COURTSHIP AND THE PAIR-BOND OF PILEATED WOODPECKERS

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ABSTRACT.—Among woodpeckers of eastern North America, the pair bonds of Pileated Woodpeckers (Dryocopus pileatus) appear to be among the strongest on a year-round basis. This report describes the courtship behavior of these birds as seen through the nesting period, chiefly at times of changeovers at the nest. While tapping was the most frequent method of intrapair communication early in the nesting period, woicks, given predominantly by the female, were more prevalent later on. Drums and high calls were forms of long distance communication. Although males did most of the excavating, females worked harder and did a larger share than is the case for smaller picines. Among other features of behavior described are the aberrant behavior of one male at times of excavating and copulating, the entrance of both birds into the nest at time of egg-laying, a greater interest in nest defense displayed by a female than her mate, and a revival of courtship after the cessation of brooding. Received 20 November 1978, accepted 23 April 1979.

PREVIOUS accounts of the courtship of Pileated Woodpeckers (listed below) have been mainly concerned with the prenesting period. Courtship as maintenance of the pair-bond, however, goes on throughout nesting. I report observations on members of pairs of these woodpeckers at 12 nests aimed to gain a more complete understanding of *Dryocopus* breeding behavior in a study that has also included the Lineated Woodpecker (D. lineatus) (Kilham and O'Brien in press). Present studies were made while I was staying as a guest at the Marine Institute of the University of Georgia in the winter and spring of 1972 and 1974 through 1978. Although it was difficult to know the exact numbers of pairs observed, as nests of one year were often located close to those of a preceding year, I estimate that five pairs were involved. The birds, nesting in woods chiefly of loblolly pine (*Pinus taeda*), were relatively tame and no blinds were used. My observations were opportunistic, totalling approximately 550 h. Other observations, made in Florida, South Carolina, and Maryland as well as Georgia, have been reported elsewhere (Kilham 1959, 1973, 1974a, 1976); descriptions of vocalizations and displays mentioned below are given in the 1959 paper. Previous reports by others include those of Bent (1939) and the Hoyts (1944, 1957).

RESULTS

PERIOD OF EXCAVATION

Tapping.—Courtship behavior was seen most consistently in changeovers at nest holes. Tapping was the most frequent form of communication in the early nesting period (Table 1). There are two types of tapping: one is slow and easily countable, and the other, drum-tapping, is more rapid. Drum-tapping was noted in 81 meetings by the nest and tapping in 56. Both seemed to be used in the same ways by both sexes.

Tapping was used almost exclusively when a pair met at a hole being considered as a nest site (Kilham 1959). Tapping (including drum-tapping) was the most frequent method of communication at nest holes. In nearly all instances the bird in the nest tapped as its mate alighted by the hole. On six occasions both birds tapped,

Table 1. Simplified presentation of greetings between members of pairs of Pileated Woodpeckers given as percentages of total numbers of changeovers at each stage of nesting.

Types of communication predominating ^a	Stages of nesting with total numbers of changeovers observed in each						
	Excavation $(n = 29)$	Egg-laying $(n = 13)$	Incubation $(n = 120)$	Brooding $(n = 41)$			
Γapping or drum-tapping	69	77	45	10			
Voicks	3	_	17	20			
High calls and/or drum	7		6				
Cuks	_	-	10	7			
ilent	21	23	22	63			

a Occurrence of low intimate vocalizations that were inaudible at a distance was not ruled out with any type.

but not synchronously. Once when a Wood Duck (Aix sponsa) and once when a Redbellied Woodpecker (Melanerpes carolinus) came to a hole, the Pileated inside tapped, as if mistaking the alien for its mate.

The amount of tapping done by Pileateds through the nesting period is unusual among picines. Many species limit tapping to the period of excavation (Lawrence 1967) or tap only irregularly thereafter (Jackson 1976).

High calls and drums.—High calls and single bursts of drumming were a form of long distance communication. They were associated with changeovers when a Pileated in the nest called to its mate who, in most instances, answered with a high call or a single drum. Occasionally, Pileateds feeding at a distance would give a high call before flying to the nest. The high calls and single drums seemed to be interchangeable.

Excavation.—Male Pileateds did twice as much excavating as females (Table 2). Male D appeared to be abnormally possessive in doing 99.2% of the excavating. This did not seem to be due to any weakness of the pair-bond, for when female D came to the hole and he refused to leave, as he did in 9 out of 11 times, he still tapped or drum-tapped. She usually replied either by tapping or giving woicks before flying away.

