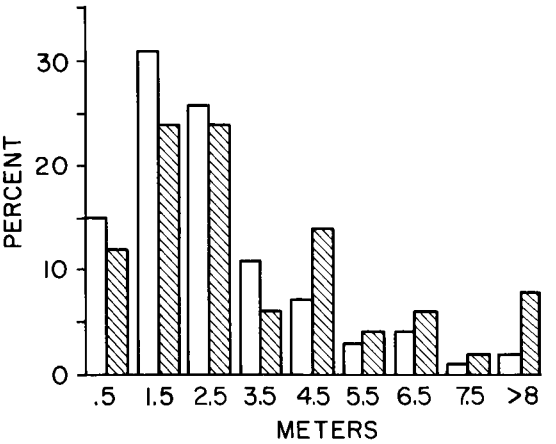

FIGURE 2. Frequency distribution of distances between nests of Barn Swallows nesting in culverts (measured to nearest cm). The white bars refer to distances between all adjacent nest pairs (N = 137) while the shaded bars indicate distances between active nests (N = 84).

I watched the birds, with the aid of 7 × 35 binoculars, from an automobile or burlap blind positioned near the entrance of the culvert. A small mirror was used to shine light into the culvert to confirm the identity of birds sitting on nests. Marked birds were watched as they entered the culvert and went to their respective nests. After nests were identified with individually-marked birds, I initiated the experiments. Often, only the female using a particular nest was marked, but in no case did two birds identified as female use the same nest.

Experimentation involved: (1) moving nests horizontally or vertically from their original location; (2) adding nests; (3) removing nests; and (4) switching nests, and/or eggs and young. Nests to be moved were carefully pried off the wall and reattached by laying down an adhesive mud base to the new location and pressing the moistened back of the nest onto the new location. Details of each manipulation are given in the results.

I observed the responses of Barn Swallows for at least 0.5 h after each manipulation. Observations were extended up to 1.5 h in cases when the final response was in doubt. The responses to nests (or nest sites) were assigned to one of four categories: (1) no response—when a swallow appeared to ignore the nest (or nest site); (2) not accepted—when a swallow investigated the nest (or nest site) by hovering in front of it, but did not land (occasionally, a swallow in this category actually touched a nest, but did not perch); (3) weak response—when a swallow attempted to incubate or feed young (or perched at nest site), but rejected these nests (or nest sites) during the observation period (a swallow who sporadically fed young in a nest was placed in this category); and (4) accepted—when a swallow continuously performed incubation or feeding activities at a nest without apparent hesitation or distress. Often, swallows in this category initially exhibited hesitation or distress when exposed to the manipulated situation.

RESULTS

In south-central Oklahoma, Barn Swallows placed their nests linearly on the wall just below the ceiling of the culvert. The outer lips of the nests were located 4 to 6 cm below the ceiling, except for one case where the nest was 58 cm below the ceiling. The mean distance between nests, for 137 adjacent nest pairs in 11 culverts, was 2.79 m (SD = 2.27 m). Mean distances between 84 occupied nest pairs (i.e., nests with eggs or young) was 3.66 m (SD = 3.12 m). The latter represents a maximal value because young may have recently fledged from "unoccupied" nests located between the occupied ones. Frequency distributions, converted to proportion of total, were prepared for distances between nests of both data sets and are shown in Figure 2. With one exception, the lowest distance between occupied nests was 0.73 m. Barn Swallows maintain some minimum distance between nests, but 60% of the occupied nests were spaced less than 3 m apart.

RESPONSE TO EGGS

I evaluated whether or not Barn Swallows are able to: discern their own eggs from other Barn Swallow eggs; distinguish Barn Swallow eggs from eggs of other species; and/or distinguish eggs from other objects. To test if females could distinguish their eggs from other Barn Swallow eggs, several manipulations were performed. When clutches with identical numbers of eggs were substituted for the original eggs, females accepted the new set in all eight cases tested. In two of these, both the eggs and nest were replaced. In two other instances, a female's nest and eggs were removed and replaced by two new nests immediately adjacent to the original location; one of the nests contained her own eggs while the other included a clutch with the

