A COMPARISON OF SOME ASPECTS OF THE BREEDING ECOLOGY OF RED-HEADED AND RED-BELLIED WOODPECKERS IN KANSAS

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Red-headed and Red-bellied woodpeckers (*Melanerpes erythrocephalus* and *Centurus carolinus*) are similar-sized species that are sympatric throughout much of eastern North America. The species are conventionally generically separated (as in the Check-list of the American Ornithologists' Union, 1957), but the distinction is questionable (Kilham 1959, Selander and Giller 1963). Agonistic interactions have been observed frequently between these species (Kilham 1958b, Reller 1972). In spite of their obvious similarities and possible systematic relationship, it is intuitive that these species are different enough in some behavioral or ecological way to allow them to exist sympatrically.

From September 1966 to July 1970, I studied various aspects of the ecology of these species in Kansas. In this paper I will compare aspects of the breeding biology of Red-headed (RH) and Red-bellied (RB) woodpeckers, emphasizing the timing of breeding, variables of the nest site, activity of the adults at the nest, and foraging behavior of the adults. The purpose of this paper is to identify those differences between the species that allow them to coexist.

MATERIALS AND METHODS

In addition to personal observations, quantitative and temporal data relating to the breeding biology of Red-headed and Red-bellied woodpeckers were obtained from the nest record files at The University of Kansas, Kansas State University, Fort Hayes State College, Emporia State Teachers College, and Bethel College.

Unless otherwise stated, observations were made at nests in Douglas County. To facilitate studying the activities of adults and nestlings in the nest, I opened three nests of RH and three nests of RB woodpeckers at the back and fitted them each with a glass window. A blind was built at the back of each of these nests (fig. 1) to allow observations from approximately 1 m away (see Jackson 1970 for details). When the blinds were not in use, the windows were covered with black roofing paper. I captured the female before the last egg had been laid at two RH nests, and by lightly pressing on the bird's abdomen was able to feel a shelled egg and thus identify the sex. These color-banded birds then enabled me to record the roles of the sexes through the remainder of the nesting period.

Frequency data were analyzed using the chi-square test, and a *t*-test was used to compare sets of measurements.

RESULTS AND DISCUSSION

DISTRIBUTION AND STATUS OF THE SPECIES IN KANSAS

Red-headed Woodpeckers are migratory, but the species can be found in Kansas at any season. In the winter, they are most common in the southeastern part of the state where they congregate in oak-hickory woods and forage primarily on acorns. In eastern Kansas the species breeds along woodland edges and in isolated trees, occasionally even in buildings or utility poles. In the western half of the state this species is most numerous along the narrow strands of cottonwood and willow that flank the larger (though often ephemeral) rivers. Some individuals can be found breeding in utility poles far from the nearest trees.

Red-bellied Woodpeckers are non-migratory and the species is restricted primarily to the eastern half of the state. Schwilling (1954) reported the species from Finney, Kearney, and Morton counties in southwestern Kansas, and Ely (1971) reported scattered sightings of the species in Ellis County in central Kansas, though he had found no evidence of breeding. Rising (1974) reported the species as an "uncommon and local resident" in Comanche, Rawlins, Decatur, and Hamilton counties.

Johnston (1964) listed one race of the RB Woodpecker (*C. c. zebra*) and two races of the RH Woodpecker (*M. e. erythrocephalus* and *M. e. caurinus*) in Kansas. Behavioral data included in this study are from eastern Kansas and, thus, refer to conventional *C. c. zebra* and *M. e. erythrocephalus*. Nest site and temporal data on nesting include records of both races of the RH Woodpecker.

PHENOLOGY OF BREEDING

Records of 38 nests of RH and 43 nests of RB woodpeckers are summarized in figure 2. These indicate a degree of non-overlap that probably reflects seasonal population movements of the RH Woodpecker in Kansas. The mean dates for records of nest excavation, eggs, and young in the nest for RB Woodpeckers are all significantly earlier than are

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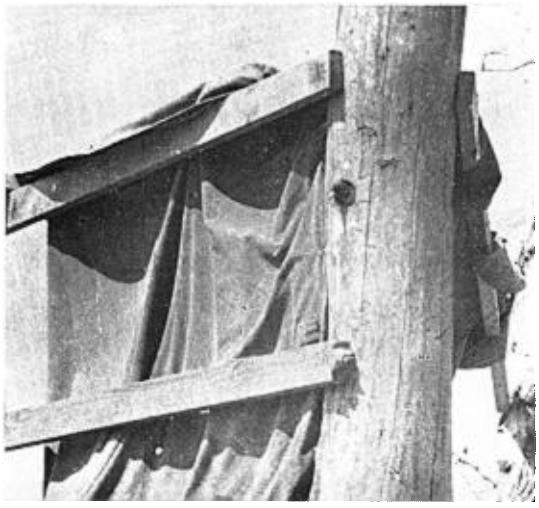

FIGURE 1. Blind erected at a Red-headed Woodpecker nest and used to study activities inside the nest.

the mean dates for RH Woodpeckers ($P \leq .05$).