Most of the work was performed silently. The members of pair P were exceptional in that, while carving the entrance to their nest, the partner at work often gave a prolonged series of *cuks* (18 to 58) when swinging its head out. These vocalizations ceased once the hole was large enough to enter. Pileateds *cuk* in a similar fashion when hanging in exposed positions of fruiting trees, as well as upon seeing hawks, and the barrage of vocalizations at this stage of excavation may be associated with a greater vulnerability to attack when the excavating bird has only its head in the hole.

TABLE 2. Comparative amounts of excavating at nest holes done by male (M) and female (F) of four pairs of Pileated Woodpeckers.

	Pair							
	A		D		E		G	
Parameters	M	F	M	F	M	F	M	F
Time observed excavating (min) Percentages of excavation time	163 69	7 4 31	780.0 99.2ª	6 0.8	311 70	136 30	194 65	106 35

^a Male D considered abnormal in both excavation and copulation; see text

TABLE 3. Percentages of total incubation times, as noted in two all-day (dawn to dusk) sets of obser-
vations on pair F of Pileated Woodpeckers, showing how the work was shared by the male and female
in the second week of incubation.

	Male			Female			
Days of incubation	In nest (min)	Per- centage	Average length of sessions (min)	In nest (min)	Per- centage	Average length of sessions (min)	
All day 8	332	55	110.7	267	45	89.0	
All day 11	274	43	91.0	366	57	122.0	
Days 8–13	786	45	78.6	952	56	95.2	
Range			(16-232)			(59-135)	

The chips produced during excavation were regularly tossed from entrances, sometimes over 40 billfuls in succession. On 28 and 29 March, when pair P had nearly completed its nest, female P twice carried sawdust about 12 m from the nest before discarding it. This behavior, seen for both sexes, has been noted for other picines as well (Kilham 1977).

It is possible that males take the greater interest in excavating because nest cavities, when large enough, become their roost holes. This was checked at six of the nests by finding a male in the hole at dawn.

COPULATIONS AND EGG-LAYING

Copulations.—Copulations took place near the nest tree with some pairs and not others, depending upon whether or not a suitable branch was present. In 16 copulations the female moved onto an open, roughly horizontal limb and squatted crosswise. The male, meanwhile, ascended the trunk and moved slowly toward her. In two of the 16 copulations the male pecked gently at the head of the female as cloacal contact was established. Copulations last 6–9 s.

Females flew to their mates making woicks prior to copulation in 8 instances. Males were generally silent. I twice heard woicks and twice low hn, hn notes. The latter were heard only when I was close and may have been missed at other times. Bill-waving dances in which heads and bills swung in arcs of about 45° were preliminary to three observations of copulatory behavior. The female squatted in all three, but the male did not mount. On the third occasion, the male gave woicks along with his bill-waving.

Aberrant male.—The majority of male woodpeckers that I have observed, including Pileateds, fall to the left after mounting and mount only once. Male D, in contrast, consistently fell to the right. In addition he mounted 2-3 times in succession, staying on for 5-10 s each time, on 26, 28, and 29 March. The pair started incubating on 30 March. Possibly Male D was an inexperienced or immature male, a point discussed by Lawrence (1967) for other picines.

Both woodpeckers in the hole at the same time.—This was seen 6 times, 4 for one pair and 2 for another, all at the time of egg-laying. On 3 and 4 April male P came to the side of the hole and rested for 9 min one day and for 16 the next while his mate was inside. She tapped from within. At the end of his resting, male P entered the hole but came out immediately. This was in contrast to the behavior of male D, who entered the nest on top of his mate. She came out after a few moments on one

occasion and he on the other. Results were the same when she twice entered on top of him. The possessiveness of the female, as demonstrated in her refusals to leave, supports my findings (Kilham 1977) that female picines become dominant at times of egg-laying.

INCUBATION

None of four pairs observed in the first week of incubation was like another. At the extremes were male D, who did 73% of the incubating, and female E, who did 78%. Eggs were unattended for periods of up to 20 min in the first few days. After that the Pileateds stayed in the nest and were nearly 100% attentive. On two occasions, early in the incubation period, a Pileated flying to the hole made a loud series of *cuks*, in the same manner as I have described elsewhere (Kilham 1974a) for Pileateds flying to roost holes.

Table 3 records two all-day sets of observations made in the second week of incubation of pair F. Observations started at dawn before the male left the nest and lasted until male F entered for the night. There were six changeovers each day. On this schedule male F did 55% of the incubating (in daylight hours) on the eighth and 43% on the eleventh day. As he spent the nights on the nest (15 h and 46 min after the eighth and 16 h and 5 min after the eleventh day), his share in the total incubating was the greatest.

