EARLY BREEDING SEASON BEHAVIOR OF RED-HEADED WOODPECKERS

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ABSTRACT.—Main phases of the early breeding season behavior of Red-headed Woodpeckers, carried on in close association with an excavation or nest hole, were: (1) Males called from holes at dawn as well as repeatedly in morning hours, for their mates to come. If a female accepted a nest site, she indicated this by mutual tapping with her mate. (2) Sexual activities fell into three stages as the season advanced. First was assumption of sexual poses when male and female perched close to one another, and later on, as a second stage, reverse mountings with the female the first to flutter on the back of the male. Abortive passing onto full copulations were a final stage, seen as nest holes neared completion. (3) Resting and preening by a hole, especially by females, were also expressive of a close pair bond. Males did almost all of the excavating. Courtship and excavating were frequently interrupted in South Carolina by territorial invaders. Owning males and females often joined in aerial pursuits of intruders, circling back to alight afterward within inches of each other on the nest stub. Sexual activity or drumming frequently followed. Both sexes sometimes assumed agonistic poses on first sighting an intruding Red-head. Similarities in courtship of Red-headed and Red-bellied Woodpeckers are stressed because they were of aid, initially, in recognition of the sexes of the Red-heads by behavioral means. The importance of Wilson's (1975) concept of behavior scaling was well illustrated in present studies by high population density, crowding, and shortage of nest stubs.-Department of Microbiology, Dartmouth Medical School, Hanover, New Hampshire 03755. Accepted 25 September 1975.

AMONG previous accounts dealing with one aspect or another of the reproductive behavior of Red-headed Woodpeckers (*Melanerpes erythrocephalus*) are those of Bent (1939); Kilham (1959a); Southern (1960); Jackson (1970, 1976); Brackbill (1970); Bock et al. (1971); and Reller (1972). While these reports cover many points, the majority of findings listed in the summary of this report are not covered, nor is the subject of early breeding behavior dealt with by any of them in any comprehensive way. One explanation of this situation is, possibly, that the sexes of Red-headed Woodpeckers are impossible to tell apart in the field, on the basis of plumage. I have found, nonetheless, in studies begun at the Archbold Research Station at Lake Placid, Florida in 1958 and 1959 (Kilham 1959a) and in visits to the Groton Plantation in Luray, South Carolina in April and May from 1973 to 1975, that the sexes are distinguishable on the basis of behavior.

Identification of sexes.—Behavior at or near nest stubs (Table 1), where nearly all courtship takes place, is distinctive enough on most occasions for one to recognize which member of a pair is the male. This is assuming that the male is the dominant partner, as appears true of all picines (Kendeigh 1952). The facts that the courtship of Red-headed and Red-bellied (M. carolinus) Woodpeckers are similar and that I had had years of experience with the latter (Kilham 1958, 1961) were important.

Among 33 pairs of Red-heads studied, 5 in Florida and 28 in South Carolina, one pair among the latter was marked by retention of late juvenile plumage by the female, the male having been identified by copulatory behavior, then by the other criteria shown in Table 1. While the pair was not essential to present studies, it did substantiate that one can learn to distinguish the sexes by their behavior. Jackson (1970) identified the sexes of a nesting pair of *M. erythrocephalus* by catching and marking them with bands of paint; he identified the male by its enlarged cloaca and the female by palpation of an egg in the oviduct.

TABLE 1

PATTERNS OF BEHAVIOR COMMON TO MALE RED-HEADED AND RED-BELLIED WOODPECKERS IN THE EARLY BREEDING SEASON

- 1. Give breeding calls from roost hole at dawn.
- 2. When female flies to the hole in response to calls, tap out of sight within the cavity.
- 3. Keep returning to the prospective nest hole or excavation periodically to call or drum, switching to tapping as mate approaches, then fly away leaving her to inspect the hole.
- 4. Do almost all of the excavating.
- 5. May initiate copulatory behavior by inviting reverse mounting.
- 6. Do more drumming and calling than the female.
- 7. Roost in the prospective nest hole at night.