The latest record for nest excavation by RH Woodpeckers is 11 June in Morton County (extreme southwestern Kansas). All other records of excavation are from eastern Kansas. Records of eggs and young for RH in western Kansas were all within the range of dates for records from eastern Kansas, though the four egg dates for the west averaged four days later (15 June) than the 11 for the east (11 June). Likewise, five records of young RH in the nest in western Kansas averaged seven days later (1 July) than the eleven records from the east (24 June). While sample sizes are inadequate to demonstrate temporal differences in the breeding schedule of eastern and western populations of the RH Woodpecker in Kansas, such a difference would not be unreasonable considering the rise in elevation from east to west.

NEST SITE VARIABLES

I compared several parameters of the nest sites of RB and RH woodpeckers (tables 1–3). Qualitatively (table 1), RH Woodpeckers prefer ($P \leq .01$) nest trees that are surrounded by 30 m or more of open space, whereas RB Woodpeckers characteristically nest ($P \leq .01$) in more wooded areas. Both species show a preference for nesting in dead trees (RH, $P \leq .01$; RB, $P \leq .05$) and, when nesting in a live tree, will excavate either in a dead limb or into the dead wood of a live limb through the stub of a broken off branch. Reller (1972) found that in Illinois RH nested in dead trees

TABLE 1. Qualitative characteristics of Red-headed and Red-bellied woodpecker nest sites.

	Red-headed		Red-bellied	
	N	%	N	%
Nest Tree				
1. Isolated	15	88.2	4	15.4
Not isolated	2	11.8	22	84.6
2. Live	3	12.0	8	26.7
Dead	22	88.0	22	73.3
Nest Limb				
1. Intact	4	25.0	3	25.0
Stub	12	75.0	9	75.0
2. Bark	1	8.3	6	54.5
No bark	11	91.7	5	45.5
3. Crack	7	100.0	1	20.0
No crack	0	0.0	4	80.0

but that RB favored a dead limb in a live tree. Both species also prefer (RH, $P \leq .05$; RB, $P \leq .10$) a broken off stub to an intact limb. Such a preference is understandable in terms of the relative ease that rain can saturate the stub from the top, facilitating decay which makes cavity excavation easier. A pair of RH Woodpeckers used the same nest limb 3 years in a row, each year excavating a new cavity below the one from the previous year. One of the RH pairs I watched used the same nest limb two years in a row, again building the second nest below the previous one. Many of the nests of both species that I found had previously excavated cavities above them, suggesting that this is a common phenomenon. It seems likely that this practice may also be related to the progressive deterioration of the limb from above. One RB nest had a passage-way connecting the nest cavity to the one above. Neither of these species practices strict nest sanitation and the combination of nestling feces, loose wood chips and bits of lost food makes a fertile chamber for the growth of fungi and decay-causing bacteria. I opened one RB nest four days after the young had fledged and found mushrooms growing in the cavity (fig. 3).

Red-headed Woodpeckers favored limbs without bark ($P \leq .01$), while RB Woodpeckers showed no preference with regard to this parameter. Excavation of all of seven RH nests examined was begun at a pre-existing crack in the nest limb. The shape of the entrance hole was usually influenced by the position and angle of the crack (fig. 4). In some cases the crack line formed the bottom of the entrance, giving it a flat surface. In other instances the birds excavated from both sides of the crack, giving the entrance the

