

REPRODUCTIVE BEHAVIOR OF HAIRY WOODPECKERS.
III. AGONISTIC BEHAVIOR IN RELATION TO COURTSHIP AND
TERRITORY

LAWRENCE KILHAM

THIS report describes the agonistic behavior of Hairy Woodpeckers (*Dendrocopos villosus*), which may take place at any time of year and with either sex, but which reaches a peak when rival males display against each other on winter mornings from mid-January to early March. Other examples of this behavior include conflicts between females in the fall, interspecific conflicts, and abnormal situations such as defeat of a mated male on his territory, stemming from inadequacies of local environment.

Present observations, like those of preceding reports, were begun in Maryland (Kilham, 1960, 1965, 1966a, 1968). They were carried on primarily, however, in Tamworth and especially in Lyme, New Hampshire over the course of nine years.

DISPLAYS ASSOCIATED WITH AGONISTIC BEHAVIOR

Some displays described in part elsewhere (Kilham, 1960, 1966a) are included below to give a more complete outline.

Threat display.—(a) Bill-waving Dance. A Hairy Woodpecker of either sex points its bill upward and at times even backward (Fig. 1), then swings its bill back and forth like a conductor's baton, while jerking head and body and making half-starting motions with its wings. The bird on the offense does the dancing. These displays are also used in interspecific encounters as against a Starling (*Sturnus vulgaris*) near a nest hole. Skutch (1955) gives some additional description.

(b) Display of white breast. This can occur briefly as an isolated performance (Fig. 1) apart from the Bill-waving Dance of which it is a main component. I saw it, for example, on several occasions when an owning male faced another male who was unresponsive to challenge, possibly due to immaturity. It is conceivable that the white breast of the Hairy Woodpecker serves a signaling purpose, since it shows up well in the bare woods of late winter when agonistic and courtship behaviors are at a peak.

Actual Conflict.—(a) Combat pose. A Hairy Woodpecker ready to strike or to meet blows holds itself with bill opened, wings held out slightly from the body, and tail well-fanned outward (Fig. 2). Outer tail feathers sometimes twitch independently of the rest of the tail.

(b) Direct clash. When antagonists grapple with each other, they use bills to seize and pull feathers rather than to strike blows.

(c) Head feathers. These are usually pressed down, giving a sharp outline



FIG. 1. Male Hairy Woodpecker in full threat display, a pose basic to the Bill-waving Dance.

to the head in conflict. Hairy Woodpeckers may raise their head feathers in mixed situations, where they are curious in regard to an intruder, whether specific or non-specific, while still holding themselves in readiness for combat.

Defense.—When threatened or about to be attacked a Hairy Woodpecker may (a) hold a frozen pose with head and bill pointed straight forward (b) spread wings out horizontally (c) swing around a trunk or branch with wings fully outstretched upward.

Displacement pecking.—A woodpecker in conflict may start pecking assiduously on places such as the bark of sound, healthy trees. This reaction is more frequent toward the end of long conflicts.

Vocalizations.—These are divisible into four groups.

(a) *Wick-a-wick-a-wick.* I have heard these notes only in male-male conflicts. They resemble a vocalization of the Yellow-shafted Flicker (*Colaptes auratus*). (Kilham, 1959a.)

(b) *Speaks* as well as *Sputters* are expressions of excitement from any cause; a *Sputter* being basically a *Whinny*, which due to its intensity carries a connotation of alarm, at least to a human ear.

(c) *Queek, queek, queek* and *chewi, chewi, chewi.* The notes express exuberance in courtship and may sound incongruous when given in conflict situations. Conflicts, however, are stimulating to courtship when both sexes are present, as they frequently are.

(d) *Teuk, teuk; chewk chewk; chewki, chewki; queek, queek* and a variety of other short, rubber-doll-like, notes may accompany bill-waving displays, giving the effect of a performance by marionettes. Excitement of the moment may explain the diversity of vocalizations used.

