

BEHAVIOR OF THE PURPLE MARTIN

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THIS paper is a descriptive account of reproductive, aggressive, and group behavior of Purple Martins (*Progne subis*). Both of us took field notes concurrently in 1959 and 1960 at a colony of Purple Martins in Lawrence, Douglas County, Kansas, and these notes form the chief materials of this report. Hardy has additional, qualitative notes on martins at a colony-house in Murphysboro, Jackson County, Illinois, covering the period 1938 to 1952. Both of us also used other colonies, chiefly in Kansas, to study certain matters that could not be studied at a single colony. The colony-house in Kansas had eight compartments and housed six pairs of martins both in 1959 and 1960. The colony-house in Illinois had 14 compartments. Notes were taken on the spot at the time of observation; 6× and 7× binoculars and a small tape recorder, from which notes were later transcribed onto paper, were also used. Birds were marked individually with paints and colored plastic leg-bands. Observations on contents of compartments were made possible by use of sliding panels on the compartments.

BREEDING SCHEDULE, PAIR-FORMATION, AND NEST-BUILDING

Breeding schedule.—The timing of events in the annual reproductive cycle of the Purple Martin is unusual in that the several activities are greatly spread out in time, compared with other birds. Purple Martins arrive in Kansas each year between 5 and 31 March; modal date of arrival is in the five-day period 21 to 25 March. Remarkably, it is not until after mid-May that eggs are laid, and the peak of egg-laying occurs in the first week of June. Thus, there is a time interval of about two months between dates of arrival and of egg-laying by martins. The prolonged gap between arrival and egg-laying could conceivably be due to either early arrival or late egg-laying (without attempting in these words to explain the gap). We may presume that timing of inception of breeding is partly a function of adaptation by the species to the seasonality of its food supply. Moreover, inception of breeding in May is advantageous in that the birds are able to meet the many hazards of late spring storms without the added responsibility of caring for eggs or young. Both of these considerations are useful in our thinking, for they emphasize that the known timing of breeding by martins has adaptive value. It is, as we shall see later, early arrival, rather than late breeding, that is responsible for the characteristic schedule of martins in spring.

A comparable schedule in spring is characteristic of the species in other regions of the United States. In Jackson County, Illinois, Hardy found that martins usually arrive between 5 and 15 March, and that most of the adult

birds are established in colony-houses by 25 March; yet, egg-laying usually occurs from mid-May to early June. In the vicinity of Ann Arbor, Michigan, martins arrive in the first week of April and lay eggs in the first week of June (Allen and Nice, 1952:611, 624); in South Carolina, martins arrive in early or mid-February and lay eggs in late April and early May (Sprunt and Chamberlain, 1949:366-367); in Minnesota, martins arrive in the first week of April and lay eggs in late May and early June (Roberts, 1932:53); in Maine, martins arrive in late April and lay eggs in early or mid-June (Knight, 1908:450-451). The period between arrival and egg-laying at any locality is about two months. This is in contrast with other North American swallows at mid-latitudes, most of which show a period of four to six weeks between arrival and egg-laying at one locality.

We are aware of only one exception to the characteristic long delay between arrival and egg-laying in the martin, but this exception is an important one. In 1946, at Murphysboro, Illinois, Hardy recorded the first arrival of martins on 5 March; most adults were in residence by mid-March, nest-building began on 24 March, eggs were laid about mid-April, and young were on the wing by early June. The delay in 1946 was therefore about six weeks for some birds, and less for others, demonstrating that modification of the characteristic time-lag is possible. The significance of this unusual schedule lies in the fact that the growing season in southern Illinois was exceptionally early in 1946; the general climate was mild, warm temperatures predominated, and trees were fully leaved by early April.

An even more unusual response by the Illinois martins to the environment of that year was that a few birds had two broods; second sets of young were on the wing in late July and early August. Parenthetically, we may note that double-broodedness has heretofore been claimed for the Purple Martin only by Audubon (1832:119) for the southern United States, eliciting long-term discussion to the contrary (see Allen and Nice, 1952:624-625). Audubon said two broods were regular, rather than exceptional, and that three broods were raised in Louisiana; this must be discounted and attributed to excessive zeal (Lowery, 1955:376).

The information discussed above suggests that time of breeding is a correlate of favorable weather and its associated influence on the timing of the biological growing season. In the absence of quantitative data it is difficult to assign chief importance to any one environmental factor or to any set of such factors, but we assume that unusual, mild weather and an early growing season are closely associated with an unusual, early breeding season in martins. By extension, we also assume that normal weather and regular timing of the growing season are associated with regular timing of breeding in martins.

Schedules of breeding of martins in northeastern Kansas are what would be expected on the basis of evidence on breeding of other swallows in the area. Data collected over several years concerning timing of breeding of five species of swallows in northeastern Kansas (Fig. 1) show that for all single-brooded species most clutches of eggs are laid in the first third of June, and the lone double-brooded species is not far from this in its first nesting effort. Such concordance in schedule in five related species suggests common response to dominant features of the general environment (those features that are factors of and responsible for the timing of the biological growing season). Because these breeding schedules show average responses of these birds to average environmental conditions, we feel reasonably sure that timing of egg-laying in the martin can be considered completely "normal." This allows us to focus on the significant aspect of the spring schedule of martins: the two-month delay between arrival and egg-laying is truly a result of early arrival, not late egg-laying.

