REPRODUCTIVE BEHAVIOR OF RED-BELLIED WOODPECKERS

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OBSERVATIONS on a hand-raised pair of Red-bellied Woodpeckers (*Centurus carolinus*) which nested in captivity, and observations on wild birds from 1957 to 1960 form the basis of this paper. I did most of my field work in swampy lands near Seneca, Maryland. Additional observations were made at the Archbold Biological Station, Lake Placid, Florida.

METHODS OF COMMUNICATION

Both sexes of Red-bellied Woodpeckers participate in the vocalizations, drummings, and displays outlined below, but males are the more active performers. My interpretations of these forms of expression are based upon the situations attending their performance on repeated occasions.

Vocalizations.—(a) Breeding call. A musical *kwirr* repeated twice or a number of times in succession—delivered in sets of three in tense situations. The call of the female may have a flatter sound, especially when the members of a pair are answering each other. *Kwirr*'s are seldom given during the fall, but may be heard, in almost explosive fashion, on days of suitable weather in early winter.

(b) Territorial call. A *cha-aa-ah*, shaking the whole body and given the year around, possibly because Red-bellied Woodpeckers have individual territories in the fall and winter in addition to their breeding territories at other seasons. The *cha-aa-ah*, like the *kwirr*, may stimulate responses of the same kind from another individual.

(c) Location and mild excitement. An often-repeated *cha*. A Red-bellied Woodpecker may give this note when disturbed by a human observer.

(d) Intense excitement. Expressed by a triple, high-pitched *kew,kew,kew*.

(e) Conflict. Red-bellied Woodpeckers usually make a loud *chee-wuck,chee-wuck,chee-wuck* when engaged in intraspecific conflicts.

(f) Intimate note. A low *grr,grr*, which may be exchanged by the members of a pair from the first days of courtship until the end of the breeding season. This note is not given by lone individuals, in my experience.

(g) Begging calls of juveniles. Young which have recently left the nest beg with a soft *psee-chew*. The first syllable is high-pitched. They clamor for food in succeeding weeks with a *grr-ick,grr-ick*, which is distinct from, but obviously related to, the *grr,grr* of breeding adults.

(h) The vocalizations of nestling Red-bellied Woodpeckers are as varied as among the young of other genera of woodpeckers (Kilham, 1959*c*). A harsh *chrr* usually accompanies feeding. Further discussion is given below.

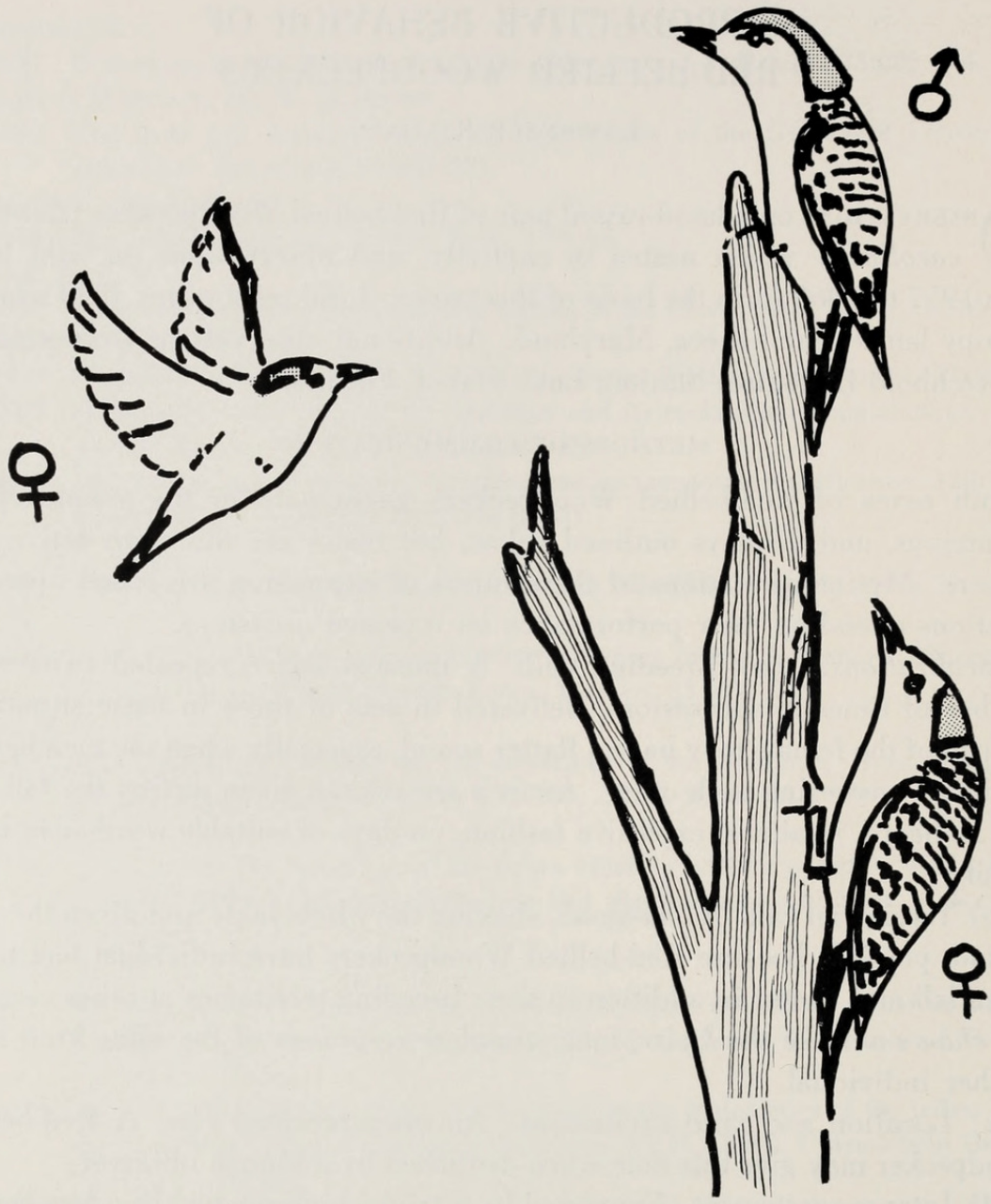

FIG. 1. Episode in a conflict observed on 30 January 1960, in which two rival females fought for a male. The intruding female is in the stiff pose expressive of tension as owning female approaches the tree from the left in a floating threat display.