VOCALIZATIONS

Breeding call.—A squeal-like "queer" or "quee-ark," "quee-o-queer (Bent 1939); "churr" (Bock et al. 1971). Breeding calls may be repeated many times when a male is seeking to attract a mate to an excavation. It can have territorial functions when given in conflicts with intruders and be an indication of general as well as of sexual excitement (Bock et al. 1971). Females also give "queers" but less frequently and with less force.

Attack note.—"Scree," "chärr, chärr" (Bent 1939); rasp call (Bock et al. 1971). These notes are often given by male and female together when chasing a conspecific intruder. The "scree" represents a pitch of excitement and reminds one of terns fishing, particularly as it is usually given when the birds are flying.

"Chrr, chrr."—A harsh, but low intimate note made when members of a pair fly toward or meet at a nest stub, often as preliminary to some form of copulatory behavior. Very similar to the "grr, grr" of M. carolinus. In both species the notes resemble the begging notes of well advanced nestlings. The "chrrs," like the breeding call and attack notes, are only heard in the breeding season. Bock et al. (1971) give structural analyses of all three.

Rattle like "quirr."—This note, described by Reller (1972) as "whirring," is almost the only vocalization heard in the nonbreeding season and is associated especially with defense of storage territories against interspecific intruders (Kilham 1959b). I have heard it in the breeding season only in the first few minutes after a Red-head had emerged from its roost hole or was preparing to roost at night. It is usually accompanied by bowing, an indication, as judged by attendant circumstances (Kilham 1959b, Jackson 1970) that the bird is disturbed for one reason or another.

DRUMMING AND TAPPING

These are indistinguishable from those of M. carolinus (Kilham 1958, 1961) in the field and are used in much the same ways.

Drumming.—Usually given as a single burst or bursts that are well spaced. Drumming is usually associated with agonistic behavior and may indicate the presence of a conspecific territorial intruder, even if it is not close by. Red-heads regularly drum, and with special force, after driving an intruder away. Both the male and the female may drum at the same time in such situations, but the drumming of the female is less forceful and of shorter duration. Drumming is also used, occasionally and in single low bursts mixed with "queers," when a male is seeking to attract his mate.

Tapping.—A slow, countable form of drumming that plays a major role in pair formation, courtship, and attachment to and acceptance of a nest site in both M.

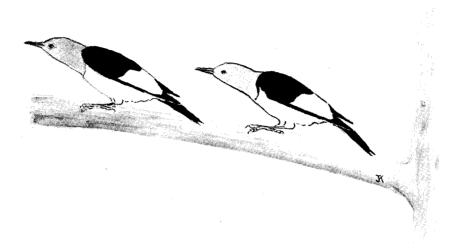


Fig. 1. Male and female Red-headed Woodpeckers in sexual pose. Female usually occupies the inner position.

erythrocephalus (Kilham 1959a, Jackson 1970) and M. carolinus (Kilham 1958, Stickel 1965).

DISPLAYS

Sexual pose.—As depicted in Fig. 1, the neck is elongated forward, the plumage sleeked down, and the upper back humped. This pose is seen at the onset of the breeding season as well as later when one partner invites mounting by the other. It is often assumed when the members of a pair fly to a nest stub after chasing an intruder, an indication of the stimulatory effect of agonistic on sexual behavior.

Agonistic pose.—While the neck and body are held as in the sexual pose, the wings are drooped and, at full intensity, the tail cocked up (Fig. 2). This pose can be assumed by both members of a pair simultaneously on the arrival of a conspecific intruder. It is not to be confused with what I call a threat display in which the wings are held well out sideways, as depicted by Hadow (1973) for the Lewis' Woodpecker (M. lewis) but common to many picines including Red-bellies (Kilham 1961). The agonistic pose appears expressive of a sudden flash of anger, as is true seemingly of the following display as well.