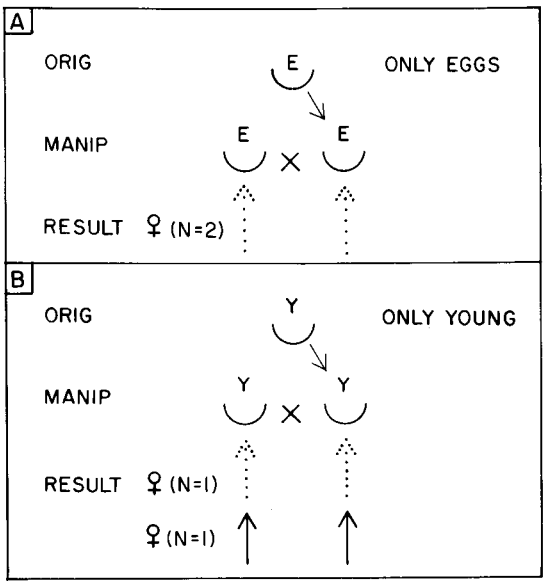

FIGURE 3. Responses of Barn Swallows to their (A) eggs and (B) young. Abbreviations and symbols indicate the following: ORIG, linear arrangement of nests on culvert wall before manipulation; MANIP, arrangement after manipulation; RESULT, choice of swallow; E, eggs; Y, young; semicircle, symbol for nest; dotted arrow, response where nest (or nest site) not accepted by swallow (see text); solid arrow, response where nest (or nest site) accepted by swallow (see text); X, original location of nest. Member of pair responding, ♂ or ♀. Sample size given in parenthesis for each result.

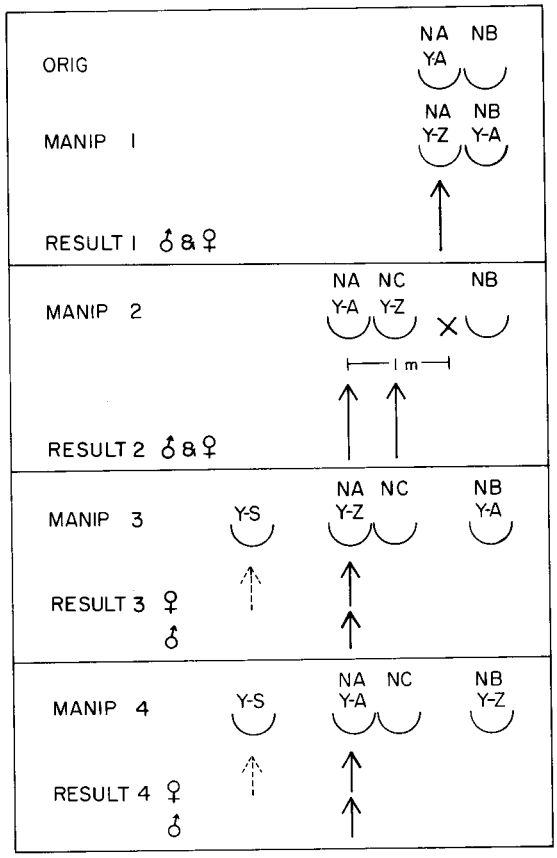

FIGURE 4. Responses of Barn Swallows to their young (see text). Abbreviations and symbols: NA, NB and NC designate particular nests; Y-A, Y-Z, and Y-S indicate particular broods; dashed arrow, weak response of swallow (see text); other symbols as in Figure 3.

same number of eggs (Fig. 3A). The females in both cases did not incubate either clutch. These experiments indicate that females could not recognize their own eggs specifically.

When I substituted House Sparrow eggs for the original eggs (3 cases), the females accepted them. In two instances, I substituted cold white stones (approximately the same size as Barn Swallow eggs) for the eggs. The females accepted and incubated them, occasionally prodding (perhaps rolling) them with their bills. These results demonstrate that Barn Swallows cannot distinguish conspecific eggs or any eggs specifically, and that they will respond to stimuli approximating their eggs.

Response to eggs does not end with recognition. Incubation behavior may be triggered internally or by the external stimulation of eggs in the nest. To determine which was the case, only the eggs were removed from the nest in four instances. Females attempted to incubate in the nests, shuffling downward into the nest bowls. Females then left the nests and returned several times, attempting to incubate several times during each visit and for several minutes during each attempted incubation bout. Later, females visited the nests and perched on the lips for several minutes during each visit. These females occasionally looked down into the nests. As long as their nests were still present at the original locations, the females did not attempt to locate other nests with eggs. When eggs were later replaced, the females accepted and incubated them. Apparently, the drive to incubate in this species is a behavioral state controlled internally or, at least, not requiring eggs to initiate the response. The tactile stimulus of eggs, however, is necessary to maintain incubation behavior.

RESPONSE TO YOUNG

In these manipulations, I tested Barn Swallows to see if they could distinguish between their young and other Barn Swallow young, or distinguish the developmental stage of their young from other stages, including eggs. In eight cases, when young up to 11 days of age were substituted for the original young of similar age, females ac-

cepted the change. In two cases, a female with young was presented with the choice of her young, or another brood in a new nest adjacent to the original site (the original nest was removed). One female investigated both nests but did not feed either set of young; the other fed both sets of young (Fig. 3B).