A satisfactory case can be made for the thesis that early arrival of martins is related to problems involved in securing a nesting cavity, something with which secondary hole-nesters generally have to contend (see, for example, Nice, 1957:315). If this is true, the character of early arrival must be a result of intraspecific "competition" for nesting cavities in past time, prior to the relatively recent availability of man-made colony-houses. Up to a point, individuals arriving early have little difficulty in finding a hole-cavity for breeding; with a scarcity of cavities, late arrivals would find fewer breeding sites than early arrivals. Such differential distribution of breeding sites would tend to give early birds a pronounced reproductive advantage over late birds, and if the tendency to arrive early on breeding grounds were genetically based, "early" genotypes would eventually come to predominate in populations. Exceedingly early birds, on the other hand, would tend over all to leave fewer offspring than others, for such individuals are periodically eliminated by severe spring weather and associated starvation. We must at this time assume that general time of arrival in martins is genetically determined.

Some support for this idea comes from the migratory and breeding chronologies of Tree Swallows (*Iridoprocne bicolor*). In this species the time between arrival and egg-laying is also prolonged and is second in magnitude only to that of the martin (see Paynter, 1954:36). The Tree Swallow is the only other North American swallow that is basically a secondary tree-hole nester.

Formation of the pair-bond.—Perhaps one-quarter of adult pairs arrive in Kansas as pairs; formation of the pair-bond presumably has occurred the previous year, for we think it unlikely that pair-formation occurs away from

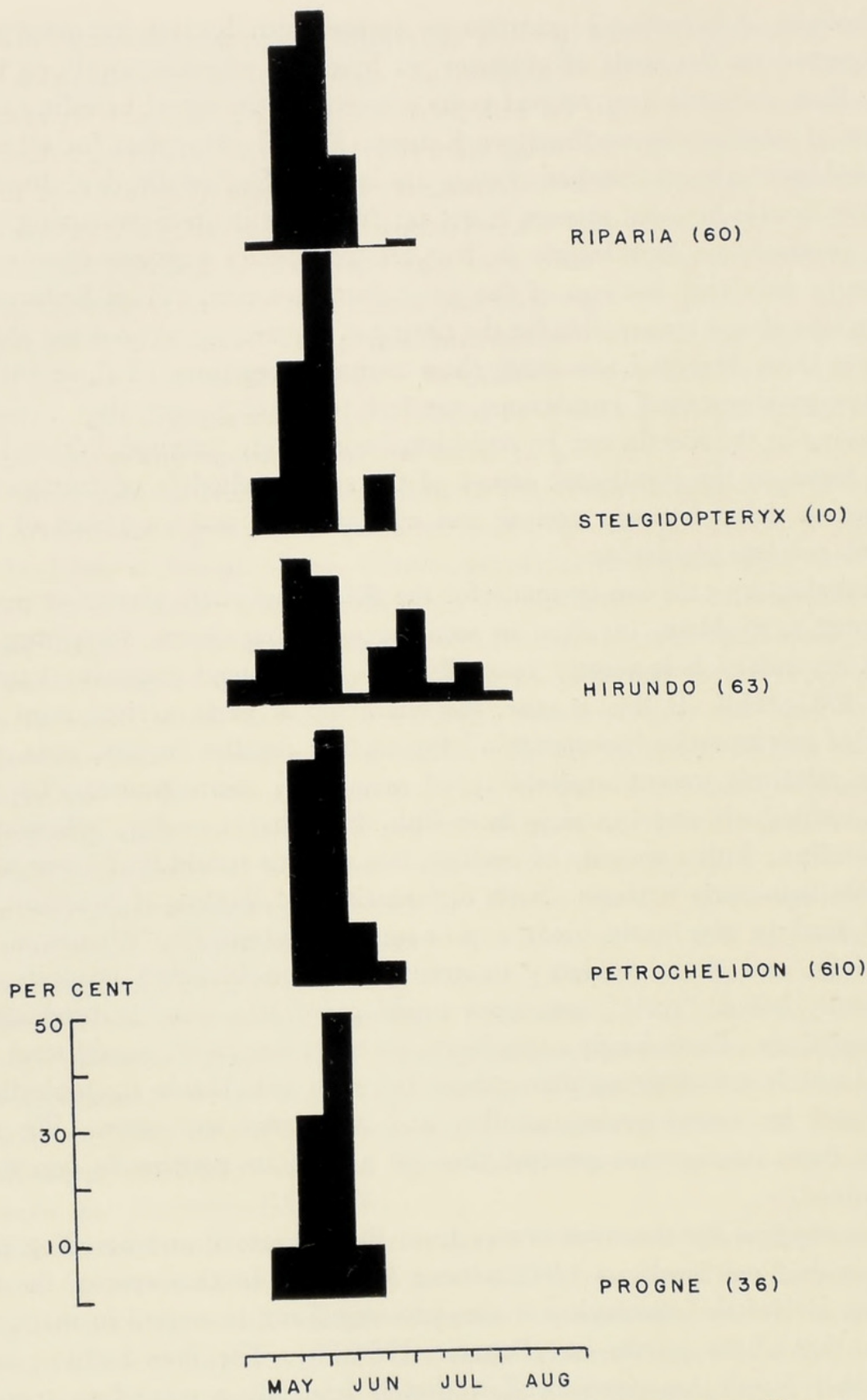


FIG. 1. Breeding seasons of five species of swallows in northeastern Kansas as indicated by dates of completion of clutches. Columns represent per cent frequency of clutch completion in 10-day intervals, with the 5th, 15th, and 25th of each month as medians. Single-peaked histograms for the Bank Swallow, Rough-winged Swallow, Cliff Swallow, and Purple Martin are representative of breeding seasons of single-brooded species; the bimodal histogram for the Barn Swallow is characteristic of a double-brooded species.

colony-houses. Nearly all birds arriving in the first migratory wave are paired on arrival, but those of later arrival are less frequently paired. All first-year birds seem to arrive without mates, and this supports the idea that pair-formation does not occur on wintering grounds. Unpaired birds, adults and first-year individuals alike, show varying degrees of a tendency toward sexual behavior. Those most likely to form pairs soon after arrival are those that seem least aggressive toward members of the opposite sex.