Erection of head feathers.—This display gives the head a bottle-brush appearance and I have seen it only a few times. It is difficult for a Red-headed Woodpecker to assume the agonistic pose unless it is perched on a limb. Erection of the head feathers may be something of a substitute when a Red-head is clinging to the bole of a tree, for this is the only situation in which I have noted it.

COPULATORY BEHAVIOR

Copulatory behavior of Red-headed Woodpeckers begins soon after pair formation. It develops in stages from token performances and increasing physical contacts to full copulations at the time of completion or near completion of a nest hole. Association with the stage of a nest hole is strong. Of 125 instances of copulatory behavior (all types) noted in April and May in Luray, 109 were on a horizontal

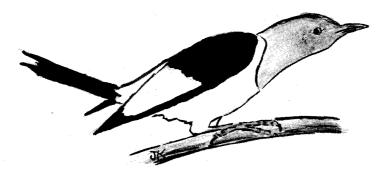


Fig. 2. Red-headed Woodpecker in agonistic pose.

branch of the nest stub within 1-2 m or less of a nest hole. It should be emphasized that while three stages are outlined below, there were intergradations.

Stage I. Positionings without contact.—After either tapping by a hole or flying together to a nest stub on sudden impulse, males and females sometimes assumed sexual poses, first with their bodies in line and pointing outward (Fig. 1), then reversing, in almost military fashion, so that both point inward. Sometimes the latter half of the performance was only a swinging to crosswise positions. The sexual poses probably involve tension, for while both birds are sexually motivated they still, it would seem, retain prebreeding aversions to physical contact.

Stage II. Mounting with brief physical contact.—As the two members of a pair became attached to each other and to their nest stub, the one occupying the inner position on the copulation branch (Fig. 1), in most instances the female, hopped or fluttered on the back of the male who then moved around to the inner position to do the same to her. These performances all took place within a second. The behaviors of the male and female were again, as in Stage 1, almost identical.

Less complete performances were limited to reverse mounting (Brackbill 1970) by the female or the male simply coming behind his mate, then flying away.

Stage III. True and abortive copulations.—Actual mounting refers to the male becoming established on the back of the female for 3 sec or more, as distinct to just fluttering for a second or less. The copulations were of two types. Abortive copulations lasted 3.5 to 4 sec and often terminated when the female fell away from under the male. Full copulations lasting 7 sec came when the pair was ready for actual nesting. Reverse mounting by the female preceded both types of copulations on some occasions and not others.

BEHAVIOR ASSOCIATED WITH A PROSPECTIVE NEST SITE

Tapping.—The main features of this display, the principal one associated with acceptance of a nest hole, have been detailed elsewhere (Kilham 1959a). Mutual tapping was noted with 4 of 28 pairs in South Carolina. Conditions associated with it were a completed nest hole, a relatively light degree of interference from other Red-heads, and repeated abortive or full copulations indicating that a height of courtship had been achieved. Mutual tapping during incubation has been described by Jackson (1970) and Reller (1972).

Features of tapping relating to the lead and eagerness of males were brought out in the following episodes: (a) Male A started tapping at a slow rate (84 taps per min) when his mate alighted 5 m away on an adjacent tree, but came no closer. (b) The male of Pair B (MB), a pair that was nearing the time of egg-laying, was resting by his nest hole on 27 April while his mate rested and preened within sight on a pine 35 m away. MB gave occasional small sets of taps, mingled with one drum and a few low breeding calls. The tapping, together with the low drum and calls, appeared to express a high degree of harmony between the two birds, as did the resting and preening. (c) Three days previously MB, when resting at the top of the tall dead pine where his hole was located, tapped when his mate alighted 16 m below. Tapping was thus not invariably associated with the nest hole. It could take place almost anywhere on the nest tree under certain circumstances.

The attentiveness with which a male may await the arrival of his mate was illustrated, amusingly, by male C. When out of sight in his hole on 26 April a Mockingbird (*Mimus polyglottos*) flew to a branch close to the hole. MC, apparently alerted by the noise of the bird alighting, started tapping immediately. This was the only time that I noted tapping triggered by anything other than the arrival of a mate, the sight of one approaching or, with advance of the breeding season, the sight of one resting nearby.