I conducted one set of manipulations on a natural "double nest" (Fig. 4)—an active nest (labeled NA) with a second nest (NB) immediately adjacent to it. Nest A (NA) contained young (Y-A) and NB was empty. In manipulation 1, Y-A young were moved to NB, and alien young (Y-Z) of similar age were placed in NA (see Fig. 4). Both the female and male fed the young in NA. In a second manipulation, NA and young (Y-A) were moved about 1 m to the left and another nest (NC) with young (Y-Z) was placed immediately adjacent to it, simulating the original situation but 1 m displaced. The female fed both sets of young equally. The male also fed both sets of young regularly, but fed the Y-A young more often. In a third modification, Y-A young (from NA) were moved back to NB and Y-Z young moved to NA at the displaced location. The female fed the Y-Z young and once fed young birds in the next occupied nest (labeled Y-S in Fig. 4). The male fed the Y-Z young. For manipulation 4, the Y-A and Y-Z young were switched again (see Fig. 4). The female fed the Y-A young in the displaced nest (NA) and again fed young in the next occupied nest (Y-S). The male fed young only in NA. These experiments and those previously described indicate that female Barn Swallows do not recognize their own young (up to 11 days of age). I was unsuccessful in conducting tests involving young older than 11 days because they fledged prematurely when disturbed.

The responses of females to young of different developmental stages than their own young were evaluated. With notable differences in the size of the young switched, females showed some reluctance, "distress," or hesitation, but accepted the change in 12 of 13 cases. If eggs and newly hatched young were switched, females receiving eggs or young (two cases each) accepted the change, sometimes exhibiting distress, but other times without hesitation. These responses indicate that females are able to distinguish between stages of development, but that similar stimuli in their nests are accepted.

Further manipulations were undertaken to determine which stimuli evoked the strongest response at various stages of the breeding cycle. Two females with young were provided with choices of nests with eggs or nests with young, both immediately adjacent to their own nests which were left empty (Fig. 5A). Females selected the nests with young which they fed, ignoring the nests with eggs. They investigated, but did not land on their original nests between visits to the nests with young. When females with eggs were given the same choice (two cases), they incubated the eggs, and brooded and fed the young (Fig. 5B); initially they appeared startled by the begging young. Females with eggs attempted to incubate in their original nests, but soon abandoned their nests for other choices. In these latter manipulations, it appeared that new stimuli of young presented to females with eggs triggered appropriate feeding responses without affecting their incubation drive. However, after young have hatched, females searching for young do not respond to eggs. Stimuli indicating advanced stages of nesting are accomodated while stimuli of previous stages are rejected.

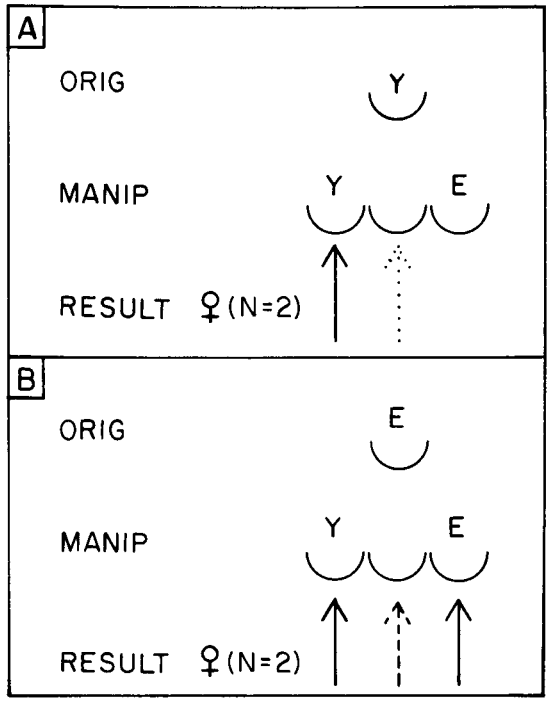

FIGURE 5. Responses of Barn Swallows with (A) young and (B) eggs to choices of eggs or young (see text). Symbols as in Figures 3 and 4.

RESPONSE TO NEST

I evaluated whether or not Barn Swallows recognize the nest itself or various characteristics of it. When the character of the nest