Displays.—(a) The feathers of head and nape are raised when a Red-bellied Woodpecker is excited. This is particularly true of the male whose red feathers, being somewhat long and silky, give him a striking appearance.

(b) Full threat display. Made with wings outstretched at an upward angle of 45 degrees and with tail outspread. The wings may be spread out like a moth's, against the trunk of a tree, in conflicts over holes.

(c) Flight display. A Red-bellied Woodpecker may float through the air toward its landing place with wings held in the position of a full threat display,

when engaged in a conflict with a rival (Fig. 1). *Centurus* appears to have no true courtship flight.

(d) Stiff pose. This display gives the woodpecker a rigid, somewhat bowed appearance (Fig. 1). The bowing results from an elevation of the patch of feathers covering the upper back.

(e) Resting motionless. The members of a pair may rest within inches of each other for minutes at a time, and in silence when close to the time of actual nesting. This form of behavior is common to a number of genera of woodpeckers, and Pynnönen (1939) has aptly described it as "*Regungslos-auf-einestelle-sitzen.*"

Drumming.—Red-bellied Woodpeckers have two types of drumming. The usual type consists of an even burst of about one second's duration. A second type is similar to the first except that it is preceded by a few well-spaced taps—*da-da-drrrrrr.* I have not discovered any different significance in these two forms of drumming, but I have heard them in the aviary as well as in the field and among the closely related Red-headed Woodpeckers (*Melanerpes erythrocephalus*) (Kilham, 1959*a*). Drumming is a far less frequent method of communication with *Centurus* and *Melanerpes* than among *Dendrocopus, Dryocopus,* and *Colaptes* (Kilham, 1959*b, c,* and 1960). The drumming of Red-bellied Woodpeckers appears to serve as an assertion of territorial dominance. It is sometimes associated with conflicts.

Tapping.—Delivered at a regular rate of 2–3 taps per second and with 4–20 taps in each burst. The members of a pair may tap together in mutual tapping. Tapping is closely associated with nest-site selection and maintenance of the pair bond, not only in *Centurus* (Kilham, 1958*a*), but also among other woodpecker genera (Kilham, 1959*a, b, c*).

EARLY BREEDING BEHAVIOR

Continuing studies of Red-bellied Woodpeckers have enabled me to complete, in some degree, an account of their early breeding behavior presented in a previous report (Kilham, 1958*a*). The additional aspects of behavior are illustrated by the histories of Pairs A and B.

Beginning of breeding season.—Observations on Pair A indicate that male Red-bellied Woodpeckers may stay on their breeding territories the year around and that females, in some instances, may compete for them early in the year.

(a) Territory of Male A.—I observed Male A excavating a nest hole in the dead limb of an elm on 22 February 1959. A subsequent wind storm broke the limb where the excavation had weakened it, but in the fall of the same year I watched Male A excavate a new hole just below the site of the old one. I did not see him in association with any other Red-bellied Woodpecker at this time. On 20 December I saw Male A fly to his excavation and start to tap as a female, making *grr,grr* notes as she flew, alit on the other side of the cavity and joined in mutual tapping. It was of interest that the woodpeckers

were using the same hole for actual nesting by 30 April 1960, when I observed them in full copulation on an adjacent limb.

(b) Competition of two females for a male.—On 30 January and again on 6 February 1960, I witnessed prolonged conflicts between two females appearing to be rivals for Male A and the hole he had excavated. Events were similar on both mornings. The females had two centers of their continually renewed conflicts, one being Male A, who called *kwirr, kwirr* from various tree tops but appeared to be indifferent to the actual fighting, and the other, the nest excavation in the elm. The intruding female might fly to either place. What I judged to be Female A would follow closely, hitch up toward her rival, then fly out in any direction in a long circular pursuit. All pursuits appeared to be restricted within the usual limits of the male's territory. The females were silent most of the time, but one might call *chee-wuck, chee-wuck*, and in two instances they clashed in bodily contact. Figure 1 illustrates an episode in the conflict. As Female A flew to the tree in which her rival and the male were resting, she floated the last 10 feet of the way with wings outstretched in a threat display. There were few respites in the conflicts. I watched one going on continuously for two and one-half hours on 6 February. I had observed a similar situation among Yellow-shafted Flickers (*Colaptes auratus*) in which two females contended for a male in mid-winter (Kilham, 1959*b*).

Events leading to actual nesting.—Pair B was well situated for observation because the nest hole was only 20 feet above the ground and remained free of molestation by Starlings (*Sturnus vulgaris*). The activities of the two woodpeckers offered many points of comparison with those of my hand-raised pair, whose breeding behavior is described later.

(a) Mutual tapping and nest-site selection.—On 9 March 1958, Male B called *kwirr* while moving about on the dead stub of a living ash. He pecked at random, as if percussing the underlying wood. There was no sign of an excavation. When I was standing directly below him a little later, he tapped four bursts of about 15 taps each, whereupon his mate flew in and joined in several seconds of mutual tapping. A fresh, shallow excavation appeared on the stub within the next two weeks. Nearly two and one-half months later, on 30 May, I removed two well-feathered young from a nest located at the spot where Pair B had had mutual tapping on 9 March.

(b) Intercommunication during the period of excavation.—The male did most of the excavating. In pauses between bouts of work he often called *kwirr, kwirr* and his mate, who was usually within a range of 150 yards, would answer *cha, cha* or a flat-sounding *kwirr*. Mutual tapping took place periodically. On 29 March, for example, the male was excavating with his body half way in the hole when he dropped down to one side and began to tap. His mate came immediately. The pair then joined in mutual tapping before she flew away. It is probable that the male had been stimulated to tap by seeing that his mate had come close by. On the following day both woodpeckers were away from their excavation when they suddenly flew to it simultaneously and joined in a bout of mutual tapping. Red-headed Woodpeckers may communicate in an analagous fashion during the period of excavation (Kilham, 1959*a*).