Drumming and breeding call.—These and tapping were methods used by males to attract their mates as is illustrated by the following examples:

- A. Unmated or lone males.—On 21 April MO, an unmated male, called "queearks" from his dead pine stub at rates varying from 40 to 60 per min. This was most rapidly heard from any Red-head, a situation noted by Bock (1970) for unmated Lewis' Woodpeckers. Two mated Red-headed males sometimes called with comparable intensity when their mates, that were unusual in foraging at a distance, failed to appear. ME flew to his dead pine on 24 April, drummed here and there as he ascended it, then called "queearks" for the next 17 min at a rate of 20 per min, without being able to get his mate to come.
- B. Calling at dawn and after.—Most males called from their roost holes at the start of a day. A male in Florida (Kilham 1959a) called every 2–4 sec for 10 min before his mate arrived. The calling ceased as soon as she arrived to join in tapping. Such males have a recurring urge to attract their mates back to their stubs throughout morning hours. MF flew to his hole on 16 April to excavate and call for the next 3 min. When his mate came he tapped, then flew away. This attracting a mate and leaving as she arrived was a common performance.
- C. Comparative uses.—The Red-headed Woodpeckers drummed chiefly in relation to conflicts and to a less extent with courtship. Males drummed more than females in either context. Some males on the plantation drummed a single burst on a nest stub before excavating or calling. The calls, in contrast to the drummings, nearly always appeared to be a long distance form of communication, directed to mates that they could not see. When a mate came into view by perching in some open place near by, males usually switched from calling to drumming. On 17 April FG flew to a nearby pine after tapping with her mate MG by their nest hole. MG switched from tapping to drumming immediately. Some minutes later MG entered the hole to tap again as FG came to the side of it, only to leave on a long flight elsewhere. MG then emerged from the hole and started calling. From such episodes as these it seemed that calling, drumming, and tapping formed a series relating to the distance of a female from the nest. In this series, the calls appeared to have two advantages. One was that, when shrill and squeal-like, they had carrying power and, another, that they appeared to be more individual. The drummings and tappings of

all Red-heads sounded much alike, but at times I could recognize individual males by their calls, even when several cornfields away.

On rare occasions males mixed drumming, calling, and even tapping in a confusing manner. On 7 May MH drummed by his hole, called "queearks" at a rate of 20 per min, tapped, called, and drummed again. In this case his mate was near by, but engaged with an intruder that flew with her when she came to the nest stub.

Excavation of holes.—Excavation of holes was not a prominent activity among the 28 pairs in South Carolina because only 12 were excavating and 4 of these were only renovating old holes. It was among the 8 pairs that were starting new, or in one case finishing a new excavation, that the differing behaviors of males and females were best observed. The males did all or nearly all of the excavating as is true of most if not all woodpeckers. The females excavated at three of the holes, but at two in no more than token fashion for only 1 or 2 min at a time, a situation seemingly described by Jackson (1970). It may have been enough for them to judge whether the sites were workable. Males of all the pairs mixed calling with their excavating, some more than others. When their mates came, they usually tapped, then flew away. This left the nest stub to the female. A characteristic behavior was for her to pay little attention to the hole but, flying lower down and working upward, to peck here and there on the nest stub, inspecting all cavities and starts of old holes. I have noticed this same behavior among other picines and, as discussed for Yellow-bellied Sapsuckers (Sphyrapicus varius) (Kilham MS), I believe it stems from females being more critical than their mates of the entire nest stub rather than just the place on it chosen by the male. The members of pair I tried many places in their pine stub over several weeks, without finding any decayed enough to excavate. In this crisis FI excavated almost as much as her mate.