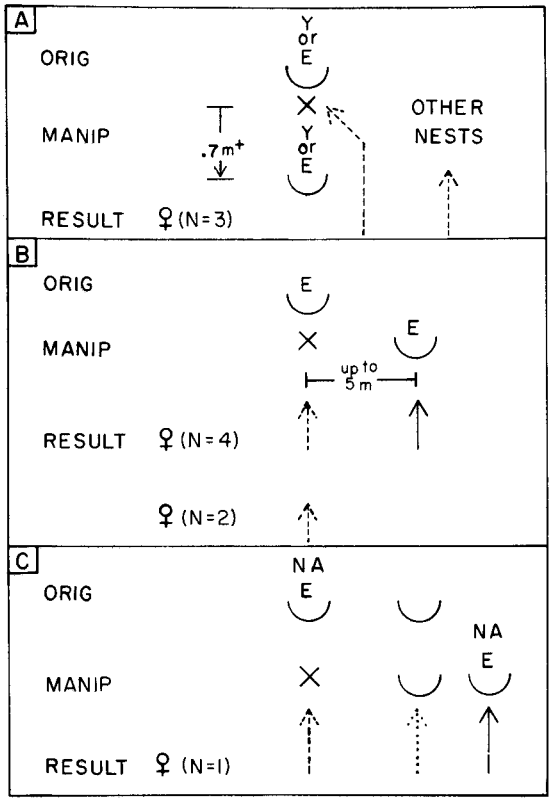

FIGURE 6. Responses of Barn Swallows to nest displacements (see text). Long dashed arrow in A indicates positive response to nest site. Other symbols as in Figures 3 and 4.

was changed by hanging paper towels from the lip (two cases), or adding excessive mud (two cases), females exhibited some distress but accepted the nests. When the lip of the nests was altered (three cases), no distress or hesitation was exhibited. When the lining of the nests was switched (three cases), females appeared "uncomfortable" at first, but accepted the change. In one case, a prominent guinea fowl feather (part of the lining of the nest) was moved to an empty nest nearby. After settling on her nest, the female rose, flew to the nest with the guinea fowl feather, picked at the feather, and then returned to incubate on her nest. The male of the pair flew into the culvert and perched on the lip of the nest with the guinea fowl feather. These results indicate that females are able to recognize gross changes in the nest and may recognize distinctive features of their nest.

Because cues used to recognize a nest may vary among individuals, females with eggs (two cases) or young (two cases) were given choices between their nests displaced immediately adjacent to the original locations, and nests with identical contents either at the old locations or immediately adjacent to the original locations. Females chose their own nests in three cases; in the fourth, the female exhibited attraction to her nest, hovering in front of it more often. In a similar experiment, the two nests (original and replicate) were placed 0.5 m (to the left and right, respectively) from the original location. The female still selected her nest. These findings indicate that females can recognize their own nests.

RESPONSE TO NEST SITE

The most distinctive attribute of the nesting situation is the nest site. Barn Swallows are able to locate their nest sites, but the cues used might differ from one bird to another. I conducted removal experiments to determine if females could locate the original nest sites if no nests were present. When nests, with eggs or young, were removed entirely (four cases), or displaced horizontally (six cases) or vertically (three cases), females would locate the original sites, hover in front of them, and often cling to the wall at the original nest locations. Nests displaced vertically downward 0.7 m or more below the original nest site were almost completely ignored (Fig. 6A). Although the females would cling to the original nest locations and look down on their nests, they never landed on or hovered in front of nests vertically displaced. They visited other nests nearby, but were chased from active nests by residing adults. These manipulations indicate that female Barn Swallows can orient to their nest site with no nest present. Vertical displacements indicate that nests must be in an appropriate position relative to the culvert ceiling to be accepted.

I also compared the relative attachment of females to their nest site with that to the combination of eggs and nest. As indicated earlier, when eggs were removed, but nests were still present (four cases), females would not attempt to find new nests with eggs. When nests with eggs (three cases) or eggs and newly-hatched young (one case) were moved 2–3 m and replaced with new nests (with identical contents), three of four females accepted the replacement nests (and contents). These results indicate that the females were more strongly attached to the nest—any nest—present at the original nest site. Also, as indicated earlier, females provided with choices of their nests and other nests near their nest sites selected their own nests. How far removed from the

original nest sites would females accept nests?

When nests and eggs were removed with no replacement (six cases), females would orient to original nest locations and then search adjacent areas, generally accepting the nearest nests with eggs (to a distance of up to 5 m) from which they were not chased (four cases; Fig. 6B). Two females did not accept nests at new nest locations (Fig. 6B). In two cases (one each for a female accepting and not accepting a nest), the female's original nest was not used in the manipulations. In one instance, a female's nest and eggs were relocated 5 m, then 4 m, then 3 m, and then 2 m from the original location toward the closest culvert entrance. She did not accept the nest in any of these cases. When this nest was then moved 2 m into the culvert from the original location, the nest was immediately accepted. Another nest moved 4 m into the culvert from its original location was not accepted; the female had been incubating at least 11 days. In the case where a nest with eggs was moved 5 m to a point where an empty nest was between the new location and the original location, the female located and accepted the original nest (Fig. 6C); this female had been incubating at least seven days. These last two experiments suggest that no increased attachment occurs with time. In general, nests displaced as much as 2 m horizontally were found and accepted. Sometimes this occurred for nests (with eggs) displaced more than 2 m.