(c) Lack of agreement in mated pair.—The nest excavation progressed slowly. It appeared in a variety of ways that the female Red-bellied Woodpecker had a breeding urge less developed than that of her mate in the unusually cold spring of 1958. First, she didn't participate in the work of excavating and second, on 5 April, I witnessed two occasions following bouts of mutual tapping, when both members of the pair held their

bodies in a stiff pose expressive of tension, for one can observe the same pose in conflicts between rival males.

(d) The lone male.—The female sometimes left the nesting territory on a long flight over the tree tops to visit, I suspected, a cornfield in the uplands. Her mate, failing to get any response from her at these times made what appeared to human ears to be "frantic" vocalizations. On 12 April, for example, he clung to the entrance of his excavation and called *kwirr, kwirr, kwirr* every three to five seconds for 40 minutes. I then saw a Red-bellied Woodpecker flying in over the leafless tree tops. The male became silent immediately. A few moments later the pair was together at the excavation. I witnessed a similar episode on 20 April in which the male called *kwirr* in sets of three as before, persisted for 15 minutes, then became silent when his mate returned.

(e) Behavior of pair at time of egg-laying.—Egg-laying probably began within a few days of 20 April. This calculation was made not only by reckoning backward from 30 May when I took two advanced fledglings from the nest but also from two concurrent forms of behavior which indicated that the female had finally accepted the nest hole. The behavior patterns were as follows: (1) Both birds remained silent and motionless for eight minutes on 20 April, the male resting inside the nest and his mate on the outside. (2) The female then entered the hole. I then heard *grr, grr* notes. The male was the first to wriggle out the entrance and another silent, motionless period of five minutes followed before the pair flew away.

CONFLICTS OVER NEST HOLES AND TERRITORY

Red-bellied Woodpeckers are territorial during the nesting season. Evidence for this territoriality is difficult to obtain in well-wooded country but two of the conflicts described below took place along a common boundary more or less equidistant between the excavations of two nesting pairs. Three other conflicts occurred close to nest holes. Features characteristic of these conflicts were that when only two individuals were engaged, they were of the same sex and fought in silence, whereas whenever three or four birds representing two pairs were in conflict, a lively combination of vocalizations, drummings, and displays usually took place. The situations observed were as follows:

Territorial conflicts between two females.—On 3 April 1958, Female A flew low over 50 yards of swamp directly at the female of adjacent Pair B. A silent conflict now took place close to the ground. One female would fly at the other, who would dodge around a tree trunk, but on one occasion the two females rose 3 feet into the air, grappling together as they flew. Both withdrew after several minutes. Their battleground was 90 yards from the excavation of Pair A and 70 yards from that of Pair B. The two females had another conflict at the same place 10 days later, so that there was reason to believe that the area represented a boundary separating the territories of the two pairs. Selander and Giller (1959) found a well-defined boundary separating a pair of *Centurus carolinus* from one of *C. aurifrons* in Texas.

Conflict between two rival pairs.—On 12 April 1958, I witnessed a conflict between two pairs of Red-bellied Woodpeckers which went on for one and one-half hours (and probably longer). Pair C owned the disputed nest hole located 60 feet up in a dead elm. A peculiarity of this conflict was that I could identify the attacking male by his aberrant call, a loud *quee-ark*. This abnormality is discussed later. The pattern of the struggle on the morning of 12 April was as follows: The owning male (OM) would bow

in and out of his nest hole, his red crest bristling straight backward while the intruding male (IM) approached from a distance calling *quee-ark*. OM would fly at IM. The intruder would then dodge under a limb and raise his wings in a full threat display. As IM was driven farther away he might suddenly dart toward the nest hole. The conflict would then renew itself. Although all four birds of both pairs were occasionally close together in this conflict, it was clear that the main conflict was between the two males. The clashes between the females were mild in intensity. One female, when pursued by the other, might remain away for 10 minutes at a time. During some intervals the two males had prolonged exchanges of their vocalizations, *quee-ark* and *kwirr*. One often drummed in between his calls. *Chee-wuck*, *cha-aa-ah*, and *grr* were other vocalizations heard in this conflict involving both sexes. Pair C retained its nest hole and I watched them feeding young in June.

Intruding male and a mated pair.—On 10 May 1958, I observed coition in Pair D. An IM came close to the nest hole on the same morning and I immediately heard a mixture of *grr* notes and *chee-wuck*'s as the pair faced their visitor. Both males had their crests raised. IM raised his wings in a threat display on two occasions before being driven away by OM, whose mate did not participate in the conflict.

Conflict between two males.—Male A was excavating on 29 March when an intruding male appeared 25 feet away and called *kwirr* a number of times. The two males rested motionless, as if frozen. Male A then flew at IM who averted contact by swinging under a limb. There was no display and no noise. After several such episodes the intruder flew away and Male A backed down to his excavation, holding a bent, stiff pose as he did so.

INCUBATION PERIOD

Red-bellied Woodpeckers become relatively quiet at the onset of egg-laying and the activities of Pair F may serve to illustrate events of the ensuing period. The entrance of Nest F was 20 feet up in the dead top of a living willow. On 18 May 1957, I cut away the wood and wired an aluminum back onto the rear of the nest cavity. There were four eggs at this time. The woodpeckers were incubating a week later, but on 30 May I found the aluminum covered with the muddy paw marks of a raccoon (*Procyon lotor*). The nest contained two eggs and two newly hatched young, all dead. One egg and one nestling were mutilated, as if punctured by the bill of some bird. Observations on the parent birds while they were incubating in the previous period were as follows:

Both birds appeared to be restless when taking turns within their nest on the week-end of 11 May. Egg-laying was presumably in progress at this time. The female would often put her head out, then withdraw it half-way. The male was even more restless, for when guarding the nest he might somersault out of the entrance, call *quee-ark* when he had righted himself, then return inside. He also called in a wide radius about the nest tree at times when the female was in the nest. His loud, aberrant *quee-ark* was easy to distinguish from the *kwirr* of neighboring males. I observed similar restlessness on 18 and 23 May while watching from a thicket 70 yards away. There was no sign of activity at the nest on 26 May. After watching for 20 minutes, I approached and stood below. At this moment the female flew up close to the entrance and I heard the male start tapping on the inside at her approach. She entered the nest after he had flown out. Had I been watching from any distance I would not have heard the tapping response of the

male to his mate's arrival. I was to hear this type of tapping many times later on, with my captive pair.