CONFLICTS OF MALES IN LATE WINTER

Early breeding season encounters of Pairs A and B were favorable for observation in taking place along a restricted area of territorial boundary (Fig. 3) in two successive years. Three of the four woodpeckers involved



FIG. 2. A Hairy Woodpecker in combat readiness as it faces an intraspecific opponent.

were present in both years. Female A (FA), however, acquired a new mate MA' in 1965. Events which involved FA and MA' were the more representative of the agonistic behavior of *D. villosus*. They fell into the following phases:

Phase I was brief for MA' when, new to both mate and territory on 31 January, he fled as if in terror on meeting neighboring Male B (MB) who was trespassing across the border. Within a month, however, MA' had become a match for MB as could be seen in displays which lasted from 07:25 to 08:30 on 28 February. Events began when MB crossed the border at 07:00 (Fig. 3). FA was alone at the time. She made many *speaks* as if nervous but did not attack MB. MA' was drumming 200 yards away. Displays began immediately when he arrived at 07:25. The two males resembled puppets operated by strings as they faced each other, a short distance apart on a limb, with bills up and tails spread, then started jerking heads to and fro, half-starting their wings and making toy-like *chewk, chewk* notes. Such bursts of activity might last for several minutes. The two would then rest for a time in strained postures until conflict was precipitated again, usually by one of the females making *Speaks* or *Sputters*, from positions that each held back from the displaying males (Fig. 3). One male might then float to another tree on out-stretched wings followed by his opponent. A common tactic was for one to get below the other on the tree. Thus the male higher up might swoop down on the one below, as the latter evaded by swinging around the tree trunk with wings outstretched. Such maneuvers brought the

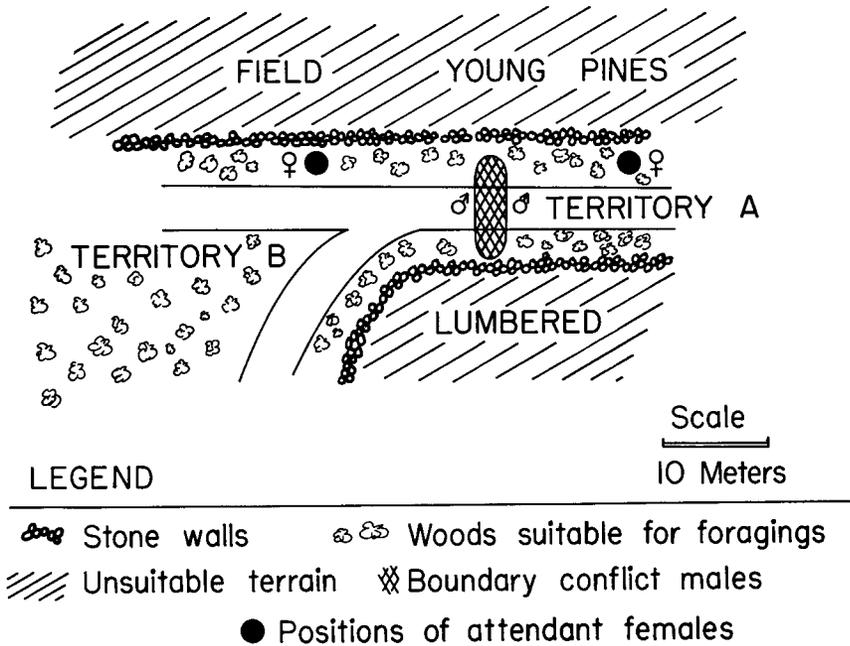


FIG. 3. The site of ritualized, early morning conflicts of two male Hairy Woodpeckers in February along a portion of their common territory boundary, showing positions of attendant females. (Pairs A and B, 1964.)

two close to the ground. Signs of fatigue began to appear as the conflict wore on, with the contestants flying more from tree to tree and taking longer pauses to peck in nervous fashion.

Conflicts in early March marked a third phase in which conflicts tapered to a close. Those on 2 March, for example, lasted only from 06:45 to 07:05. MA' swooped repeatedly at MB. He now appeared the more aggressive of the two. The two males spent much time resting motionless. FB flew toward her mate in one such pause in fluttering, gliding flight, making *chewki* notes, and this precipitated a renewal of displays. At the end of the encounter FB assumed an invitatory pose, crosswise on a limb (Kilham, 1966a). MB came within a few feet. The two, however, flew off without copulating, although the conflict had obviously aroused FB in this direction.