In one series of manipulations (Fig. 7), a female (with nest containing eggs) was presented with a choice of her nest and a second nest, both with eggs and immediately adjacent to the original location. She investigated the second nest, but selected her nest. When her nest was moved 1 m away from the original location (manipulation 2), the female investigated both nests but did not accept either. When her nest (at the new location 1 m away) was moved 2.5 m farther from its original location and replaced by an unfamiliar nest (manipulation 3), the female selected the nest nearer the original location. In manipulation 4, her nest was moved back to the position of the first manipulation. The female investigated all three nests before selecting her own. In two other cases, females' nests with eggs were moved more than 2 m and replacement nests with eggs were placed at the original locations. The females accepted the replacement nests at the original locations. These results indicate that attachment to and recognition of

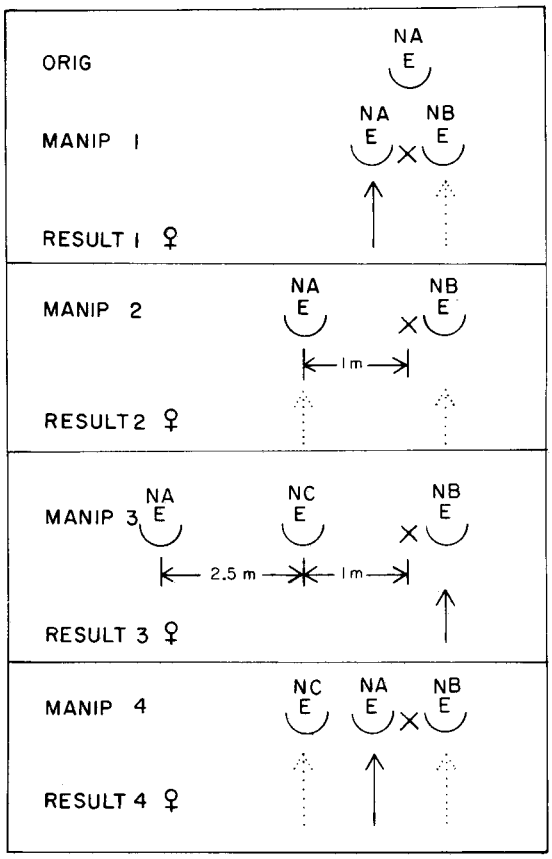

FIGURE 7. Responses of Barn Swallows to nest and nest site (see text). Symbols as in Figures 3 and 4.

the nest are secondary in importance to an attachment to the nest site.

Although females oriented to their nest sites, they could find nests (with eggs) that had been moved. These females continued to orient to the original nest sites before going to the relocated nests in subsequent visits (see Fig. 8A, manipulation 1). Females may find new locations by using cues for orientation to the old nest sites, or may still be attached to the original sites. To test which was the case, three females whose nests had been moved to new locations without replacements were given replacement nests with eggs at the original location of their nests. (Remember from previous experiments that females provided with substitute nests at the original locations did not attempt to find nests elsewhere.) The three females tested continued to orient to the original locations (with nests present), but then flew to the relocated original nests to incubate (see Fig. 8A, manipulation 2). In manipulation 3, eggs were removed from nests at the new locations. The females oriented as usual, flew to the nests at the new locations, and attempted to incubate. After

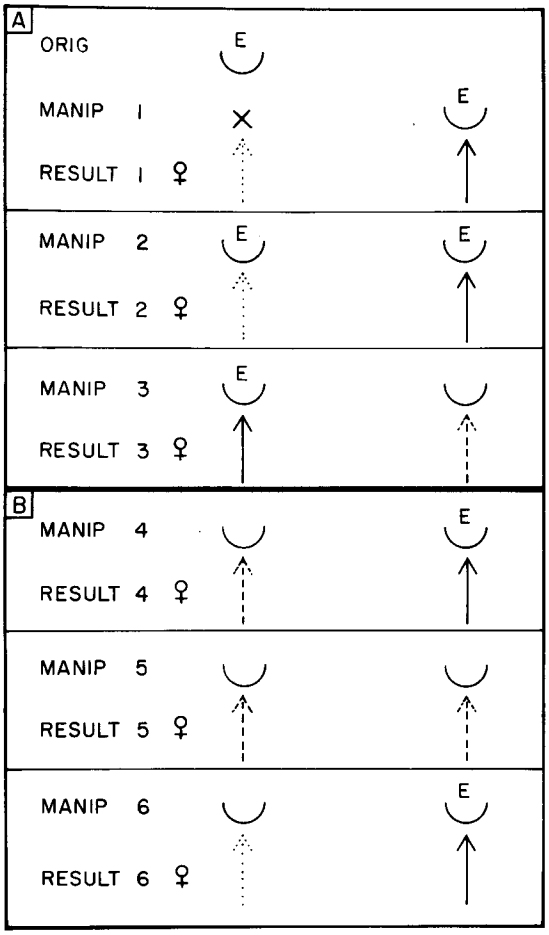

FIGURE 8. Responses of Barn Swallows to nest site and eggs (see text). Manipulation 1 refers to the same experiment depicted in Figure 6B. Unlike Figure 6B, however, the result shown for manipulation 1 indicates the response of female Barn Swallows *after* initial acceptance of the displacement nest. Symbols as in Figures 3 and 4.

attempting incubation, they left the displaced nest and went to the one at the original location and incubated. In subsequent visits, these females went directly to the original nest sites and incubated.