THE NESTLING STAGE

I observed 10 pairs of Red-bellied Woodpeckers while they were feeding their nestlings. The following is a generalized picture of their activities.

Feeding of young.—When the young were recently hatched, one parent stayed with them until the other arrived with food to take its place. Parents usually had many insects protruding from their bills on arrival, and this prey, while small in size in the early nestling period, was larger later on when big beetles, long-legged, gauzy-winged insects, and even butterflies were brought in. The woodpeckers captured most of their prey on tree trunks. On 30 May 1958, for example, I watched the female of Pair A alight on one tree after another, landing low on each trunk and then ascending rapidly. She managed to catch insects even when her bill was already loaded. She then flew to a broken branch where she appeared to store some of her prey, for she returned to the same spot after flying away to feed her young. Parent birds occasionally brought in fruits, carrying two or three nearly one-quarter inch in diameter in their bills at one time. Some of these fruits may have been wild cherries. Parents disappeared inside nest cavities in order to feed the young when they were small. At later times the tails of the old birds projected from entrances as they fed their offspring, and at a still later period the young climbed to the entrance where the parents fed them from outside. Feeding visits varied in frequency with the weather and the time of day. They were apt to be most frequent early on a warm day, as on 18 May 1957, when the two birds of Pair E fed their young 10 times in the 26 minutes after 7 AM. The female made eight of these visits. On 7 June 1958, the male and female of Pair D made two visits each within an eight-minute period.

Greeting ceremonies.—Red-bellied Woodpeckers usually fly directly to their nest holes when carrying food. On 11 May 1957, Male E alit on the bark below the hole and rested quietly for a few seconds. His mate then appeared from within the entrance and made a slight chatter as she flew off. Hungry young ones greet an entering parent with harsh *chrr*'s. These *chrr* notes are not easy to hear and I usually heard them only when standing close to the nest. Adult Red-bellied Woodpeckers were relatively silent when away from their nests gathering food for their young. The vocalizations they made included *kwirr*, *cha*, *cha-aa-ah*, and *kew*, *kew*, *kew*; most of these expressing some degree of excitement at such times, for example, as when I stood near the nest tree while a parent bird waited nearby with a bill-full of insects. Males might drum under these circumstances. In the course of 41 feeding visits observed for Pair E, the male started drumming on two occasions when I came close and, from my usual observation post at a greater distance, I witnessed the chatter greeting ceremony

of the parents in four of the 41 visits. On most visits the two birds did not encounter each other. I have not heard tapping during the nestling period.

Nest sanitation.—Methods of nest sanitation were not obvious among the Red-bellied Woodpeckers. Parent birds were often making motions with their tongues as they emerged after feeding and I came to believe that they had just swallowed the excreta of their young. I never saw a recognizable fecal sac in their bills at any time. Of six Red-bellied Woodpeckers taken as nestlings, none produced fecal sacs. But two young Flickers, hand-raised under similar circumstances, produced well-formed sacs. Two of the nest cavities, from which I removed well-feathered young, were remarkably clean. The third nest cavity had one-half inch of damp detritus on the bottom, and three nestlings with early pin feathers.

Observations on nestlings.—Woodpecker nests are usually too inaccessible for close study but I was able to observe some features of nestling behavior by removing the young. Three nestlings were taken from a nest on 23 May 1959. Their eyes were beginning to open and they had pin feathers up to one-quarter inch in length. It was apparent at the time of removal, as well as in ensuing weeks, that the three were of different ages in regard to feather growth and behavioral development. The tips of upper mandibles and the protuberant knobs at the corners of the bills of the young were sharply white in color. Young Flickers, among other woodpeckers, have a similar white point at the position of the egg tooth. One may speculate that parent birds, when darkening nest entrances on arrival with food, may be guided to the mouths of their offspring by these white points which disappear only as nestlings become well feathered. The knobs at the corners of the bill are sensitive areas. We found that if we brushed these knobs with a toothpick carrying a morsel of food, the bills of the nestlings would open widely as their necks stretched upward. This begging response could be induced by passing a hand between the birds and a source of light, if the nestlings were on a lighted surface. It seemed likely that the sudden shading was the effective stimulus, for jarring or movement alone had no effect. Results were different in the dark. The nestlings were kept in a dark cabinet, and any scratching on the door or miscellaneous jarring, such as the closing of a nearby refrigerator, was sufficient to elicit a gush of begging cries. These cries were harsh and as steady as if one had turned on a faucet. Once the young had been fed, however, they sank back and made soft, musical *wee-urp*'s which had a contented sound to human ears. The cabinet was equally dark at all times. At night, however, the nestlings would settle down to a low *purp, purp, purp* continuing even after midnight when they were apparently asleep. Nestling Pileated Woodpeckers (*Dryocopus pileatus*) exhibited similar patterns of vocalization (Kilham, 1959*c*).

Young Red-bellied Woodpeckers, when well feathered, developed an urge to

scurry away and cower in the darkest place available after being fed and, a little later on when they might have been leaving their nest under natural circumstances, they became wild and pugnacious, as evidenced by attacks on each other as well as on our fingers. This aggressiveness appears to be a specific characteristic of Red-bellied Woodpeckers. I have not encountered it among the young of *Dendrocopus*, *Dryocopus*, *Colaptes*, and *Sphyrapicus* raised under similar circumstances.

Time of nest leaving.—I watched two Red-bellied Woodpeckers feeding their young over four week ends from May into June 1958. On 22 June the female fed the last young one in the nest at 7:15 AM. There were no more feeding visits over the next half hour in which the young one perched well out of the entrance, giving a frequent harsh chatter, not only in response to the *kwirr*'s of its parents who were farther down in Creek Wood, but also to the vocalizations of other neighboring Red-bellied Woodpeckers.