Pairs A and B came to their mutual border again on 4 March. On this occasion they did no more than idle about for a short while, each remaining on its own side. They left by 07:15 and this was the last time I saw the four woodpeckers together.

Conflict of females, 1965.—I saw no further conflicts between Pairs A and B in the spring of 1965, but on 24 July FA and FB had an encounter in the border zone used by the males in February (Fig. 3). The two females were resting motionless three feet apart when first observed. They soon started Bill-waving Dances accompanied by doll-like *queeks* which continued for only a few minutes. FB then flew back to the vicinity of MB who, accompanied by a juvenile, was back from the boundary in his own territory and did not participate.

I have observed a total of four such conflicts between female Hairy Woodpeckers in New Hampshire, of which three took place in September and October. One on 8 October 1961 resembled the one described above in that FX in Tamworth was accompanied by MX at the time she faced her rival at what had been the boundary of the breeding territory. The males in both situations remained back from the encounter and uninvolved.

Disequilibrium between males A and B in 1964.—MA, who was FA's mate in 1964, appeared to be atypical in at least three aspects of his behavior which were, a) failure to reciprocate in full to the courtship advances of his mate FA (Kilham, 1966a); b) hyper-excitability in the nesting period (Kilham, 1968) and, c) lack of interest in either territory or in the challenge of neighboring males.

Observations on MA began in mid-December when I located his roost hole 150 meters within Territory B and 15 meters from that of FB. The two woodpeckers belonging to different pairs paid little attention to each other on emerging in the morning. Male B began to seek out his mate soon after dawn by the end of the month, but it was not until 25 January 1964, that he became aggressive toward the intruder MA. By this time FB had gone to roost elsewhere. MB came to the wood at 07:05 and took a position above the roost hole of MA who first put his head out at 07:16. MA emerged the day before and the day after at close to 07:12, but on 25 January he remained within until 07:26. MB meanwhile, preened, scratched, and drummed demonstratively as if waiting for his rival to come out. When MA finally did so, MB put on a full display, with bill back and white breast rounded forward (Fig. 1). MA kept well away, however, and soon flew off to his own territory pursued by MB.

MB sought a conflict again on 13 February, for he invaded territory A at 07:20 and, coming to an aspen where MA was resting 40 meters beyond the boundary, he made the same exaggerated breast display as on 25 January (Fig. 1). Neither the trespassing nor the display aroused MA. He moved away, pecking on places of no special interest as he did so and MB, returned to his own territory.

MB came to the border again on the following morning. This time he

did no more than cling to a tree trunk and look across for several minutes. He then gave a Sputter and flew back the way he had come. On 19 February both MB and FB came to tree on the border at 07:30 and remained there, either motionless or preening for 20 minutes. Such occasions suggested that the borderline, defined by conflicts in 1965, was recognized, at least by Pair B, and I believe by FA as well, in 1964.

MA was not only indifferent to the intrusions of MB, but also about moving into Territory B to feed, which he did on 7 and 22 February. FB met him on both days. She attacked him by advancing rapidly up the trunk or along the limb where he happened to be, without displays, but moving directly at him. MA's only response was to fly to another tree. FB desisted after several such attacks.

One might assume from MA's unresponsiveness that he lacked a will to fight. Two observations, however, indicated that he was aggressive in other situations. One was at a time, 25 December 1963, when FB approached his roost hole in Territory B after he had emerged. MA popped inside hurriedly and faced her at the entrance. The two woodpeckers then had three sharp exchanges of blows, with MA striking so hard from within that FB lost her hold on the bark several times. A second instance of MA's aggressiveness was at a suet holder, two kilometers away, where FB was feeding on 22 February. MA drove her off and when a Starling attacked him a minute later, he swung under a limb in a full-wing threat display, then attacked and drove this bird away as well.