No postures of any degree of ritual expression are involved in epigamy; the vocalizations and physical attitudes are the same as those that result in the formation of temporary social units, such as groups "investigating" a set of nest boxes or groups engaged in preening or foraging. This is well to emphasize, because formation of pairs seems in part dependent on the fact that the birds engage in periodic flurries of group behavior. Yet, in the final analysis, it is not such group behavior that results in formation of the pair-bond; given the matrix of social interaction around colony-houses, the final establishment of a pair is a function of choice by a female.

The typical pair-bond comes about in the following way. A male sets up operations at one or two compartments in a colony-house; here he roosts, sits when calling to other martins, and acts aggressively in the presence of other males. Eventually, among the many females that periodically visit the colony-house, one or two display interest in the male and his site. Initially it is the site that seems to be most attractive to the females, but those sites lacking males are never used as much as those having males in attendance. Females go in and out of the boxes, fight among themselves, and accompany the male, and *vice versa*, in aerial activities. A male seems to show no preference for one female but is likely to encourage the entry of any female into a compartment; "encouragement" is effected by the male going into and out of the aperture, and by his profuse song and a display flight probably identical with the Claiming-Reclaiming display (which see below under aggressive behavior). These display flights often terminate in a dive toward and rapid entry into the compartment, and may serve to "steer" to the box females that seem on the verge of leaving the vicinity of the colony-house. In time the male and a female show some increased awareness of the presence of each other, and with no overt sign that a bond has been established, subsequently behave as a pair: they tend to forage, preen, loaf, and fly with the group together; they have elaborate "greeting" vocalizations; and they show excitement at seeing each other at a distance. It may take from three hours to three days for such a pair to become established, but in the absence of extensive observations on marked individuals we do not know what the most characteristic time period really is.

The events mentioned above that contribute to formation of the pair-bond

are most evident in birds active in early morning hours, from dawn until 9:00 to 10:00 AM. It is in this time that the social activity of the flock is greatest, and the time that individual martins having weak bonds to the colony-house and to other individuals are most likely to strengthen these bonds. This is probably because all the resident birds are present, are strongly advertising their ownership of compartments, but at the same time are most active in encouraging the presence of new birds at the colony-house. The least aggressive birds can at this time appear to lose their equivocal behavior and assume the attitudes characteristic of established, resident birds.

Pair-bonds seemingly formed in morning hours are subject to a kind of test in the evening prior to roosting. At this time birds with established residency and strong pair-bonds act with an air of confidence and forcefully exhibit ownership of a part of the colony-house. More importantly, in the evening established birds show a lesser tendency to accept the presence of new pairs. Thus, new pair-bonds (and "residence-bonds") that seemed strong eight hours earlier can disintegrate at nightfall. Results of such disintegration vary; the pair may actually separate and occupy different compartments, one or both birds may depart, or they may attempt singly to crowd in with established pairs and usually end up roosting on porches of the colony-house.

Pair-formation, establishment of residence, and formation of the colony are closely bound together, as indicated above. The following examination of these activities will emphasize just how close such relationships can be.

In 1959, the first pair of adults, P-1, to establish residence at the colony-house of eight compartments showed marked aggressive behavior throughout the season. This behavior possibly was responsible for a relatively slow increase in colony size and the ultimate number of but six breeding pairs. Five of these were of first-year birds and only one of these managed to occupy a compartment on the side of the colony-house occupied by P-1. P-1 established residence on 10 April and initially claimed all eight compartments in the house, roosting at one time or another in most of them. Gradually they concentrated their activity on two compartments, one above the other, on the southeast side of the house.

A second pair of adults, P-2, arrived at the house shortly after P-1 and likewise showed preference for the southeast side of the house, although the entire northwest side was empty. There was much aggressive interference by P-1 into the activities of P-2, and consequently we were never certain that P-2 was firmly paired. They usually roosted in separate compartments and were nearly always silent, which may be taken as evidence of an equivocal relationship to each other and to the house. Male No. 2 frequently showed behavior typical of an established male in the morning, but his behavior at dusk was that of a nonresident.

Until 22 April P-2 was in evidence, but the two only occasionally showed attachment to one another. Once it seemed that they might roost together, but the male attacked the female, they fought, and eventually roosted in separate compartments. By 26 April P-2 had deserted the house. P-1 participated in the failure of P-2 to establish at the colony by occasionally preventing their entrance into compartments, causing them to fly from the house, and by interfering at their attempts at intrapair sociality.

On 22 April P-1 began to collect nesting material and to carry it to compartments on both sides of the house. However, by 26 April the building activity was confined to two compartments on the southeast side of the house. Other martins then became frequent visitors to the house. On 1 May another adult pair, P-3, appeared; P-3 seemed to have a strong pair-bond and they began to contend with P-1 for space on the southeast side of the house. The fighting was occasionally severe, but P-3 did acquire use of the two remaining compartments on the southeast side. Yet, conflict did not cease at this point, for P-3 also showed tendencies toward using all compartments on the southeast side. P-3 remained at the house only until early June.