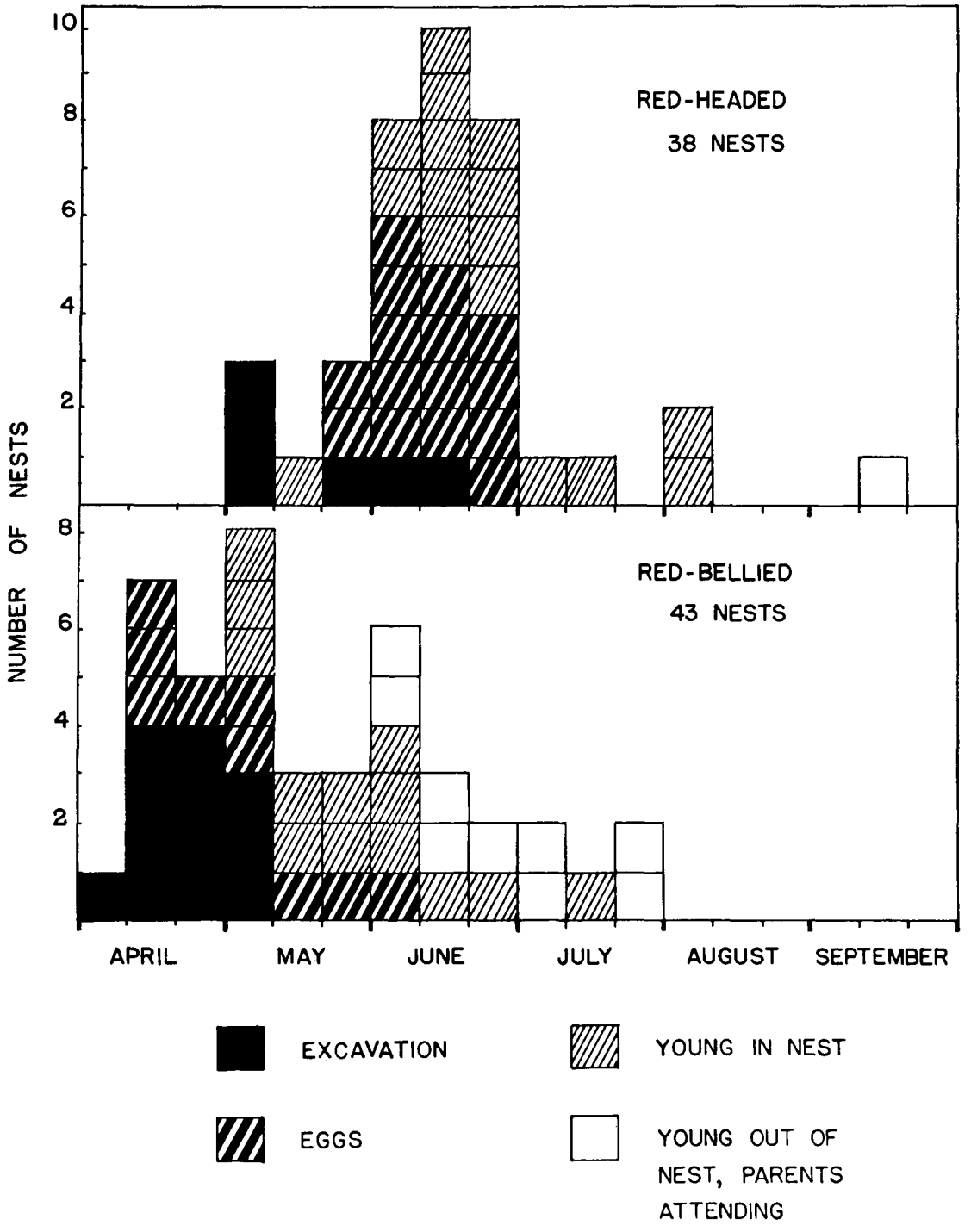

FIGURE 2. Nesting phenology of Red-headed and Red-bellied woodpeckers in Kansas.

shape of a pointed ellipse. Of five RB nests examined for cracks, only one had a crack passing through the entrance; this crack did not influence the shape of the cavity entrance. The preference of RH for using a crack as a starting place for excavating a nest hole is an adaptation which facilitates initial excavation and also provides access and a suitable environment for fungi that can weaken the inner wood.

The means for height of the nest tree, height of the nest within the tree, and the diameter of the nest limb are similar for the two species (table 2). Reller (1972) also found no sig-

FIGURE 3. A Red-bellied nest cavity opened four days after the young had fledged. The dampness of the cavity and accumulated debris facilitated the growth of mushrooms shown here.

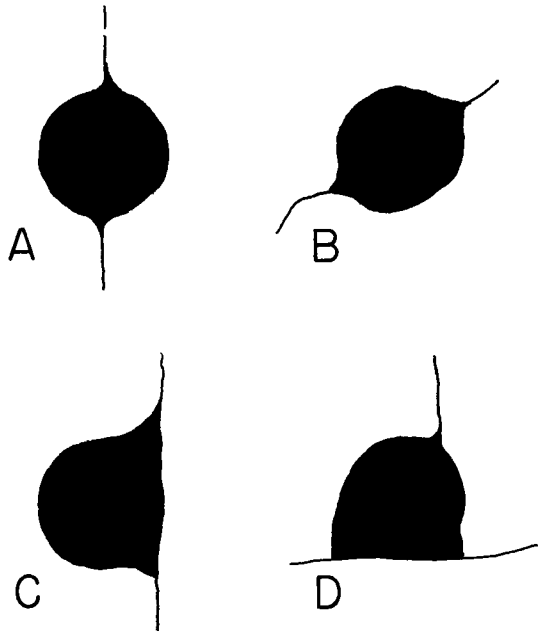

FIGURE 4. Outline of four Red-headed Woodpecker nest entrances indicating the influence of existing cracks on entrance shape.