PARENTS AND YOUNG AFTER NEST LEAVING

Full foliage in the woods and the comparative quietness of the Red-bellied Woodpeckers after their young had left the nest made it difficult to follow them in summer months. Creek Wood, however, was an open area favorable for observation. Young were raised there in two succeeding years and as juveniles, in each year, they followed their parents about for nearly two and one-half months. These young ones were relatively inactive much of the time, resting while their parents moved up tree trunks or flew into clusters of leaves to catch insects. Adults dismembered large insects before feeding them to their offspring. The begging cries of the juvenile were of two types and were well illustrated by a hand-raised female who would have left her nest at the end of May under natural circumstances. She often fed from my hand. In June her begging note was a high-pitched *psee* or *psee-chew*, but by July her cry under similar circumstances became *grr-ick*. Both of these vocalizations were of help in locating the family groups in Creek Wood. During the summer of 1958 the wood was occupied by an adult male and a juvenile which followed its parent closely at all times. The adult female was attended by the second young one of the family in a similar fashion. These two, however, rarely returned to Creek Wood where the nest had been located. I had reason to suspect that the male had become hostile toward his former mate. On 13 September, for example, he was moving about with his attendant offspring in a peaceful fashion when he suddenly flew to the edge of the wood where I saw the female and her young one. The male had his crest raised, and there was an outburst of vocalizations which included *chee-wuck,chee-wuck*, *grr-grr*, and *kew,kew,kew*. The female held a stiff pose. After a minute of this confused conflict she flew away followed by her young one. During the same summer I observed another family of Red-bellied Woodpeckers by the canal which appeared to be divided in a similar fashion.

In the summer of 1957, the family which occupied Creek Wood consisted of three offspring, and these juveniles had noisy conflicts among themselves. On 20 July I heard two of them calling *chee-wuck* before grappling together in mid-air. A week later all three juveniles were together on a dead tree. One would perch on the top and the others would fly to replace it with noisy *kwirr*'s and *chee-wuck*'s. This conflict behavior could be interpreted as play.

SECOND NESTINGS

I have had no evidence that Red-bellied Woodpeckers raise more than one brood a year in the vicinity of Seneca, Maryland. Thick foliage, however, makes complete observation difficult in the late spring and summer. The situation appears to be different farther south. Hauser (1959, and personal communication) has had good evidence that a marked male raised a second brood in South Carolina in two successive years, and, while in Florida in mid-June 1960, I observed a pair of Red-bellied Woodpeckers finishing the excavation of a nest hole. The two birds had full copulation on 14 June. On the same day and 300 yards away I watched a juvenile bird for several hours. It appeared to be independent of any parents.

BREEDING BEHAVIOR IN CAPTIVITY

A pair of Red-bellied Woodpeckers, raised in a preceding year, nested successfully in the spring and again in the summer of 1960 in my aviary—a modified indoor garage. The development of their breeding behavior was as follows:

Early breeding behavior.—(a) Fragmentary interest in the fall.—On 22 October 1959, the female tapped vigorously and called *grr,grr* when the male alighted near her. I had witnessed an almost identical episode with a wild pair five days previously, but there was no sustained development of breeding behavior, either in the field or in the aviary, until the beginning of winter.

(b) Female flies to male at dawn.—The female was flying to the male's roost hole at dawn by mid-December and she continued this habit through the next July, except for periods when larger young were in the nest. This visit was in the nature of a greeting. She would tap on the outside of the box and, by 3 January, he was joining her by tapping on the inside at the same time. The male was slow about emerging from his roost hole. He would rest inside for 20 to 30 minutes after the greeting ceremony. I have described this type of behavior at dawn, as observed among wild Red-bellied Woodpeckers, in a separate report (Kilham, 1958*a*). The roosting place of the captive male later became the nest box and his mate developed a constant habit of resting in it for an hour or so every late afternoon.

(c) First breeding calls.—We began to hear *kwirr*'s coming from the aviary on 28 December 1959, and for some weeks the woodpeckers made most of these vocalizations while light was still dim at dawn. We had never heard them give

kwirr's in previous months. There were variations in the numbers of the vocalizations given from day to day; on some mornings the woodpeckers were noisy for several hours but on others they were quite silent. On 3 March, for example, a morning of heavy snowfall, our Red-bellied Woodpeckers gave *kwirr*'s in sets of three every four to five minutes after 5:45 AM, although they did not leave their roosting places until nearly 6 AM. On the following morning we heard only one *kwirr* prior to 8 AM. I have described an outburst of breeding behavior among the Red-bellied Woodpeckers of Seneca Swamp on a morning of freshly fallen snow (Kilham, 1958*a*). Whatever meteorological conditions affect avian activity, as judged by the volume of song and other vocalizations, they appeared to influence our indoor birds. Cardinals (*Richmondena cardinalis*), for example, were doing their greatest amount of singing in the yard on mornings when our captive Red-bellied Woodpeckers were calling an unusual number of *kwirr*'s in the aviary. Such correlation was fairly regular during the spring.

Increasing intimacy.—The new forms of behavior outlined below indicated that a closer pair bond developed between the two woodpeckers in the last weeks of March.

(a) Greater association with the nest box.—The male entered the nest box on 24 March when his mate was already on the nest and the pair remained out of sight for a few minutes before she emerged. This togetherness within the nest became of frequent occurrence in succeeding weeks. The male spent increasing periods of time resting on the box during the day and, if his mate came close, he would start to tap or make the *grr,grr* note. The pair engaged in mutual tapping on the box at other times. I observed a new behavior on 3 April when the female, who had been resting on the inside of the nest hole, dropped down and tapped out of sight when her mate alighted on the stub above. Later on the same morning both birds rested, silent and motionless, he within and she on the outside of the cavity. Such episodes became more frequent.

(b) Head-swinging and bill-touching.—It was apparent by early April that the two woodpeckers were meeting on the top of a tall stub, both birds swinging their heads somewhat as the male, with crest raised and calling *grr,grr*, kept trying to touch the female's bill with his own. This performance was of interest in retrospect, for it became the prelude to copulatory behavior on the same stub. Attempts at bill-touching may represent courtship feeding. On 6 April, when the male had carried a small chip of wood to the top of the stub, his mate ran out her tongue to explore it, then seized it and flew off. I observed a closer simulation of parent-young feeding, however, on 24 April. The male was looking out from the nest entrance when the female made repeated attempts to seize his bill within her own. This event occurred five days before the first egg was laid.