Nest O was watched prior to and during the incubation stage, and I climbed up to it periodically to determine the length of incubation. On 27 March neither the male nor the female spent much time near the nest during 3.5 h of observation. On the following day the woodpeckers took turns staying in the nest in what appeared to be the first day of incubation. On the 14th day (10 April) there were four eggs, one infertile. On the 16th day there were 3 young in the cavity plus the infertile egg. The incubation period was thus estimated to be 15–16 days, as compared to the 18 days estimated by Hoyt (1944).

NESTLING PERIOD

The day of hatching is known for most woodpeckers by the presence of food in the bills of the parents as they come to changeover at the nest. This is not possible for Pileateds because they feed by regurgitation. One can estimate the time that incubation ceases and brooding begins, however, by using Hoyt's (1944) observation that young Pileateds first climb to the entrance when 15 days of age. Counting backward from the time nestlings were observed at the entrance, I estimated that pair J brooded for 10 days (3–12 April) and pair I for 8 days (11–18 April). As observed over the course of 21 h, male I did 47% and female I 53% of the brooding during daylight hours. These sessions in the nest were during the first 5 days of brooding when the two were close to 98% attentive. Brooding diminished over the next 3 days, one bird or the other flying away without waiting for its partner to come. As shown in Table 1, silent changeovers were noted most frequently at the time of brooding.

The work of feeding nestlings after cessation of brooding was shared equally by the two sexes (Table 4). Few fecal sacs were removed visibly from nest I because the feces were swallowed when nestlings were small. At nest J, with older nestlings, female J removed twice as many as her mate.

Woicks.—As shown in Table 1, these vocalizations increased during incubation

TABLE 4. Comparative amounts of feedin females (F) of two pairs of Pileated Wood		tation done by males (M) and
	Fecal sacs	Intervals between

	Feeding visits		Fecal sacs removed		Intervals between feeding visits (min)	
Pair	M	F	M	F	Average	Range
I	29	26	3	3	27.15 (40 vis	3-81 its)
J	36	39	12	29	23.40 (44 vis	2-75 its)

and brooding. They differed from tappings, for while tapping or drum-tapping were used equally by both sexes, the *woicks* were given predominantly by females. Second, females gave *woicks* when males changed over with them in addition to when they came to relieve the male. On only one occasion did a male and female give *woicks* at the same changeover. The *woicks* were often loud and repeated 3–5 times in succession.

Courtship.—The courtship of pair J became active during the days after cessation of brooding on 14 April. After feeding the nestlings at 0829, female J (FJ) flew to a drum stub 33 m away. Here she rested with head drawn into her 'shoulders,' preened, and drummed 9 times in 15 min. Four of her drums were answered by her mate in the distance. After 10 min, male J (MJ) flew to a pine 12 m away. FJ flew to him, and the two exchanged woicks, then remained close to each other (within 40 cm) for 10 min. Once, when she moved up the pine trunk, he did a bill waving dance. FJ drummed on the following morning. MJ flew to her and they exchanged woicks. In these two meetings it was she that took the lead. On 16 April MJ started drumming, and FJ appeared within a minute, crest raised and giving woicks. The two then rested motionless for 6 min.

DEFENSE OF NEST HOLE

Avian hole-nesters [including Red-bellied Woodpeckers, Starlings (Sturnus vulgaris), Wood Ducks, Eastern Bluebirds (Sialia sialis), and Great Crested Flycatchers (Myiarchus crinitus)] that approached Pileated nests were chased away silently by the owners, with a rare use of threat displays (two instances). The same applied to intruding Pileateds of either sex. Although there was no apparent difference in the way male and female Pileateds defended their nests in mild encounters, one female (FJ) took the lead in a severe encounter with a gray squirrel (Sciurus carolinensis). FJ was in the vicinity of her nest with young on 25 April when the squirrel started to climb a vine-covered pine 7 m away. FJ flew to it with crest raised, pushed her way through the tangle, and pursued the squirrel up the trunk. The squirrel soon turned and drove the Pileated from one limb to another. FJ faced the squirrel on each occasion with crest raised and wings outspread. When male J arrived he attacked the squirrel but was driven away. He did not return. His mate was more persistent and attacked the squirrel three times after MJ had left, facing it each time with wings out in threat displays that flashed the white of the underwings. The reaction of FJ to these attacks persisted. Later on the same day and for several days thereafter she spent 40–45 min lingering by the nest after feeding the nestlings.

An account of a female Pileated that took the lead in a physical conflict with an

intruding male is given elsewhere (Kilham 1973). Lawrence (1967) describes a Downy Woodpecker (*Picoides pubescens*) making persistent attacks on a Great Crested Flycatcher in which her mate, although nearby, took no part. Female woodpeckers may at times, therefore, take a stronger role than males in defense of nests.