nificant differences in the heights at which these species excavated their cavities, though her data from an Illinois population differ significantly from those presented here ($P \leqslant .05$). Reller found the mean nest height for these species to be 14.3 m for the RB and 12.4 m for the RH—nearly double the means for Kansas. Reller did not include data on nest tree height, but it appears that the trees at the Illinois sites are larger, and the geographic differences, while real, are a consequence of the available habitat.

I found no significant differences between RH and RB with regard to the tree species they use for nest sites (table 3). Both species relied on American elms (*Ulmus americana*) for nearly fifty percent of their nests. This apparent dependency on elms probably reflects death of large elms to Dutch elm disease in recent years and their consequent availability to the woodpeckers.

I measured the dimensions of 3 nests of each species that I opened for study of the activities inside (table 4). These measurements included the vertical and horizontal diameter of the entrance at the outside, the depth from the bottom of the entrance hole to the top of the chip layer at the bottom of the cavity, the thickness of the front and back wall of the cavity on a plane with the bottom of the entrance, and the greatest and smallest diameters of the cavity, measured on the plane of the greatest diameter. The dimensions for the two species are similar though the size of the entrance of each of the RH nests was

TABLE 2. Mensural characteristics of Red-headed and Red-bellied woodpecker nest sites.

	N	Mean	Range	S.D.
Red-bellied				
Height of nest tree (m)	14	9.9	5–18	3.43
Height of nest (m)	38	7.6	2–18	3.31
Diameter of nest limb (cm)	16	21.6	13–38	8.94
Red-headed				
Height of nest tree (m)	10	10.9	4–24	5.89
Height of nest (m)	34	7.0	3–15	3.53
Diameter of nest limb (cm)	10	21.8	13–36	7.77

TABLE 3. Tree species used for nest by Red-bellied and Red-headed woodpeckers.

Nest trees	Red-headed (N)	Red-bellied (N)
American Elm (*Ulmus americana*)	14	19
Cottonwood (*Populus deltoides*)	9	3
Willow (*Salix* spp.)	3	7
Oak (*Quercus* spp.)	2	3
Box elder (*Acer negundo*)	0	3
Shagbark hickory (*Carya ovata*)	0	3
White Ash (*Fraxinus americana*)	0	2
Sycamore (*Platanus occidentalis*)	0	1
Utility pole	2	0
Total	30	41

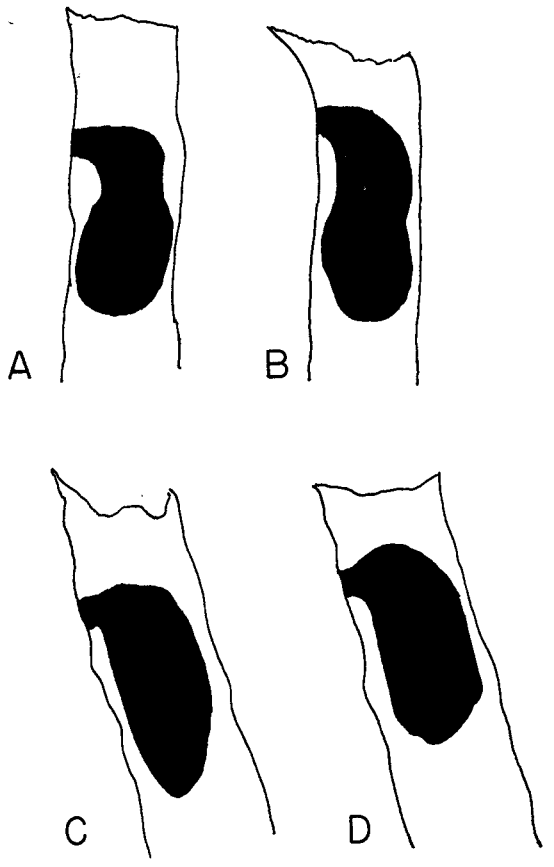

FIGURE 5. Side view of two Red-headed (A, B) and two Red-bellied (C, D) woodpecker nest cavities.

slightly larger than that of any of the RB nests. All cavities were generally gourd-shaped, but there was considerable variation as exemplified in figure 5.