The ultimate failure of P-3 to maintain residence probably was the result of their increased fighting with other birds, all of which were subadults. These increased in numbers after the second week in May. Adult birds are clearly dominant in aggression with younger birds, but as long as conditions of space permit, little conflict occurs between the two age groups. Thus, three first-year pairs became established on the northwest side of the house with no aggressive interaction from P-1 or P-3. Two of these pairs themselves attempted to hold the one remaining compartment on the northwest and vigorously attacked any birds attempting to claim the box.

This concerted action by these first-year pairs seemed to result in the fact that the next three males (all of the first year) that attempted to establish residence did so first on the southeast, where two compartments seemed to be available. The three males appeared in succession so that there was continual conflict on the southeast between them and P-1 and P-3. P-1 seemed to have no difficulty holding two compartments, but P-3 was unsuccessful. On 2 June all other established pairs had at least one egg, but P-3, the second pair to become established, had none.

P-3 did in fact maintain residence in the face of conflict with Male 6 (which left the colony) and Male 7 (which with great difficulty claimed the remaining compartment on the northwest), but deserted the colony following challenge from P-10, a first-year pair that of necessity tried to claim space on the southeast. P-10 eventually laid eggs in the compartment farthest from the main compartment of P-1.

The first-year pairs that established residence on the northwest side were

initially represented by males and each was later joined by a female. There was no "competition" between males for females. In each instance females seemed to choose a combination of a male and compartment. Once a female for several days delayed "choice" between two males. The choice of one of the males was influenced by the intermittent hostility of the other male toward the female. Significantly, this male frequently prevented the female from entering his compartment.

We may summarize the main points concerning pair-formation and establishment of residence as follows:

(1) Males select compartments as sites of social and (ultimately) sexual activity.

(2) Being variably sporadic to concerted heterosexual group behavior allows individuals, chiefly females, to find sites of eventual sexual activity.

(3) Partial disappearance of dominant aggressive behavior in both sexes enhances formation of the pair-bond.

(4) Females have definitive control over pair-formation, because they choose a nest box-male combination, and not a male alone or a nest box alone.

These points apply equally to adults and first-year birds. It should be emphasized, however, that first-year birds arrive on breeding grounds later than adults and probably never, or infrequently, are paired on arrival. They avoid conflict with adults more often than adults avoid conflict with each other. Yet, first-year birds occasionally contend more readily against small numbers of established adults than against large numbers of established sub-adults. The description of pair-formation by Allen and Nice (1952:617-619) essentially agrees with ours.

It is evident that formation of the pair-bond can be relatively obscure, especially with any one pair, but the bond itself is not obscure; it is typical of pair-bonds found in migratory passerine birds. As such it differs notably from the pair-bonds of certain other swallows. Emlen (1954:28) wrote of "mutual tolerance" in Cliff Swallows (*Petrochelidon pyrrhonota*), a pair-bond similar to an armed truce, resulting from a welter of vague, early meetings, chaotic aggression, and site-tenacity. Peterson's remarks (1955:240-241) concerning Bank Swallows (*Riparia riparia*) suggest that this species has a pair-bond similar to that of the Cliff Swallow. It is possible that "mutual tolerance" describes a condition characteristic only of sexually isomorphic swallows. Adult martins are clearly dimorphic sexually; males know males from females, and *vice versa*. The important thing is that there is no ill-defined aggression in martins, as there is in Cliff Swallows; males treat females one way and males another. That the primary factor governing this dichotomous aggressive behavior is visual perception of sex is strongly

indicated by the fact that adult males usually treat first-year males as though they were females, which they resemble in plumage.

However, visual perception of sex includes awareness both of morphological and behavioral characters. This is shown by the behavior of established adults toward the occasional male in adult plumage that arrives late in the season. These atypical adult males are not only late, as are first-year birds, but behave otherwise like younger birds. This may be due to a hormonal regime similar to that of first-year birds. In any event, although they are indistinguishable by plumage from adult males, they are reacted to by adults in precisely the same manner as are first-year birds, and they typically contend with first-year birds for space in the colony-house. On 12 May 1959, such an adult male appeared at the colony in Lawrence and began to investigate the northwest side of the house, where one empty compartment existed amid three others held by first-year birds. This adult ignored the southeast side of the house where two compartments were potentially available but where two pairs of adults were established. This late adult was eventually driven from the colony by actions of two first-year males that attempted to hold the empty compartment.

Nest-building.—Purple Martins start to bring nesting material to compartments about a month before eggs are laid. In 1959 building began on 22 April and first eggs were laid on 30 May; in 1960 building began on 16 April and first eggs were laid on 19 May. Typically, building proceeds for about three days, ceases for perhaps two weeks, and then is evident in morning hours until eggs are laid. Materials brought in the first three days include dead leaves, sticks, and papers; in the week or two prior to laying eggs, mud and sticks are brought, to form a relatively solid mat near the entry hole. The mat slopes toward the rear of the box and has a small, shallow cup.