DISCUSSION

Downy Woodpeckers, whose pair bonds last only through nesting season, stand in contrast to Pileateds, which have strong ones the year around (Kilham 1976). I think that this relates to food supply. As recently stated by Armstrong (1977), "food supply and foraging . . . are fundamental elements to which other characteristics are related in an integrated pattern." Because of the nature of the food of Pileated Woodpeckers, i.e. carpenter ants (Camponotus sp.), termites, (Isoptera), and woodboring larvae, etc. (Hoyt 1957, Kilham 1976), pairs are able to stay on the breeding territory the year around, the male usually roosting in the nest hole of a previous season. They thus fit the Heinroth and Heinroth (1958) idea that ". . . on the whole . . . a lasting pairing takes place in birds which share responsibilities of brooding or which stay around the nesting place outside of the breeding season." Downy Woodpeckers, in contrast, are opportunistic feeders in winter, moving to areas where they find concentrations of the superficial prey on which they live (Kilham 1970).

Female woodpeckers do less excavating of nest holes than do males. Why then, do they share the later tasks of incubating, brooding, and feeding the young (Lawrence 1967) on a fairly equal basis? One reason, I think, is that the nest hole becomes the male's roost hole. He therefore might be expected to feel more possessive toward the hole while it is being constructed. A second factor possibly influencing this pattern is the need of the female to build reserves of protein (King 1973, Jones and Ward 1976) and other nutrients as the time of egg-laying approaches. If this is so, one may ask why the females of small woodpeckers, such as the Downy (31 g), the Yellow-bellied Sapsucker (Sphyrapicus varius) (47-64 g), and the Hairy (Picoides villosus) (80 g), do very little excavating (Lawrence 1967, Kilham 1977 and MS), and the much larger female Pileated (311–358 g) (weights from Roberts 1932) a lot more one third of the total. This may be a matter of egg weight as related to body size. As stated by Skutch (1967), "the larger the bird the smaller the fraction of her weight that her egg represents." Applying this rule, it would seem that it is less of a metabolic burden for a female Pileated to produce four eggs than it is for a Downy, a sapsucker, or a Hairy to produce, on the average, a larger clutch size (Bent 1939). From this point of view a female Pileated can afford to devote more time to nest building, working as hard in her sessions as the male in his.

Two cautions should be kept in mind. One is that, of all that has been written on woodpeckers, few observers other than Lawrence (1967) have studied the excavation of nest holes long enough to determine reliably the shares of the work done by the male and female. Studies need to be both qualitative and quantitative. As noted by Lawrence (1967) and also by Kilham (1977, MS), female Downies, Hairies, and sapsuckers spend much time idling (preening, resting, etc.) rather than actually working when taking a turn at an excavation. Another caution relates to the time in the breeding season an excavation is made. If a good nest site is found early and all goes well, a female of the smaller species of woodpeckers does very little work. If, on the other hand, there are few good nesting sites and the pair has to make repeated tries, a female may work hard (Kilham 1977).

A source of confusion to any discussion of pair-bonding can be the relationship of courtship to agonistic behavior. There are four situations that should be kept in mind in regard to Pileateds. One is that a mated bird may attack and drive away conspecific intruders of either sex. Therefore a male pursuing a female with wings outspread in a threat display is not likely to be engaged in courtship, as some earlier writers (Bent 1939) believed. Another source of confusion is that a male or female Pileated may occasionally strike at its mate. The only instance of this I have seen (Kilham 1973) was when a female, after a prolonged encounter with an intruding male, struck at her mate. This seemed to be a case of a redirected attack, a consequence of being under stress. Lawrence (1967: 123–124, 130–131) has described similar situations among Hairies.

A fourth source of confusion relates to bivalent displays such as crest-raising and bill-waving. Crest-raising is expressive of excitement from any cause and may, therefore, give rise to confusion. Bill-waving is complicated by the fact that, among Hairy and Downy Woodpeckers, it is used almost exclusively in intraspecific conflicts. With Pileateds, in contrast, it is used in relation to copulation and courtship and often in association with the pair-bonding *woick* vocalization (Kilham 1959, 1974b, 1976). Why then should it also be used occasionally in conflicts? This, seemingly, is due to its function of drawing attention to the performer. It is apparently a way of emphasizing what the performing Pileated has to communicate with a mate or an intruder, the context giving the cue.

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ERRATUM

In our paper "Female-female pairs and other unusual reproductive associations in Ring-billed and California gulls" (Auk 96: 6-9, 1979), we erroneously stated on page 8 that Ryder and Somppi (Auk 96: 1-5, 1979) had reported a 31% fertility rate for eggs from female-female pairs. The actual level of fertility should have been 66%, making their findings similar to our own.—MICHAEL CONOVER