Extended experiments were performed with one female (Fig. 8B). In manipulation 4, her eggs were again moved to her original nest at the new location. She tried to incubate on the nest at the original location, then finally settled on the nest at the new location. In subsequent visits, this female first oriented on the original nest site, and then flew to the new location. For manipulation 5, her eggs were removed so that both nests were empty; the female attempted to incubate on the nest at the new location, then moved to the old location, attempted to incubate, and then alternated between nests. Finally, she visited the nests alternately, perching on the nest lips for several minutes at a time. When the eggs were restored to the nest at the new location (manipulation 6), the female came into the culvert, checked the nest at the original location, flew to the nest at the new location, and immediately incubated. She raised her young in this nest.

In any situation, when the eggs were removed, the females first attempted to incubate on the last sites where they had successfully incubated eggs. If these were new locations, they would then accept eggs at the original locations; if old locations were involved, females would accept eggs at the new locations. Barn Swallows can reorient very quickly to new nesting situations, but probably use old cues from previous situations. However, attachment to nest sites can be weakened when no stimulus for incubation is present, at least for females with eggs.

To test what cues may have been employed in orienting to nest site, several manipulations were performed. In one instance mentioned previously, where a "double nest" occurred naturally, a female was misled into picking the wrong nest site by simulating a "double nest" nearby (Fig. 4). In this case, the female's original nest was used in the simulated "double nest." In a second case, the simulated double nest (nests NB and NC in Fig. 9A) included the unused member of the "double nest" (NB). The female's original nest (NA), with eggs, was left in place (Fig. 9A); the female first perched on the next nest nearest the culvert entrance (ND in Fig. 9A) facing her nest location. She then flew to her nest (NA) and incubated. In one instance, where an artificial series of three nests was previously arranged (NC, NB, and NA in Fig. 9B), later manipulations misled a female (with original nest, NA) into temporarily selecting the wrong nest. Her first choice was ND (the middle nest in the new triplicate nest series NA, ND and NF) from which she was chased by a second female (the residing adult). She then momentarily landed on NA (her original nest now in the new triplicate series) before going to NE (the replacement nest at the original location) to incubate. The second female made the correct choice of her nest the first time, indicating that she was using different cues than the first female. In another case, where a nest (with eggs) was moved 3 m with a replacement nest at the original site (Fig. 9C), the female selected her relocated nest; in this case she may have been using a characteristic of the

nest to recognize the nest site. Cues for recognition of nest site appear to be learned and these cues differ among females. Characteristics of the nest are among the cues used in nest site recognition in many cases.

My observations of Barn Swallows' behavior during removal experiments gave additional insight as to the nature of cues used to orient to nest sites, and the locations of these cues. Females whose nests were manipulated often hovered at various locations near the nest sites (sometimes in front of the opposite wall of the culvert). When new nests were placed on culvert walls, some swallows occasionally investigated noisily, attracting other swallows to these recently modified locations. These observations (and results of manipulations given above) indicate that cues inside the culvert are used to orient to the nest sites. The following observations suggest that cues outside the culvert may also be used. Females whose nests were manipulated often flew in and out of the culverts several times, flew through the culverts or hovered at the culvert entrances. One isolated experiment was conducted on a culvert of north-south orientation which contained only two nests located directly opposite each other; one with eggs on the west wall, and a nest with large young on the east wall. I switched the eggs and young. The female of the nest with eggs flew in the north entrance and up to the nest (now with large young), was startled by the young, and left by the north entrance. She proceeded through a series of maneuvers alternating between short circular paths just outside the culvert and approaches to and retreats from her nest site. She exhibited distress during the first approaches, but never landed on her nest during the hour of observation. Sometimes she flew out for some distance from the culvert, and then back in, always approaching her nest on the west wall and never orienting to the opposite wall. She never accepted the young, but accepted her eggs when they were reintroduced into her nest.