Also just prior to laying eggs, and continuing through much of the time of incubation, pieces of fresh, green leaves are brought by both sexes to the nest. This material is not nesting material in one sense, for not only is the nest essentially completed when the pieces are brought, but the leaves are placed around the rim of the cup, not initially in the cup as Allen claimed (Allen and Nice, 1952:622). Eventually the pieces of leaves dry out, curl up and get worked into the body of the nest. Their primary function, however, is still to be determined; this function probably has nothing to do with nest-building. The oldest hypothesis concerning use of the leaves is that, as the leaves dry, moisture is given off that makes the microclimate of the eggs more nearly optimal. There is no good evidence that this is so.

Another, and more nearly plausible, hypothesis can be derived from the work of Dr. Frank W. Preston and Mr. Earl Shriver (personal communication). Preston and Shriver have been investigating the habit of certain

hawks (Accipitridae) in bringing green tree limbs to nest sites in time of late incubation and feeding young. At present it appears that decay of the vegetation results in release of hydrocyanic acid, notably toxic to animals. The HCN is conceivably a control of numbers of the variable and numerous arthropod and bacterial parasites that habitually live in the detritus of a hawk's nest and which occasionally contribute to mortality of nestling hawks. A martin nest also offers an exceedingly rich medium in which parasites, chiefly bird mites in Kansas, develop large populations. It is possible that the green leaves brought by martins also release a fumigant and thus act as a check on the development of large populations of such parasites.

AGGRESSIVE BEHAVIOR

Aggression in Purple Martins is effected by a few simple postures and sounds. This is true when territory is being maintained and in interspecific exchanges. Aggressive behavior in martins may occasionally be as vigorous as any recorded in birds, but most often consists of postural and auditory threat. Although most birds rely on threat, rather than actual physical contact, the large role that threat plays in martin aggression seems particularly adaptive because these birds are organized at all times of the year into working social units: they migrate, roost, forage, preen, seek nesting material, etc., in flocks, and they breed in colonies. Any tendency toward a breaking up of such groups would presumably rank as non-adaptive. Thus, the only real instances of physical violence to be seen in martins result from flagrant trespass of the ultimate territorial bound, the nest box itself. Moreover, such flagrant trespass can itself be tolerated, and trespassers are frequently allowed to move away without being bitten, hit with wings, or otherwise assaulted.

Such variation in response to trespass is not an indication of territorial ambivalence in martins, for individuals do maintain areas of exclusive use in and around compartments. One of the first activities of the newly arrived male is to find and take possession of a compartment, or if early in the season, two nest boxes. The box itself and the perch around the entry hole are maintained by the male, and later the pair, for his or their exclusive use. Territorial agonism drops in intensity as eggs and young appear and the adults are occupied with primary breeding activities. The frequency of occurrence of intruders also drops at this time because most potential intruders are themselves occupied with breeding activities.

Artificial nest boxes probably only in part duplicate the naturally occurring cavities to which the birds are primarily adapted. The chief new element in the artificial situation is one of increase in colonial density, and it would be to this feature that martins might be expected to be least well adapted. Nevertheless, the only significant item of behavior supporting such expecta-

tion is the action of a strong male holding exclusively more than one compartment throughout one season. This conceivably can be considered not a true adaptation to colonial nesting, because it obviously prevents at least one additional pair from nesting and attempting to raise young. We think it is unlikely that this behavior is a part of a mechanism limiting density, for less than half the adult males behave in this fashion, and its incidence does not seem to rise under conditions of high density.

Postures.—The chief posture of threat may be called the Horizontal Threat posture: individuals orient on a perch so that the axes of their bodies run parallel with the surface on which they are perched, their necks are neither extended nor withdrawn, and their feathers are moderately appressed save for those of the nuchal area, which are usually erected in a short crest. The wings and tails are flicked upward repeatedly; such flicking is, however, typical of anxiety in any context, not only that associated with threatening attitudes. In territorial agonism singing is frequent. In a period of intense social activity around the colony-house, a frequently singing and aggressive male seems to proclaim residence by song; the more another male exhibits exploratory behavior toward the house or one of its compartments, the more vigorous and frequent is the song of the resident.

Song also accompanies another non-ritualized display that we call the Claiming-Reclaiming display. A male thus engaged exhibits occupancy of a compartment over and over again by repeatedly entering and emerging from the compartment, usually about as fast as he can move. This process is punctuated by occasional stops for song when the bird perches in the compartment and projects its head slightly through the hole. The bright yellow lining of the mouth is strikingly revealed by song in such a situation, for the color is emphasized by its contrast with the bird's dark head in the even darker hole.

Claiming and reclaiming of the compartment involves a flight display (which we consider also to be an element in group behavior). A male flies from the house, sails in a wide arc having as much as a half-mile radius, and abruptly returns to the house, terminating the flight in a steep dive with wings flapping as brakes in a curiously lowered fashion. In the same motion of landing the bird enters the compartment, turns, projects its head slightly from the hole, and sings vociferously. Claiming-Reclaiming as such seems to be chiefly a territorial display with some aggressive content. It probably prevents naive, nonresident birds from investigating an occupied compartment and thus eliminates one cause of physical contact. The behavior may also reinforce the bond of residence of the displaying bird.

On the other hand, the flight component of the Claiming-Reclaiming display unquestionably serves to attract other birds to the colony-house, espe-

cially early in the season. Such attraction is discussed below under considerations of group behavior.

The Gape, in which the mouth is opened widely directly toward an individual to be threatened and which is sometimes accompanied by a short lunge or feint, is used chiefly in high-intensity threat display. Gaping is also used under conditions of low-intensity threat, or interspecifically (most frequently with House Sparrows, *Passer domesticus*). In any such rendering, gaping is almost always effected from the Horizontal Threat posture with the bird standing on extended legs. Gaping sometimes precedes an actual attack; the Gape can therefore be considered to be a signal of intention to attack. Both sexes use the Gape. Females occasionally thereby threaten males, and the rare instances of females attacking males are always signaled by a Gape.