COPULATORY BEHAVIOR

I observed full copulation on 12 occasions between 28 April and 6 May. A first egg was laid on 29 April. Inspection of the nest appeared to upset the pair and I did little further inspecting until 8 May, when there were three eggs. The phases of copulatory behavior were as follows:

(a) Initial signs of interest.—The male fluttered on the female's back on 11 April and by 24 April this pseudo-coition was being preceded by reverse mounting on the part of the female.

(b) The full copulations which began on 28 April frequently took place when I turned on the lights in the aviary at about 6:20 AM, but they might occur at almost any time later in the day. The pair nearly always copulated in the same place. This was the top of the tall stub where the two had done their bill-touching in previous weeks.

(c) Preliminaries.—The female flew to the male as if on signal, just preceding most of the copulations. Indications of the male's readiness might consist of his giving a single *kwirr* or simply arriving at the top of the stub. There were no set preliminaries so far as I could determine.

(d) Reverse mounting.—When the female flew to the male, he was usually in a low crouch as if inviting her by the time she arrived (Fig. 2-Left). She would immediately flutter on his back in reverse mounting (Fig. 2-Center). A medley of *grr*'s at this time might alert me to what was going on, even if I were in another room.

(e) Full copulation.—The male mounted the female directly after the reverse mounting. She assumed no special pose. He sometimes waved his wings during the whole process of copulation but usually only briefly and at the start. Once

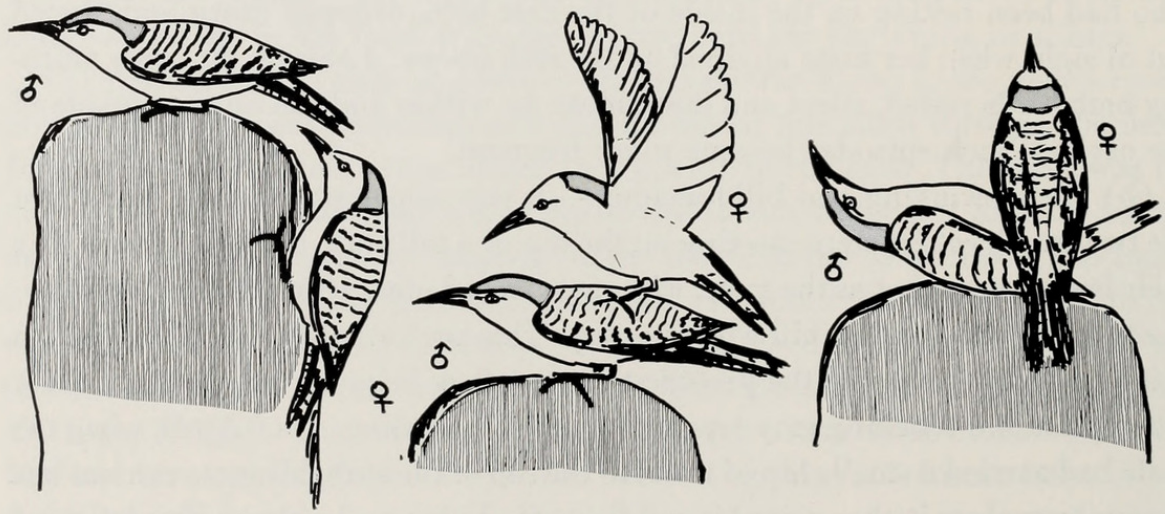

FIG. 2. Copulatory behavior of Red-bellied Woodpeckers. (Left) Male assumes crouching position as female flies to him. (Center) Female flutters on back of male in reverse mounting. (Right) Final position of full cloacal contact, after male had mounted female and fallen to left.

established on her back, he always fell down to the left. His final position was on his back with his body at right angles to hers so that the tails of the two birds were overlapped in cloacal contact (Fig. 2-Right). Southern (1960) has given a description of similar copulatory behavior among Red-headed Woodpeckers.

(f) Female's drive the more persistent.—The female's sexual drive apparently persisted longer than that of her mate as indicated by the fact that the pair might return to the stub within 10 minutes of full copulation, but only reverse mounting would take place. In addition, reverse mountings continued from 7 May through 11 May, although copulations stopped on 6 May.

INCUBATION AND CARE OF YOUNG

(a) Greeting ceremonies.—The female continued to greet her mate at dawn. He would start tapping at the bottom of the cavity when she appeared but there was no mutual tapping or tapping on the outside of the box during the incubation period. The female might respond to the male by tapping at the bottom of the excavation at other times of day. She would then slip out and leave the nest to him. He did the greatest part of the incubating by day as well as remaining in the nest at night. The pair became increasingly quiet as incubation progressed. On 12 May the female came below the entrance and gave a low *grr-ick, grr-ick*, the first time I had heard her give this vocalization since she had been a juvenile.

(b) Hatching.—Events were similar on 18 May and on 9 July, the dates on which the young of the first and second broods, respectively, began to hatch. The female exhibited a sudden change of behavior. She greeted me in the morning by alighting on my head and pounding my skull (which I interpreted as meaning that she needed some new kind of food and quickly). I brought meal-worms which she prepared with much careful crushing and nibbling. She then carried one to the nest and I could hear *chrr,chrr,chrr* notes as the first hatchling was fed. Hatching took place over the course of two days in the case of both broods.

(c) Guarding, brooding, and feeding the young.—The male remained so close to the young during the first week after hatching that we rarely saw him. He would not move, even when I put a light and mirror into the nest. The female continued to be bold and demanding, taking great numbers of meal-worms from our fingers, which he would not do. This led to a peculiar situation. She would take meal-worms to the nest and either enter in spite of his being there or, more frequently, she would give the food to him at the entrance and he would relay it to the young. This relay system took place in both nestings. It was the reverse of what I have described for another species of hole-nesting bird, the Casqued Hornbill (*Bycanistes subcylindricus*), in which the male always feeds the female at the nest entrance (Kilham, 1956).