One nest site characteristic that I did not collect quantitative data on but which appears to influence these species in different ways is the angle of the plane of the potential nest entrance with respect to the ground. Every RB nest I have seen has been on the underside of a limb or leaning trunk. The advantage of such a nest site is that it is protected from the weather. Red-headed Woodpeckers, however, do not seem to be so selective. I watched a RH excavating a cavity on the upper side of a barkless American elm stub; the plane of the nest entrance was about 100° with respect to the ground. A similar nest was usurped by a pair of Starlings (*Sturnus vulgaris*), but after a heavy rain, was filled to the entrance with water. The preference of RH for limbs with cracks in them may not only facilitate excavation, but also provide drainage for their more exposed nests. In the case of the Starlings, their bulky nest plugged the crack and prevented drainage.

NEST EXCAVATION

Both sexes assist with the excavation of the nest cavity in RB and RH woodpeckers. In April of 1969 I watched for about 5 hours as a pair of RB excavated at a cavity that a bird could almost completely enter. During that time the male worked for periods of up to two hours without a break. Periodically the female would come to relieve him. He was generally gone from the cavity for no more than 5 to 10 minutes. She generally inspected the cavity, gave a token peck or two, and rarely threw a few chips from the hole. Only once did she appear to make any real effort to assist with the excavation, and this lasted for 8 minutes. On the other hand, a female RB at a nest in Linn County worked shifts of 22 and 25 minutes to those of 8 and 12 minutes for her mate. During one of the female's shifts the male preened in a tree about 20 m away. Kilham (1958a) and Stickel (1965) noted that participation of the female RB in nest excavation increases as the cavity nears completion.

In a similar manner, one of a pair of RH did most of the early excavation at a cavity. On the afternoon of 25 May 1969 a RH worked continuously at a cavity for an hour and 42 minutes. Once the cavity was large enough for a bird to enter out of sight a sec-

TABLE 4. Dimensions of Red-bellied and Red-headed woodpecker nest cavities (cm).

	Mean limb diameter	Entrance diameter		Cavity depth	Wall thickness		Cavity diameter	
		Vertical	Horizontal		Front	Back	Greatest	Smallest
Red-headed								
	21.6	7.0	5.4	24.1	14.0	1.3	13.3	8.3
	16.5	7.4	7.6	26.7	2.5	3.8	10.8	10.5
	15.9	6.4	5.7	22.9	3.6	1.9	11.2	8.6
Red-bellied								
	19.8	5.7	5.7	23.5	3.2	6.4	12.8	8.3
	17.8	6.2	6.4	22.9	5.1	1.5	12.1	9.5
	21.6	5.1	5.7	32.4	—	—	14.6	—

FIGURE 6. Newly hatched Red-headed Woodpeckers and two unhatched eggs resting on wood chips provided by the parents during incubation.

ond bird assisted equally with the excavation. This cavity was begun on 20 May 1969 and was complete by 5 June (the first egg was laid on 6 June); thus excavation took about 17 days.

While the nest cavity is essentially complete before egg-laying begins, in the case of one RB and two RH nests that were opened before the clutch was complete, I found that the first eggs were laid on a thin layer of small wood chips (chips between .3 and .5 cm long and .2 and .3 cm in diameter). After the second or third egg, however, the birds continued adding chips to the bottom of the nest, the chips now ranging from .5 to 1.0 cm in length (fig. 6). Throughout the first three to four days after the eggs hatch the adults occasionally pecked more chips from the walls of the cavity. After this no more chips were added and the nests became quite dirty.

In both species the excavating bird used its beak as a chisel, hitting the wood at an angle of less than 90 degrees. Generally the beak was slightly open while the bird excavated. Occasionally a bird would grab a splinter in its beak and break it off. While excavating from the outside a bird would toss chips over a shoulder; once a bird was working inside the cavity it seemed as if it allowed chips to fall to the floor, since only occasionally did it come to the entrance with a beak full of chips to be released.

COURTSHIP AND OTHER INTERACTIONS OF ADULTS AT THE NEST

As pointed out by Kilham (1958a, 1961), the nest site seems to be the focus of RB courtship activities; this is also true for RH. Three distinct behavioral components have been described as part of the courtship of Red-bellied Woodpeckers: mutual tapping, reverse mounting, and copulation. Excellent accounts of these components have been presented by Kilham (1958a, 1959, 1961), Stickel (1965), and Reller (1972). My observations of RB Woodpeckers do not differ from these earlier studies, but confirm that all three components do occur from the beginning of nest excavation until the end of incubation. Further, the components are often performed sequentially as well as individually. When two or all of these patterns are linked, the sequence always observed has been: mutual tapping, reverse mounting, copulation. The complete sequence is not necessary for successful copulation.