What may be called heterosexual gaping, wherein a squatting male gapes at a female (the reverse seems not to occur), seems to be of a different order of behavior, possibly related to solicitation of some thing or action, and is at present obscure. However, the male uses a posture characteristic of nestlings begging food, suggesting an "appeasement" display. "Appeasement" seemingly to reduce intraspecific aggression has been commented on for finches (Hinde, 1956:12-13). Hinde made the point that "appeasement" associated with connubial or courtship feeding has a possible function in habituating the male and female of a pair to one another. Although it is necessary to note the possible operation of such a mechanism in Purple Martins, because the posture suggests that of a fledgling begging for food, connubial feeding has never been recorded for these birds.

Bill-snapping, in which the mandibles are forcibly brought together in an audible, high-frequency *click*, is a frequent accompaniment of the feints or lunges from the Horizontal Threat posture; such snapping is less common than gaping.

The Stooped-Submissive posture is relatively infrequent but is one of the most distinctive attitudes of Purple Martins. It is assumed by a male that has been decisively defeated in an aggressive encounter with another male. The defeated martin flies with the upper back humped, with head lowered, and with the tail held low; the rectrices are abnormally constricted so that the tail resembles a tapered spine (Fig. 2). The action in flight is labored and seems to lack the coordination otherwise typical of martins. The bird may remain in this posture when perched; the wings are drooped and the crown feathers are greatly appressed. Such a posture may be maintained for a few seconds or as long as a half-hour. Emergence from the posture, however, is usually gradual. The posture seems to indicate complete defeat of the individual; it is significant that no further aggression is directed toward



FIG. 2 (upper left). The Stooped-Submissive flight posture, a signal of defeat following a fight in male Purple Martins; abnormally uncoordinated flight and constricted rectrices are characteristic.

FIG. 3 (upper right). Male Purple Martin showing the white tuft of feathers exposed laterodorsally following scratching of the head.

FIG. 4 (lower). Sunning posture of the Purple Martin. There are various degrees of expression of this posture; the feathers of head and rump may be ruffled more extensively, the wings may be partly opened, and the bird may be lying nearly on its side. Drawing made from a 35 mm Ektachrome transparency.

Drawings by Robert M. Mengel.

the vanquished bird so long as it maintains the Stooped-Submissive posture. We have never seen a female martin in this posture.

Vocalizations.—The song of the male martin is a complex series of distinct notes running three or four seconds in time. An initial series of notes, most frequently just two (phonetically, *chürr*), is followed by two notes (*sweet*) of different quality, and is rounded off by a warbled set of heavy, guttural, but musical clicks. The song may be given in aggressive interchanges, in the greeting of a mate on its return, or in proclamation of territoriality. Only in aggression is the song rendered from the Horizontal Threat posture so that apparently the same set of sounds has different meanings when used with

different postural attitudes and in different social situations. It is well to emphasize that the distinct elements of this complex song (but, chiefly the doublets) are frequently used by themselves, and usually not in aggressive exchanges; such use is described below under considerations of group behavior.

The notes of alarm, given when the birds are frightened by a hawk or cat or human are *kiv-kiv*, *kiv kiv keer keer keer keer*, *kiv keer keer*. *Kiv* is uninflected; *keer* has a downward inflection. The initial notes *kiv-kiv* may actually be the important notes of stress and alarm; the notes *keer*, etc., are given while the birds are in flight or engaged in mobbing the agent of alarm. *Kiv* and *keer* may also be given under conditions of intraspecific stress, but more commonly the birds use the social calls *chürr* and *sweet*. Infrequently (specifically, near a mounted dummy Long-eared Owl, *Asio otus*, placed near the colony), a note of possible alarm, probably denoting strong fear, is given; phonetically this is *yenk*.

The note of high-intensity aggression is *zwrack*! This note was used by a single male in aerial pursuit of a Sparrow Hawk (*Falco sparverius*) and by two birds harassing a House Wren (*Troglodytes aedon*) that ventured onto the colony-house.

There are minor differences between vocalizations of males and females and of adults and first-year birds. Most of the notes of females are slightly muffled counterparts of the notes of males. However, what seems to be the counterpart of male song in females is a hardly describable series of grunts, phonetically something like *gerunkee-gerui*, *gerunkee-gerui*. Hardy heard an adult male give this song once and also recorded a female, mated to an adult male, rendering a male-like song. The only consistent difference between vocalizations of first-year birds and adults is also in the song; the song of many first-year males is shorter than songs of most adults, lacking so full a series of guttural clicks in the terminal part.

GROUP BEHAVIOR

The Purple Martin maintains itself in groups of one kind or other at all times of the year, and, to paraphrase Köhler (1959), a single martin is not really a martin at all. Much of the behavior of the species is thus geared to forming or maintaining the several kinds of groups that may be evident in one day. We have already noted that some of the territorial mannerisms are attractive to other martins, as well as being responsible for spacing in the colony. Such duality in response to signal behavior is characteristic of martins, and is exactly the kind of behavior that would seem to be adaptive for a bird that on the one hand is monogamous and territorial and on the other hand colonial and group-oriented. We would like to emphasize that this

duality in response is achieved without any apparent conflict in behavioral tendencies.