(d) Nest sanitation and continued excavation.—The nest remained fresh and

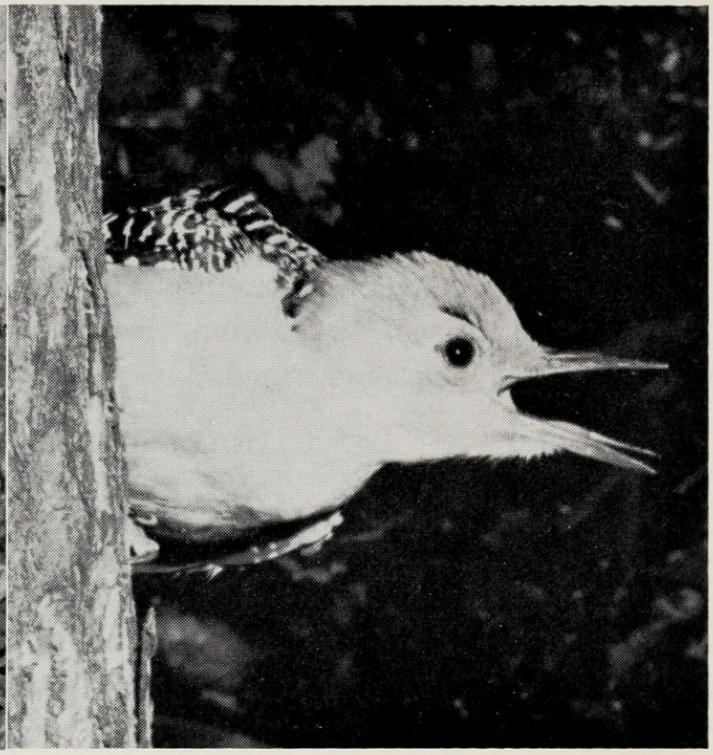

FIG. 3 FIG. 4

FIG. 3. Young Red-bellied Woodpecker on eighth day after hatching in indoor aviary. The position is natural.

FIG. 4. A hand-raised female Red-bellied Woodpecker in threat display, faces a rival female in an adjacent cage.

clean throughout the nesting period and I believe that the parents swallowed the excrements of the young, for they never carried anything away from the nest which we could perceive. It is possible that the male's occasional bouts of excavating provided fresh litter on which the young could rest (Fig. 3).

(e) Young leave the nest.—The three young ones left their nest between the morning and evening of 13 June, 26 days after the onset of hatching. They appeared to leave without any special encouragement from their parents. All three continued to re-enter the nest hole for the next few days. They often made a prolonged, harsh chatter when about in the aviary. These young remained as wild as if they had hatched under field conditions and, since they were unsatisfactory for observation, I had them banded and liberated within three weeks, by which time their parents were already incubating a second clutch of eggs.

(f) Second nesting.—I placed a new nest box in the aviary on 17 June when I noticed a renewal of copulatory behavior. The male did a considerable amount of excavating. I observed full copulation on 25 June, but it had probably taken place before this time, for there were two eggs in the nest on the following day. This was 13 days after the young had left the old nest. The final clutch of four eggs hatched on 9 and 10 July. Due to the lack of a steady supply of meal-worms,

three of the young died within a few days. The fourth one remained in good condition until eight days of age, when I cut the nest box in order to photograph it within the nest (Fig. 3). Both parents were suspicious of the nest after I had wired it together. This led to a neglect of the one remaining young, which died.

DRUMMING

The Red-bellied Woodpeckers did little drumming in the course of their breeding activities. Neither of two captive females, one mated and the other unmated, has ever drummed so far as I know. The male of the pair did his first drumming on 11 April, when he was showing his initial interest in copulation, but there were no indications that the drumming had any special relation to either courtship or pair formation. It appeared to serve as a demonstration against rivals. Most of the male's drumming was done at the edge of a window looking out onto a yard where a wild male called *kwirr* many times a day. I was able to precipitate drumming in another way. On 29 May 1960, when the Red-bellied Woodpeckers had been feeding their young for 10 days, I introduced a female Pileated Woodpecker into an adjacent cage. The reaction was immediate. The male Red-bellied made continuous efforts to attack the Pileated Woodpecker through the wire, calling *chee-wuck,chee-wuck* as he did so and making full threat displays. The two birds jabbed at each other, back and forth. When the larger woodpecker finally lost interest and went about her usual activities, the male Red-bellied drummed for over an hour, completely neglecting his young and keeping as close to his adversary as the wire would permit. The female Red-bellied Woodpecker's reaction to a rival was somewhat different. She paid no attention to the Pileated in the above episode and when faced by a female of her own species in the adjacent cage, the two birds engaged in brief bouts of jabbing and threat displays (Fig. 4). These encounters were always silent affairs, unaccompanied by drumming. Evidence is given below that the male Red-bellied probably regarded the Pileated Woodpecker as being a specific rival.

UNUSUAL BEHAVIOR

Unusual behavior, from unusual circumstances, may influence one's interpretation of more usual activities and this is true of the three examples outlined below, which involved wild as well as captive Red-bellied Woodpeckers.

Relations of captive birds to Pileated Woodpecker.—The hand-raised Red-bellied Woodpeckers have lived in association with flickers, sapsuckers (*Sphyrapicus varius*), and Hairy (*Dendrocopus villosus*) and Downy (*D. pubescens*) Woodpeckers but have not responded to these cage-associates in any special way. They have, on the other hand, reacted in a definite fashion to a female Pileated Woodpecker. Thus it was apparent over many months that both the male and the female Red-bellied Woodpeckers regarded the larger bird as a near approach

to being a male of their own species. My guess is that the crest of the Pileated served as an exaggerated releasing mechanism. The fact that this bird was the only one in the aviary to have a crest of the same red color and silky texture as that of a male Red-bellied Woodpecker offered some support for this hypothesis. I have described phenomena of a similar nature elsewhere (Kilham, 1959*c*). In this latter situation it was the lone female Pileated Woodpecker which exhibited a vigorous and constant reaction to a female Yellow-bellied Sapsucker. The reactions of the captive male and female Red-bellied Woodpeckers to their larger associate may be outlined as follows:

(a) Reactions of female.—One of our two hand-raised female Red-bellied Woodpeckers has never had a mate. This female began to show an interest in the Pileated Woodpecker when she first assumed adult plumage in the fall of 1958. The attraction has persisted over the course of two breeding seasons, as indicated by the following activities: flying to the Pileated's roost box and tapping at dawn; following the Pileated about and tapping wherever it might be pecking and, in addition, calling *grr, grr* when the larger bird came close. These forms of behavior were similar and comparable to those of the mated female described in a separate section above.