I have observed the same behavior to also be characteristic of RH Woodpeckers. Kilham (1959) described mutual tapping as it occurs in RH and, indeed, suggested that RH and RB are more closely related than previously supposed because of this shared behavior pattern. On 5 June 1969 I observed reverse mounting followed by an unsuccessful copulation attempt at a nearly completed RH nest. Southern (1960) described the copulatory behavior of RH Woodpeckers; it is remarkably similar to that of RB. Kilham (1961) mentioned that the male RB Woodpecker occasionally flutters his wings during copulation; I have observed this in RH as well. Southern (1960) suggested that the female RH may always perch parallel on the branch for copulation. I observed a copulating pair of RH in Linn County on 18 May 1969, with the female perched across the branch.

Vocalizations from or near the nest were common in RB but infrequent in RH. This difference between species was also noted by Reller (1972). The *kwirr* call of RB seems to be the equivalent of the *queeark* of RH as suggested by Kilham (1959). These calls serve not only to call the mate back to the nest (Kilham 1959, Reller 1972) but may also call a mate from the nest. On 1 June 1969 as I was sitting in a blind watching an incubating male RB, I heard another RB give two *kwirr* calls about 20 m away. The male immediately lifted his head, gave a responding *kwirr* while still down within the nest, went to the cavity

entrance, paused, then left. The female immediately entered to incubate.

Both RH and RB frequently exchange a chattering call as one parent arrives at the nest with food and the other parent is present. Kilham (1961) reported this call for RB. The chattering is hard to describe, but I have it recorded as *rrr rrr* and *cuh cuh cuh cuh*, each repeated many times, for RH and RB respectively. In both species the chattering is most frequently heard for the first four to five days after hatching while the young are still being brooded.

In one instance I observed tapping in response to chattering. On 19 June 1969 as I watched a brooding female RH, the male arrived at the cavity chattering, the female immediately moved to the front wall of the cavity and began tapping slowly. She then moved to the entrance and left. The male entered to feed and brood the young without response.

TIME OF LAYING, CLUTCH SIZE, INCUBATION PERIOD, AND TIME OF HATCHING

I have records of complete clutches for 8 RH nests (2 nests of 3 eggs, 4 nests of 4 eggs, 2 nests of 5 eggs) averaging 4.0 eggs/clutch and for 7 RB nests (1 nest of 6 eggs, 5 nests of 5 eggs, 1 nest of 4 eggs) averaging 5.0 eggs/clutch. In the RH and RB nests that I opened, inserted a window and watched from a blind, the birds began sitting on the eggs for short periods after the second egg had been laid. It wasn't until the last egg had been laid, however, that incubation began in earnest. In both species one egg was laid before 08:00 each day until the clutch was complete. The incubation period was about 12 days for both species, though there was variation within a single nest if the beginning of incubation is reckoned from the laying of the last egg. For example, at a RH nest the last of 4 eggs was laid before 08:00 on 9 June 1969 and the birds began nearly continuous incubation. The first two eggs hatched between 07:45 and 08:30 on 20 June, the third egg hatched between 17:50 and 18:30, but the fourth egg didn't hatch until approximately 14:00 on 21 June. At another RH nest in the same area, 2 young hatched the morning of 20 June, the third hatched early on 21 June, and the fourth hatched before 08:00 on 22 June. Similar asynchronous hatching was characteristic of RB Woodpeckers. After 12 days of full incubation one egg hatched at about 11:30 on 2 June 1969. A second egg had hatched by 13:30, though it hadn't been pipped at 11:30. At about 09:00 on 3 June the third egg hatched, and by 09:00 on 4 June the last egg had hatched.

INCUBATION AND BROODING

I collected too few quantitative data to statistically demonstrate differences in the roles of the sexes in incubating and brooding during the day. The males of both species did all of the incubating and brooding at night. In both species periods of attentiveness during the day averaged longer during incubation (RH = 35.5 min., RB = 18.9 min.) than during brooding (RH = 7.6 min., RB = 10.4 min.). Perhaps because of large variances and small sample sizes (incubation periods: RH N = 8, RB N = 16; brooding periods: RH N = 24, RB N = 37), I could discern no significant differences between the species.