The generalized group.—This heading refers to the social units of martins that engage in loafing or resting, and in investigation of neighboring colonies. Individuals composing such groups are those recently arrived from wintering grounds or those recently completing breeding activities. Three birds is the minimum number of individuals in such groups but the upper limit cannot be effectively set; ordinarily less than 15 birds are involved. These generalized groups are usually conspicuous in the time prior to and coincident with pair-formation, but established pairs frequently join groups, especially as they move around to various colonies. It is difficult to assess just what the birds are doing in such activity; we know that they "investigate" neighboring colonies, but this in no way tells us what the birds are really doing. It is possible that some group interaction, of doing something in a group, is all that is involved. Yet, the birds in fact learn about their immediate environment (as, isolated food sources, disposition of neighboring colonies, the place of nearest water, etc.), and this is clearly adaptive. In the end, however, it is not obvious why a group has to be the behavioral unit; therefore, the moving, loafing, and chattering communication may be engaged in for their own sakes.

A few examples of activities of martins in early spring are of use in consideration of generalized groups. In February 1959, we established a new colony-house about a quarter of a mile from a set of three colony-houses, two of which had been used by martins for more than 15 years. A pair of martins and one or two other individuals appeared at the new house in late March and continued to visit for several days. On one or two occasions the pair roosted, but mostly their visits and those of the others were confined to early morning and evening hours. Meanwhile, by the second week in April, the three-house colony had increased to six pairs. In all this time the pair that occasionally roosted in the new house showed strong ties to the old colony-houses, and at dusk usually flew from the new house to the old houses to roost or to attempt to roost. This pair actually had difficulty finding a space at the old colony. So the birds went back and forth between the old and new colonies many times a day, and several times each evening, seemingly attracted by the concentration of their fellows (but finding competition for space rigorous) and at the same time also attracted by the new, suitable but, significantly, unoccupied house. For the first two weeks only one or two other martins ever accompanied the pair to the new house in midday; all of these were residents of the older colony.

The new colony-house ultimately attracted none of the birds already established at the older colony. Additional residents at the new house were

adults and first-year birds that arrived late in migration, after the older, established colonies had acquired most of their residents. Gradually the one pair broke its social ties to the older colony, and, especially in midday, spent more time at the new house. Concurrently, more birds arrived and seemed to be partly responsible for the pair finally establishing residence at the new house; conversely, the pair in a real way attracted newly arrived birds to the new house. Late migrants probably always are attracted first to the old, thriving colonies, where most of the martin activity is actually occurring. Attempts to gain space at full colonies are, as has been described, severely discouraged, but at new houses such attempts are "encouraged," up to a point. So it is that in April and May the morning hours are taken up with these groups of birds visiting one house after another, remaining or leaving after investigation, depending partly on the availability of compartments not defended by residents.

One way that newly arrived birds learn about the availability of colonies at a distance is by means of the flight display of Claiming-Reclaiming activity, described earlier. Such flight seems to be initiated by a male when other martins are nearby but not right at the colony-house. Presence of the group may effect cessation of the behavior. In the absence of success in attracting other birds by means of this display, the flights are infrequent. Yet, some individuals persist in the behavior for prolonged periods of time without attracting other birds. Hardy saw a lone male use the display flight about 20 times within one hour in early March when no other martins were known to be in the area. Although one stimulus for such flight is presumptive availability of other birds, the autochthonously motivated flight is qualitatively identical with that used in the presence of other birds.

The last houses to be occupied are variously unsuitable, as ones with excessively small openings, ones with small compartments, ones situated too low to the ground, or ones packed with nesting material of House Sparrows and Starlings (*Sturnus vulgaris*). Suitable, new houses made available after the majority of adults have been established are also colonized late, as would be expected. One such house was erected in southern Illinois on 30 April. It was visited by an adult male for several days but finally was completely occupied by first-year birds, the first of which were attracted to the house by the actions of the adult male. First-year birds were seemingly attracted by adult males established nearby to two other houses erected in late May.

The criteria of suitability differ according to the histories of individual houses. An originally suitable house tends to keep its colony of birds, even after undesirable changes have occurred, such as trees growing up around the house, or heavy use of the house by Starlings. Yet, martins avoid houses that are unsuitable from the start. Also, houses originally unsuitable that

have been modified to suitability without changing their locations may continue to be ignored by the birds. Such behavior by martins probably shows that habituation learning is an important modifier of the behavior of the birds; old birds tend to respond to a colony-house as if it were in the condition it was when they originally learned about it. There may also be "traditional" or nongenetic transmission of information about colony-houses from old birds to young birds.

Foraging.—Groups of martins forage together, especially early in the season of breeding. Birds most frequently fly at about 100 to 200 feet above the ground, but may operate from a few feet to more than 500 feet; the organization of flocks in flight is loose and fluid. There are social calls given by the birds when foraging, so it may be presumed that there are at least vocal attempts made to maintain a foraging flock. A real value can be attached to group foraging, particularly early in the year. A group of birds is more likely to find food of restricted occurrence than is a single bird. Small samples of data from northeastern Kansas strongly suggest that the food of martins in March and April is localized, and for these months group foraging would seem to be highly adaptive.