MA was possibly an immature male, less than a year old. This might explain his lack of agonistic and courtship behavior, as well as sense of territoriality. These deficiencies did not keep him from successful nesting later on. Here two further explanations are conceivable; one, that he matured as the season progressed and second, that his mate, FA, had a territorial sense established by occupancy dating from the preceding fall, if not from a longer period beforehand, and this was sufficient to hold the pair together in the early breeding season. The unusually prolonged courtship endeavors of FA in relation to MA are described elsewhere (Kilham, 1966a).

Intense conflict followed by coition.—The territory of Pair E lay on the east and that of Pair F on the north slope of Lyme Hill, with an area of continuous woodland in between. Above this was a small, more open area where winds swept around a shoulder of the hill, which was attractive to the pairs of Hairy Woodpeckers for at least two reasons; one, the blown-down or broken trees provided a supply of wood-boring insects and second, it was the only piece of terrain between their territories which had well defined topographical features. Both causes may have operated to make this segment of border, roughly 10 meters in extent, the scene of conflicts

between Males E and F. ME and FE, for example, had worked on the wind-blown trees from 08:15 to 08:35 on 13 March 1965. These quiet activities were interrupted at 08:35 when ME began giving Speaks, then flew at Male F who had just arrived. The two males now engaged in a Bill-waving Dance accompanied by *wick-a-wick-a-wick* vocalizations. They separated after a few minutes to feed near their respective mates. This momentary quiet was broken when MF suddenly flew at ME and knocked him from his feeding place, the males then falling through the air as they grappled together. The rival males had several more of these clashes during the next three to four minutes. Female E had meanwhile flown to a tall dead stub and drummed, as well as giving Whinnies. When MF flew to her directly from his last clash with ME, she broke into a medley of exuberant *teuk, teuk* notes, moved out to take a copulation pose by crouching low on a limb, then broke into a frog-like *quare* as ME mounted in what appeared to be full coition. There was thus a rapid change, within seconds, from agonistic to sexual behavior. It was as if a drive built up for one was directly transferable to the other.

I observed that ME and FE moved uphill toward the wind-blown area on four other mornings in March, between 06:00 and 07:00. The only other conflict with their neighbors, however, was a brief one on 22 March. It seemed possible that this early morning movement toward the border area was actually appetitive behavior, in which displays with rivals were sought, as if the male and female of the pair felt a need for these activities.

Comment on territory and terrain in relation to sites of conflicts.—The territories of Hairy Woodpeckers are large, being roughly 500 meters in length as figured in two previous publications (Kilham 1960, 1966a) and having borders that are ill-defined in most directions in New Hampshire where much terrain consists of young woods, fields, or other unsuitable habitats. There is thus no crowding of pairs but rather the reverse. If conflicts were random affairs under such conditions they might be comparatively infrequent. This is especially true in the early breeding season when unfavorable weather may interrupt courtship and agonistic activities for days or even weeks at a time. The fact that pairs seek conflicts in the first hour or two after dawn on favorable mornings and at a set section of the boundary where conflicts have taken place before may thus have importance. The border sections were about 10 meters in length. As observed for Pairs A and B, and for Pairs E and F, in two successive years, the section in each case was an area of woodland favorable to feeding. For Pairs A and B, the area consisted of large maples bordering a dirt road (Fig. 3) while for Pairs E and F, the strategic meeting place was an area along a ridge where high winds had killed or weakened trees and thus increased the supply of wood-boring prey. Each of these places was where the woodpeckers would have been likely to

meet when feeding. Once contact was made, they may have returned when seeking conflict at other times. This tendency of *D. villosus* to have successive conflicts in one segment of boundary was also noted in Maryland (Kilham, 1960).