Boone (1963) stated that female RB did most of the incubating at nests he studied in Kansas. Stickel (1965) found no significant difference in the time spent incubating by male and female RB when data from nine Illinois nests were pooled. He noted that at some nests the female did more of the incubating. Reller (1972) indicated that Kendeigh (1952) stated that male and female RH Woodpeckers share incubation duties during the day and that the male incubates at night. However, Kendeigh did not mention *Melanerpes erythrocephalus*, but rather, referred to *Melanerpes* (*Centurus*) *chrysauchen*.

In both species, when a parent entered the nest to incubate or brood the young, it entered head first, walked head first down the entrance wall with feet spread far apart, turned around while raising the tail so it wasn't in the way, bared the brood patch, then settled down over the eggs or young. Once down, the parent typically fluffed its feathers, then relaxed its wings so they rested on the bottom of the cavity. The bill was either rested against the wall of the cavity with the head held up, or it was tucked under the feathers on the back. Often the parent closed its eyes as if asleep.

During very warm weather both species perched inside the entrance of the cavity, panting instead of incubating or brooding. At times with both species, the parents took turns at the nest without actually incubating or brooding for two hours or more. During cool or rainy weather both sexes of both species incubated and brooded for longer periods.

By viewing the incubating and brooding birds within the nest from a blind I was able to observe that both species are easily dis-

TABLE 5. Observations of foraging behavior of Red-bellied and Red-headed woodpeckers from April through July.

	Red-headed		Red-bellied	
	N	%	N	%
Pecking	2	3.2	1	2.9
Gleaning	3	4.8	21	61.8
Excavation	1	1.6		
Flycatching	27	43.5		
Fruits and seeds	11	17.7	10	29.4
Sap			1	2.9
Stooping	18	29.0	1	2.9
Total	62		34	

turbed by human activities. For example, as I watched a male RH incubating on 14 June 1969, it hurriedly left the eggs and scrambled to the nest entrance 12 times in two hours and 37 minutes, as ten vehicles and a boy on a horse passed along a gravel road 7 m away and as an airplane flew by at least a km away. RB behaved similarly.

FORAGE BEHAVIOR OF ADULTS AND FEEDING OF THE NESTLINGS

I divided the foraging behavior of the adult birds into six categories: pecking or brief excavation, lengthy excavation, surface gleaning, eating fruits or seeds, drinking sap, and stooping. I use the term, "stooping," to refer to a bird flying to prey on the ground. Characteristically stooping occurs from an observation post where the woodpecker will regularly perch. Flycatching also is generally from such a perch in RH Woodpeckers. Table 5 summarizes observations of foraging in these species from April through July. Red-headed Woodpeckers devote much of their foraging activity to flycatching and stooping, RB Woodpeckers get most of their food by gleaning tree surfaces. Both species make frequent use of ripening mulberries and other fruits and seeds.

The sexes of each species shared equally the task of feeding the nestlings for about the first 12 days (table 6). From day 13 to fledging the female of each species fed the young more frequently—significantly so in RH ($P \leq .05$). This division of nestling life is clearly marked by the opening of the nestlings' eyes and the emergence of the first sheathed feathers.

The food brought to nestlings (table 7) clearly reflects the differences in foraging behavior of the adults. The frequency with which RB Woodpeckers brought wood roaches (Blattidae) to the young prompted me to search for these myself to see where the birds were getting them. I never found wood roaches on the surface of a healthy tree, but found them readily in crevices and under the loose bark of dead, dying, and injured trees. The RH Woodpeckers caught the grasshoppers by stooping and the adult beetles by flycatching.

ENCOUNTERS BETWEEN RH AND RB

I observed few encounters between RH and RB. These are described below:

7 June 1969. A pair of RH were at their nest tree where two eggs of an eventual 4-egg clutch had been laid. A male RB landed on a utility pole about 30 m from the nest. He gave no call, but was immediately seen by the RH. One RH flew toward the RB; the second RH followed. The RB left with the RH chasing him.

8 June 1970. A male RB was incubating when a RH landed in the nest tree. The RH peered and poked around the tree, coming within 3 m of the RB nest without a response from the RB.

13 June 1970. A RH landed in the nest tree of a pair of incubating RB and began hitching around the tree as if gleaning insects from the surface. The male RB immediately stuck his head from the entrance of the nest and remained quietly in this position. The RB withdrew into the cavity and the RH flew to the cavity and briefly stuck his head inside. The RH then flew to an adjacent limb. Within seconds the RH flew directly at the RB cavity in a fluttering flight, all the time giving very loud *kuk kuk kuk* calls. The *kuks* were given at 3–5 second intervals. The female RB, apparently attracted by the calls of the RH,

TABLE 6. Division of labor between the sexes in feeding nestling Red-headed and Red-bellied woodpeckers. Data are from two nests of each species.