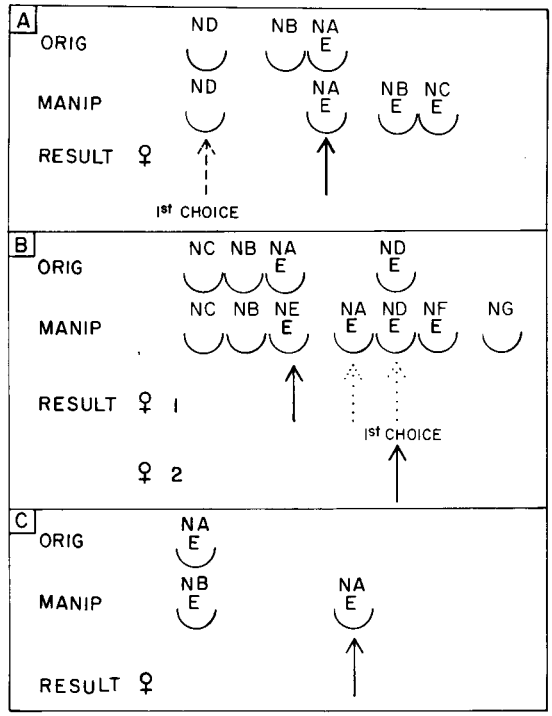

FIGURE 9. Responses of Barn Swallows to cues used in nest site recognition (see text). ND, NE, NF and NG designate particular nests; other symbols as in Figures 3 and 4.

RESPONSE OF MALES

Although extensive manipulations were not made to test specifically the responses of males to nesting situations, observations made during the experiments imply that attachment to and ability to recognize young and nests are perhaps greater in the males than the females. I observed males landing on their nests proportionately more often or quickly than females during various manipulations involving young. When conspicuous elements of the nest linings were moved, males in three of four cases tended to find the nests with the original linings and perch on them. In these instances, I recognized males belonging to a nesting pair behaviorally and by compatability with females, as males were not individually marked. In a few cases, where both the young and the nests were new, males showed no special ability to select nests.

DISCUSSION

If the context of the situation precludes making "errors," no selective pressure for egg or chick recognition should exist. Few species of birds recognize their own eggs specifically. Where recognition has been demonstrated, the species have (at best) rudimentary nests and nest in dense colonies, where eggs can easily be displaced (Johnson 1941, Buckley and Buckley 1972). These species possess highly variable eggs, a condition which undoubtedly aids in egg discrimination. Some passerines can discriminate between eggs of their species and those of other species or of a different color (Rensch 1925, Rothstein 1975). Many bird species, both passerine and non-passerine, accept eggs or egg-like objects placed in their nests.

Parasitism by conspecifics is highly unlikely among Barn Swallows. Copulation and egg laying are part of a sequence of behaviors which includes nest building. While it is possible for an occasional nest accident to create a situation for egg dumping, such behavior would not persist beyond that generation or that incident. Parasitism by Cuckoos (*Cuculus canorus*) has been observed in Barn Swallows in Europe (Dod 1892, Atkinson 1894, Heath 1973). Friedman (1963), citing only five cases, indicated that the Barn Swallow is an infrequent host of Brown-headed Cowbirds (*Molothrus ater*). I saw no evidence of parasitism by cowbirds in my study. Parasitism by cowbirds is unlikely in Barn Swallow colonies, since some swallows are always present. Barn Swallows have been seen mobbing Starling (*Sturnus vulgaris*) intruders (Snapp 1976) and would probably do the same to a cowbird. Thus Barn Swallows, as expected, do not recognize their own eggs specifically and accept eggs of another species and stones placed in their nests. These results are in agreement with those by Burtt (1977) on Barn Swallows and Tree Swallows (*Iridoprocne bicolor*), and Hoogland and Sherman (1976) on Bank Swallows.

Recognition of young has been demonstrated in several studies (e.g., Beer 1969, Buckley and Buckley 1972, Peek et al. 1972) and generally occurs just before the young become mobile (when the chance for error in progeny care is high). Barn Swallows (Burtt 1977), Bank Swallows (Hoogland and Sherman 1976), and Red-winged Blackbirds (Peek et al. 1972) recognize their own young near fledging age. However, Hoogland and Sherman (1976) found that Rough-winged Swallows (*Stelgidopteryx ruficollis*), a non-colonial species, could not discriminate their young from other young able to fly. The authors suggested that these differences between Bank and Rough-winged swallows were accounted for by colonial and non-colonial habits. Nesting pairs of Rough-winged Swallows may occupy habitats disjunct enough so that mixing of young is less likely than for other species tested.

Fledglings in colonial situations could benefit from attention of several adults. In Barn Swallow colonies, such behavior could be most advantageous for young of early nesting individuals. Burtt (1977), however, presented evidence of aggression toward alien fledged young by adult Barn Swallows. In my study, Barn Swallows demonstrated an ability to recognize the developmental stage of young, but accepted young in their nests even if these young were at a different stage. Fledged or nearly fledged young were not introduced into nests with young at earlier stages in either Burtt's or my study.