Resting and preening.—A way of communicating acceptance of a nest stub and pair bond among Red-headed and other woodpeckers is, sometimes, just by resting quietly. Females on the plantation did not join their mates in tapping on most occasions when they flew to a nest hole being excavated, but they frequently clung near the male as he worked, either resting with head drawn in and body feathers fluffed out, or preening in leisurely fashion, scratching, or at moments sunbathing. Female A flew to her mate four times between 0642 and 0720 on 28 April to rest for some minutes. A detail noted for such resting females, especially for females D and I, was that they made slight outward motions of their wings while spreading their tails, as though pressing their bodies close against the stub.

Males, in contrast, seldom rested or preened when actively searching for a nest site or excavating. It was only when a hole was completed and mutual tapping and copulations were taking place, that they also became silent and leisurely. MB, for example, flew to his hole silently on 26 April to rest and preen for 8 min, giving occasional low taps. His mate, meanwhile, rested motionless on a pine branch 30 m away, the two being in sight of each other. Their quiet behavior, to me, represented the height of courtship and a readiness to begin the stage of egg-laying and actual nesting. Similar behavior states have also been noted, among other woodpeckers, for Downy (Dendrocopos pubescens) and Hairy (D. villosus) Woodpeckers (Kilham 1966, 1974) at the close of the early breeding season.

AGONISTIC BEHAVIOR

Some aspects of the agonistic behavior of the Red-headed Woodpeckers limited observations, such as the impossibility of distinguishing the sexes of the intruders, or

indeed of any of the individuals in fast-moving conflicts. Other features of conflicts were discernible and these are outlined below.

Background of conflicts.—The early season conflicts of *M. erythrocephalus* in South Carolina in both 1974 and 1975 centered on efforts of invading pairs or individuals to win nest stubs in territories of pairs already established. In mid-April 1974 I located six pairs in an area of 5 ha. By the end of the month 13 pairs had nest stubs and many of these were spending much time trying to drive out still others. This fighting was due, it seemed, to a shortage of stubs. Reller (1972) gives quantitative descriptions of conflicts among Red-heads under conditions, seemingly, of similar high population density. But she does not give details, such as those given below, of the spectrum of agonistic behavior observable.

Mutual defense of nest stubs by members of pairs.—A feature of interspecific conflicts among Red-headed Woodpeckers was the way members of pairs acted together in the face of intruders. Intruders were persistent whether coming as single individuals or in pairs. Some flew to or close to the nest stub of owning pairs day after day and hour after hour. The owners, male and female, flew at them in swift flights giving "screes." Pursuits commonly looped about only to circle back. On reaching the stub the Red-heads of the owning pair frequently alighted within 5 to 10 cm of each other and on some occasions token copulatory activity followed. Mutual defense, possibly aided by the fact that the sexes of M. erythrocephalus are alike in plumage (Kilham MS) thus seemed to bring members of pairs together.

Drumming and "queers."—Owning males often drummed and called "queers" in pauses between conflicts. On 25 April male E (ME) alighted on a broken branch of his nest stub and his mate close by on another after chasing intruders. ME drummed for 10 min at a rate of one to two bursts a minute. As noted with other males, ME drummed furiously in the first few minutes, pounding the spike with great vigor. His mate, meanwhile, drummed two low bursts and left.

Defense by single individuals.—In prolonged conflicts males did the most chasing while females stayed near the nest stub. But sometimes the reverse took place. On 25 April MA was excavating when his mate flew the length of the pine grove in silent pursuit of an intruder. From this and other occasions it seemed that the "scree" notes were given primarily when members of a pair were acting together.

Agonistic pose.—This (Fig. 2) was assumed when an intruder had come into view on 10 of the 13 occasions when I noted it. On 26 April 1974 the two Red-heads of pair E had alighted on their nest pine when an intruder returned to alight 10 m away. Both members of the pair took agonistic poses immediately. Only once did I see an owning Red-head face an intruder in this pose and only twice see the pose assumed by an intruder.

Physical clashes.—In spite of the large number of conflicts that took place at the South Carolina plantation (I took notes on 123) I saw physical encounters (grappling in midair) in only three. Two of these were unusual in involving two Red-heads fighting low to the ground on what was possibly a territorial border.