(b) Reactions of the male to the Pileated Woodpecker.—The aggressiveness of the male Red-bellied Woodpecker toward the Pileated, also described above, has persisted for one and one-half years, making it impossible to keep the two birds in the same cage. Whenever I have done so, the Pileated Woodpecker has hidden in its roost box all day. The male has kept it there by perching within a few feet of the entrance, constantly bowing its head and making the vocalizations *cha* or *cha-aa-ah.*

Aberrant breeding call.—The following situation, in which a wild male Red-bellied Woodpecker in Seneca Swamp gave the breeding call of a Red-headed Woodpecker in complete exclusion of that of its own species, may have reflected the relation which appears to exist between *Centurus* and *Melanerpes* (Kilham, 1959*a*). Red-headed Woodpeckers over-winter in the swamp in some years. In 1956–57 they began to give their breeding call, a *quee-ark*, before migrating to breed elsewhere (Kilham, 1958*b*) and on 2 May, after the last of them had left the main swamp, I observed a male Red-bellied Woodpecker calling the same *quee-ark*. The vocalization was in sharp contrast to the *kwirr*'s of neighboring males. I located the nest hole of the *quee-ark*-male three days later and I was able to follow his activities and those of his mate for the next three weeks. The male never called *kwirr* during this or subsequent periods of observation. His other vocalizations were typical of those of his own species. I did not hear him again until 15 December 1957, when the Red-bellied Woodpeckers of Seneca Swamp experienced a short ourburst of breeding behavior. The *quee-ark*-male was still in the same area in which he had nested in May. My next encounter with this

individual was 500 yards away when, on 12 May 1958, he and his mate had a prolonged conflict over a nest hole which belonged to the latter birds. I have never heard a male Red-bellied Woodpecker call *quee-ark* since that time.

Attacks of lone female on nesting pairs.—The following incidents parallel those which I have described among breeding Casqued Hornbills (Kilham, 1956). Whether the females of both species of hole-nesting birds were prompted to attack the nests of others of their own kind due to the lack of a mate or to the loss of one, I could not determine. The observations on the Red-bellied Woodpecker were as follows:

I was standing below the nest hole of Pair E on 4 May 1957, when an intruding female (IF) flew to the entrance 15 feet above me. Female E was on the inside, presumably incubating her eggs. The two females jabbed at each other vigorously and small feathers floated down. IF had flown in to renew these attacks four times within a minute when Male E arrived and pecked savagely at the rear of the intruder while his mate engaged her head-on within the entrance. The intruder then took flight with Male E in pursuit. By the next morning IF had transferred her attacks to Pair F. This pair of Red-bellied Woodpeckers had a nest 100 yards from that of Pair E and I watched the conflicts which centered on it from 10:15 until 11:40 AM. They followed a rather constant pattern. Male F would chase the intruder through the surrounding woods to the accompaniment of *cha*'s and *chee-wuck*'s, then return to his nest hole and pop inside. IF would return immediately. Male F would come out to drive her away and another pursuit would follow. Female E took almost no part in the conflicts, even when all three woodpeckers were together in the same tree. It is possible that the IF was attracted by the noise of young within this second nest for at one time she arrived with food in her bill, only to be driven away as abruptly as before.

SUMMARY

Vocalizations, drummings, and displays of Red-bellied Woodpeckers have been studied in relation to their breeding behavior. Observations regarding this behavior may be summarized as follows:

(1) The male takes the initiative in location of a nest hole and seeks the approval of his mate in a ceremony of mutual tapping. He spends more time by the nest hole than she does. The members of a pair, however, remain in contact with each other by an exchange of vocalizations within their nesting territory. If a female leaves her nesting territory, her mate may call incessantly until she returns.

(2) Red-bellied Woodpeckers are pugnacious birds. Described are various types of conflicts centering on issues such as the possession of a nest hole, or on the rivalry for a mate and territorial boundaries.

(3) Acceptance of a nest hole by the female may be delayed until seasonal conditions are favorable. Full acceptance by the female is indicated by the two members of the pair completing the excavation, entering the nest hole together and resting motionless in each other's proximity either within or on the outside of the nest cavity. Copulatory behavior increases in frequency at this time.

(4) The phases of copulatory behavior usually consist in the male assuming a crouching pose as the female flies to him and flutters on his back in reverse mounting. The male then mounts her in full copulation, gradually falling to the left.

(5) Paired Red-bellied Woodpeckers become quiet at the time of egg-laying and incu-

bation. The newly hatched young are brooded by one parent or the other for much of their first week and, as they grow older, they are fed insects of increasing size.

(6) Fecal sacs have not been seen among either wild or captive birds. Parent Red-bellied Woodpeckers apparently keep their nests clean by swallowing the excreta of their young.

(7) The reactions of nestlings were studied by means of hand-raised individuals. Their begging and begging cries were stimulated by sudden shading if they were on a lighted area or by jarring if they were in the dark. The range of their vocalizations was considerable.

(8) A pair of hand-raised Red-bellied Woodpeckers bred in their first year in an indoor aviary. They reared three young in their first nesting and a second nesting was equally successful to the point of hatching but had to be interrupted due to extraneous circumstances.

(9) Copulation, including the preliminary reverse mounting by the female, is described in detail.

(10) Juveniles may leave their parents within a few weeks in the event of a second nesting. Otherwise, they may remain with them for several months until family groups break up in September.

(11) Three examples of unusual behavior are described. One concerned a male Red-bellied Woodpecker which gave the breeding call of a Red-headed Woodpecker to the exclusion of its own; and another, a lone female which attacked the nest holes of two mated pairs. A third situation concerned the peculiar and persistent reactions of male and female hand-raised Red-bellied Woodpeckers to a Pileated Woodpecker kept in the same aviary.

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