In most species tested, the nest site was more important than any other aspect of the nesting situation (Lashley 1915, Meise 1933, Allen and Mangels 1940). Nest site would certainly be the most distinctive aspect of the nesting situation. Proper orientation to the nest site would avoid contributing to competing genotypes in both colonial and non-colonial species and would be favored by selection. Colonial species are expected to be most rigid in their response to nest site. Black-crowned Night Herons (*Nycticorax nycticorax*) preferred to incubate blocks of wood rather than their own eggs in nests placed nearby (Allen and Mangels 1940). Negative responses to nests moved short distances have also been recorded for Sooty Terns (Lashley 1915) and House Sparrows (Meise 1933). Herring Gulls did accept nests displaced about 30 cm (Tinbergen 1953). However, Peek et al. (1972) and Nero and Emlen (1951) found Red-winged Blackbirds, a non-colonial species, would find nests displaced considerable distances. Responses of Barn Swallows to nest site in this study were intermediate between those of these colonial species and of Red-winged Blackbirds.

In a New York study (Snapp 1976), Barn Swallows rarely nested less than 3 m apart. I found 60% of the active nests were closer than 3 m to another active nest, indicating that swallows were more densely packed in the Oklahoma culverts. Barn Swallows prefer to feed along edge habitats, where wind speeds are reduced and insects are more abundant (Samuel 1971). Heavy-duty roads in Oklahoma provide a continuous wind break (whether in open or wooded terrain), and swallows may be attracted to these strips of suitable habitat. Swallows nesting in the longest culverts, or in colonies of less than 10 pairs, seldom occupied the middle sections of culverts; nests were concentrated near the entrances. This crowding may have been a factor in my study, modifying responses to nest site which may be more similar to responses of non-colonial species in other situations.

While kinesthetic memory may be credited for locating nest sites, Barn Swallows were occasionally misled by changes in the position of various cues. It is likely that response to the nest site in this species is de-

termined by several, if not many, visual cues which vary among individuals. Barn Swallows reoriented quickly to moved nests. The birds in this study usually oriented to the original locations first, and then to new locations, a simple adjustment. The new location then became the nest site and reorienting to the original situation meant readjusting in the same manner as after the first manipulation. Nests left in new locations for several days were approached directly. Such response abilities are probably advantageous for locating nests in situations where cues for nest site recognition are altered or destroyed. The possibility of contributing to foreign genotypes is precluded by the nest defense of residing adult Barn Swallows.

Attachment to nest and nest site may be interrelated. Two female Red-winged Blackbirds did select their nests 0.5 m away from their nest site where a replacement nest was located (Peek et al. 1972). However, this occurred after one day of incubating on the replacement nest at the original nest site. Barn Swallows could locate their nests when given choices near their original nest sites. When their nests were displaced more than 1 m, with no replacement, the birds usually found their nests. One female went directly to her nest displaced 3 m with a replacement at the original site (Fig. 9C). This may indicate that the nest itself is among the cues used to orient to the nest site. Barn Swallows recognize the nest, and it may be used to recognize the nest site.

Barn Swallows could be coerced into taking care of two nests under certain circumstances (Figs. 3B, 4 and 5B). This capability has not been tested in other species, but may be common in multi-brooded species. Several "double nests" (nests placed close together) may be results of pairs beginning second nestings before the first has been completed. In only one case was a nest with a complete clutch of warm eggs situated next to a nest with almost-fledged young. Since Barn Swallows defend an area near their nests, such a situation is best explained by assuming that both nests belonged to one pair of adults.

SUMMARY

Responses of Barn Swallows to eggs, young, nests and nest sites were determined in colonies located in culverts under roads in Oklahoma. Active nesting pairs maintained some minimum distance between nests, but 60% of the occupied nests were less than 3 m from another active nest.

Female Barn Swallows do not recognize their own eggs specifically and cannot distinguish conspecific eggs from other eggs or egg-like objects placed in their nests. Incubation behavior appears to be controlled internally and the presence of eggs is not required to initiate the behavior. Tactile stimulation of eggs, however, is necessary to maintain incubation behavior.

Barn Swallows could not distinguish their own young, up to at least 11 days of age. They could distinguish young of different developmental stages but accepted such young placed in their nests. A few females with eggs could be coerced to attend two nests simultaneously, and such behavior may reflect an adaptive response of a multiple-brooded species.

Females selected their own nests in multiple-nest situations if nests were placed near the original nest sites, but they did not show any preference for their nests (with eggs) displaced more than 2 m from the original nest sites. The swallows were strongly attached to their nest sites and recognition of nest is part of recognition of the nest site.

Swallows oriented to their nest sites with no nest present. Manipulation of prominent nest site features misled some swallows into selecting nests at sites other than their own, indicating that visual cues are used for recognition of the site. These cues varied greatly among individuals. Cues both in and outside of the culverts were used for orientation. The swallows quickly adapted to new nesting situations.

Barn Swallows responded most strongly to the nest site, then nest, and then eggs or young. They found nests which had been moved, but only if no replacement nest was present at the original nest site. They did not accept nests displaced vertically downward.

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