	Red-headed				Red-bellied			
	Male		Female		Male		Female	
Age of young	%	(N)	%	(N)	%	(N)	%	(N)
1–12 days	48.6	(18)	51.4	(19)	51.7	(30)	48.3	(28)
13 days—fledging	24.2	(8)	75.8	(25)	41.7	(10)	58.3	(14)

TABLE 7. Food items brought to nestling Red-bellied and Red-headed woodpeckers.

	Red-headed		Red-bellied	
	N	%	N	%
Vegetable				
Mulberry	7	28.0	6	26.1
unidentified	1	4.0		
Animal				
Earthworm	1	4.0		
Spider	1	4.0	1	4.3
Lacewing			1	4.3
Wood roach			10	43.5
Grasshopper	6	24.0		
Katydid	1	4.0		
May beetle (adult)	3	12.0		
Beetle (adult)	3	12.0		
Beetle (larva)	2	8.0	3	13.0
Moth			1	4.3
Caterpillar			1	4.3
Total	25		23	

appeared and actively chased the RH from the area. The male RB remained in the cavity.

EVOLUTIONARY AND ECOLOGICAL SIGNIFICANCE OF THE SIMILARITIES AND DIFFERENCES IN THE BREEDING BIOLOGY OF RED-HEADED AND RED-BELLIED WOODPECKERS

The data presented above further demonstrate similarities between RH and RB woodpeckers. The two species are similar not only in size, but also in their courtship, copulatory behavior, vocalizations, choice of tree species and limb stubs for nest sites, nest height, nest limb diameter, incubation and brooding period and behavior, and in their use of mulberries as food for their nestlings. Nest site and food selection might be interpreted in terms of availability and similarity in size of the species without invoking a close phylogenetic relationship. The similarities in courtship and related behavior coupled with the occurrence of interspecific territorial conflict demand a phylogenetic interpretation. I concur with Peters (1948), Kilham (1959), and Mayr and Short (1970) that these species should be treated as congeners.

Competition between these species in Kansas is minimized and their coexistence made possible by differences in nesting habitat (RH nest in more open areas than RB), by differences in foraging behavior (RH forage more by flycatching and stooping during the breeding season and rarely by tree surface gleaning as RB typically forage), and by differences in breeding phenology (RH nest later than RB). Some of these differences have been noted in other geographic areas (e.g., Selander and Giller 1959, James 1971, Reller 1972). These differences may have originated as a result of the seasonal movements of RH Woodpeckers and the sedentary existence of RB Woodpeckers. RB, because they are non-migratory, don't have to establish a new territory each spring and may initiate their reproductive cycle earlier. Because of the interspecific territoriality and the established RB territories, RH (even if they preferred the same nesting habitat as RB) might be expected to be relegated to marginal areas just as late arrivals within some migratory species have to settle for "less desirable" territories (Brown 1969). The differences in breeding phenology likely facilitate the coexistence of the species not only by effecting their spatial separation, but also by minimizing conflict when the species do meet. If the species were establishing territories, courting, and selecting nest sites simultaneously, coexistence might not be possible. As it is in Kansas, RB territories are established before most RH arrive and by the time RH begin establishing territories and courting, the RB are literally too busy with nest excavation and incubation to get involved in more than an occasional skirmish near a nest.

Since the nest site characteristics of the two species are similar except for general habitat, it seems reasonable that the lesser quality of the RH's habitat (in terms of the preferences of most woodpecker species) may largely be related to the availability of food. In adapting to a habitat with fewer trees, ancestral RH, like ancestral flickers (*Colaptes* sp.) (Short 1972), had to abandon typical woodpecker modes of foraging and were successful in doing so.

SUMMARY

Red-headed (RH) and Red-bellied (RB) woodpeckers in Kansas have similar courtship, copulatory behavior, vocalizations, choice of tree species and limb stubs for nest sites, nest height, nest limb diameter, nest dimensions, incubating and brooding behavior, and preference for feeding mulberries to their nestlings. Red-headed Woodpeckers prefer nest limbs without bark and start their nest cavities at a pre-existing crack. The species differ in that the RH breeding cycle starts later than that of RB, RH prefer to nest in open areas whereas RB nest in more wooded sites, and RH forage extensively by flycatching and stooping during the breeding season whereas RB forage more by tree surface gleaning. These differences between the

species may be related to migratory and nonmigratory habits of RH and RB, respectively, and are likely the factors that allow these species to exist sympatrically over much of eastern North America.

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