Territorial boundaries.—The extent of territories and the nature and numbers of conflicts varied. In South Carolina, where strips of pines and cultivated fields were interspersed and the numbers of Red-heads high, the territories were small. Neighboring pairs respected common boundaries once these were established. Pairs C and K had nest stubs 68 m apart, with pines forming a boundary 20 m from the nest cavity of pair C. The conflicts noted for these pairs were always with intruders and

never between themselves. While such territories were small in some directions the Red-heads had extensive room to forage in others.

DISCUSSION

Comparative courtship.—The courtship of Red-bellied and Red-headed Woodpeckers is so similar that what Stickel (1965) wrote of the former applies equally well to both: "An integral part of the establishment of a bond between adults concerned selection of a nest site and excavation of a cavity. The male took the lead and did most of the early excavation. However, periodic visits of the female to a cavity usually in response to the male's breeding call, followed by 'mutual tapping' and 'reverse mounting' (Kilham 1958) at the cavity, were extremely important in the maintenance of the male's interest in the place. If the female did not come to the cavity which was being excavated, the male started elsewhere."

In present studies I did not see the type of copulation Southern (1960) noted in a pair of Red-heads. I did, however, see it frequently with a pair of Red-bellies that nested in an aviary (Kilham 1961) and once in Yellow-bellied Sapsuckers (Kilham MS). In the case of all three of these species I believe that the situation depends on the type of substrate; the broad top of a stub being particularly favorable.

The role of drummings among Red-headed and Red-bellied Woodpeckers also has peculiarities. Among species of more "typical" woodpeckers such as the Hairy and Downy, neither of which has a breeding call, drumming can convey a variety of messages (Kilham 1966, 1974). With *C. carolinus* and *M. erythrocephalus* the role of drumming is reduced in favor of breeding calls. An advantage of breeding calls is that they can be given anywhere and are not dependent, as is drumming, on a place of special resonance. The loudest and most frequent drumming in these two species is agonistic; low drumming, especially in single bursts, appearing to be more associated with courtship. A source of confusion in studying Red-heads in South Carolina was that many pairs were carrying on courtship and agonistic behavior simultaneously. Drumming by the male may serve a double function in such situations; drawing the members of a pair together sexually while at the same time serving notice to the territorial intruder.

The behavioral scale.—Courtship and breeding proceeded peacefully in Florida (Kilham 1959a) where Red-heads were separated from conspecific neighbors in contrast to South Carolina where a high population density plus a shortage of nest stubs led to almost incessant conflicts. Behavioral variations of this type are instances of behavioral scaling. Wilson (1975) writes of this concept that "at low population densities, all aggressive behavior is suspended. At moderate densities, it takes a mild form such as intermittent territorial defense. At high densities territorial defense is sharp," while if densities are too great there may be a breakdown into "social pathology." Sometimes at the plantation I wondered how pairs could fight for hours without, seemingly, taking time to feed.

The behavior of Red-heads on the plantation was comparable in the amount of aggressiveness to that of Yellow-bellied Sapsuckers observed in lumbered parts of New Hampshire (Kilham 1962, MS). In both cases, north and south, environmental change had led to crowding of nesting pairs. Such high population densities are probably not possible for all picines. Sapsuckers and Red-heads may be especially prone because they are mobile opportunists, quick to move into areas that are favorable for nesting in terms of dead trees and stubs.

It would seem in conclusion that if one wants to see the spectrum of courtship and agonistic behavior, one should study woodpeckers under varying conditions. Learning about a species in a comprehensive way is not easy. It is only by comparing species with species and studying each species along the different points of its behavioral scale that one can hope for any breadth of understanding.

(After the foregoing was written Jackson (1976) published an important article that describes various aspects of the breeding behavior of Red-bellied and Red-headed Woodpeckers. He also found that the courtship of the two species is closely similar and takes place, for the most part close to the nest stub.)

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