Preening.—Small groups, ordinarily but not necessarily from one colony, periodically engage in preening; preening usually follows a successful foraging bout and is most frequently seen in late afternoon. There is less vocal communication between preening and non-preening individuals than among any other groupings of martins. To compensate, as it were, for this lack of vocal signal another sign seems to be used; this signal is a patch of white feathers that is brought into view at the level of the tertial feathers on either side of midline following scratching of the head by a preening bird (Fig. 3). Martins bring their legs up and over their shoulders to reach their heads. In so doing a tuft of silky, white feathers on the anterior flank, ordinarily covered by the dark feathers of the middorsal region of the spinal feather tract, and, when perched, by the folded wing, is uncovered and brought to lie exposed laterodorsally. In adult males this white spot can be seen by a man from a distance of perhaps 50 yards, and in first-year males and females from nearly as great a distance, although the contrast is somewhat reduced.

The white tufts are never fully exposed except under the routine of movements associated with preening, but the tuft can be partly exposed under other conditions, as in a bird with ruffled feathers of the sunning posture (Fig. 4). It would thus seem that the significance of the white tuft is associated with preening and, because little vocal communication is involved with preening, the tuft could serve simply to indicate martins that are preening.

Sunning.—The least social behavior of Purple Martins is that of sunning.

Some other swallows engage in group or socially oriented sunning (Jon Barlow, unpublished field notes), but martins seems to restrict sunning behavior to individual efforts. Martins assume an obligatory, Level III posture in sunning, to use the terminology of Hauser (1957). The rump and head feathers are ruffled, the bird visibly pants with mouth agape and tongue extended, the wings are drooped, and the body is partly rolled over on one side (Fig. 4). The eyes remain open and there is no conspicuous action of the lids or nictitating membranes, in spite of the fact that one eye is exposed to direct sunlight. The posture can be held for three to five minutes in the absence of disturbance.

Colonial nesting and the Fraser Darling Effect.—In certain respects (extremely high density, restriction of territory to a small region around the nest, a tendency to maintain flocks at all times) Purple Martins are like various colonial sea birds in general pattern of nesting. Emlen (1952:196) maintained this to be true also for the Cliff Swallow and suggested that some social coordination of nesting phenomena was evident. Specifically, the synchronization of nesting activities, presumably enhancing reproductive success, "social facilitation" or the Fraser Darling Effect (Darling, 1938), was the chief element suggested by Emlen to be of consequence for Cliff Swallows. The Fraser Darling Effect has been cited by numerous workers as potentially operative in diverse species, and has received considerable recent attention; Fisher (1954) and Coulson and White (1956, 1960) have presented the only real evidence against its operation (in Fulmars, *Fulmarus glacialis*, and in Black-legged Kittiwakes, *Rissa tridactyla*), but others, notably Lehrman (1959:490), still feel that it is ethologically, if not ecologically, a useful construct.

Our evidence bearing on this point is ecological, as far as it goes. If the hypothesis concerning social facilitation were valid, we should expect Purple Martins to show (1) close synchrony of inception of breeding within any one colony, especially in large ones, (2) earlier breeding in large colonies and later breeding in small ones, and (3) a high efficiency in reproductive effort (best possible ratio between number of eggs laid and number of young fledged) in those colonies showing high degree of synchrony of breeding. The most interesting ramification of point 3 cannot be pursued here, due to lack of information, but points 1 and 2 are not supported by martins in northeastern Kansas.

The reason individual colonies lack synchrony to any phase of the breeding cycle is that adult and first-year birds alike are found in all colonies, and adults breed relatively early and first-year birds relatively late. There can be as much as a month's delay in any one phase of breeding in first-year birds *versus* adults. An implication of this is that a colony composed strictly

of one age-class would show close synchrony in breeding effort; at present this would seem to be true, judging from the timing of inception of breeding in adults only or first-year birds only at a colony in fact composed of mixed age-classes. But, basically, no colony of any size shows real synchrony to inception of breeding or to any other phase of breeding. These observations are nearly parallel to those of Fisher and Coulson and White (op. cit.); namely, the relative timing of events and success in the breeding cycle is a function primarily of age, and any tendency toward colonial synchrony is a result of birds of like ages being together.

SUMMARY

This report describes some elements of the reproductive, aggressive, and group behavior of the Purple Martin in spring and summer in Kansas and Illinois.

Purple Martins arrive on breeding grounds some two months before they lay eggs. Such timing is unusual for a swallow and is a result of early arrival, for their breeding schedules seem to be wholly in line with schedules characteristic of other swallows in temperate North America. Early arrival is advantageous in securing a nesting cavity.

Formation of the pair-bond is accomplished without ritualization of behavioral elements. Pair-formation is a function of interaction between a male, a female, and a colony-site. Females exert ultimate control over pair-formation because they choose a nest-box-male combination, and not one of these alone.

Nest-building is sporadically engaged in for about a month prior to egg-laying. The green leaves brought to nests by both sexes may serve as a source of fumigant acting against ectoparasites developing in the detritus of the nest.

Aggression is effected by few and simple postural and auditory mechanisms. Horizontal Threat, Gaping, Bill-snapping, Claiming-Reclaiming, and several vocalizations are described. The Stooped-Submissive posture is a notable sign of defeat in a male martin.

Purple Martins operate at all times of the year in groups. Activities significant in formation of colonies include general investigatory behavior and Claiming-Reclaiming. Formation of preening groups seems to be facilitated by a white signal-mark on the backs of the birds. An obligatory (and probably nonsocial) sunning posture is described.

Social facilitation of reproductive activities seems not to be significant for Purple Martins. It is fairly clear that timing of the reproductive effort is partly dependent on ages of the birds, and any tendency toward colonial synchrony and increase in reproductive success is a result of birds of like ages being together.

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