TERRITORIAL DRUMMING

The larger part of the drumming of Hairy Woodpeckers in winter and spring appears to be related to courtship, while drumming made in response to territorial neighbors is less frequent. Examples of this territorial drumming are as follows:

ME and FE were feeding well within their territory at 08:00 on 21 March 1965, when a member of Pair A began drumming across the valley. ME became excited immediately as indicated by Speaks and Sputters. He flew 100 or more meters to a position on his boundary opposite to where the sound was coming from, then started drumming in reply. After a few minutes, he began preening between bouts as if having no sustained interest. This brief episode brought out features of territorial drumming. One was that it was not related to FE, since ME had flown directly away from her, and second, it was precipitated by the action of the neighboring woodpecker. An interpretation of events was that ME had flown to the border as if eager for a conflict, presumably with Male A', but the nature of the terrain was unfavorable to any direct encounter since fields and a highway separated Territory E from Territory A.

An almost identical episode took place with MB on 4 March 1965. He was working on the entrance of a potential nest hole at noontime, with FB not far away, when drumming began in Territory C. MB gave a Whinny, then flew to some tall basswoods which grew along his border and began drumming in reply. The terrain separating the basswoods from Territory C was of an indifferent nature, in terms of places to feed since it consisted of small pines and a field. MB drummed at a leisurely rate of four bursts a minute. One would have thought, to see him fly to his border so promptly, that he was eager for an encounter, but, as in the case of ME, the nature of the terrain made an actual conflict unlikely.

I have been unable to determine by sound whether a male or a female Hairy Woodpecker is drumming and possibly a Hairy Woodpecker cannot either when the sound comes from outside its own territory. This may make no particular difference in regard to territorial drumming. Males such as E and B appeared to have a high level of eagerness for conflict as judged by their prompt and excited response. Drumming by either member of a neighboring pair might, therefore, be enough to bring male woodpeckers to opposite borders, well separated though these might be.

TERRITORIAL INTRUSIONS OF AN UNMATED FEMALE

In March and April 1965 an unmated female (UNF) wandered about in portions of territories A, B, and C arousing responses from the respective mated pairs, as may be illustrated by an encounter on 5 April. MA' and FA had reached a quiet phase of breeding behavior at this time. FA had been inspecting a birch stub as a potential nest site when she flew to the ground among some low pines to face UNF, who had appeared suddenly. The intruder was seemingly unconcerned as FA came within a few feet. FA did not attack, but pecked indifferently on a dead limb, then gave shrill *chewkis* and flew up to rest on a limb in a crosswise pose, inviting coition, as MA' arrived. He came within a few inches of her, then turned to swoop down to the intruding female. UNF continued to be unconcerned as MA' approached in a Bill-waving Dance, then flew at her, giving shrill *chewkis* as he did so. FA joined her mate. She remained to one side, however, and uninvolved in the displays. All three finally flew off together.

On 10 March, UNF invaded Territory E. FE had been drumming and preening in leisurely fashion at 08:50 when she suddenly made *queek, queek* vocalizations as UNF alighted on a neighboring tree. FE pursued the intruder up the tree trunk, but in quiet fashion, without displays. Both females then rested motionless until UNF departed.

A feature of these episodes was the lack of agonistic response to the invading female shown by owning females A and E. Male A', on the other hand, had immediately resorted to a Bill-waving Dance, then a direct attack. These events suggested that female Hairy Woodpeckers are not much concerned about the defense of breeding territories in the first half of the year when males are the active partners, but become so only subsequent to the breeding season when males are no longer interested.

CONFLICTS IN NESTING PERIOD

Conflicts between two male Hairy Woodpeckers in May 1963 were unusual, a) in being carried on at a time when pairs are normally occupied with nesting and b) in that an intruding, unmated male (MZ) ultimately defeated a mated male (MX) in the latter's territory in Tamworth.

Defeat of a male on his own territory.—4 May. Speaks and sputters attracted my attention at 07:00 to a series of Bill-waving Dances going on between males X and Z close to their common boundary (Fig. 4). The conflict was a mild affair, carried on in silence, and ending with departure of intruder MZ.

5 May.—MX and his mate FX were feeding close together on the following morning when MX suddenly became alert, then flew through woods to meet MZ who had invaded his territory again. There was a brief encounter before MZ left. MX flew back to his mate and copulation followed as if an emotional intensity engendered by the conflict had carried over directly.

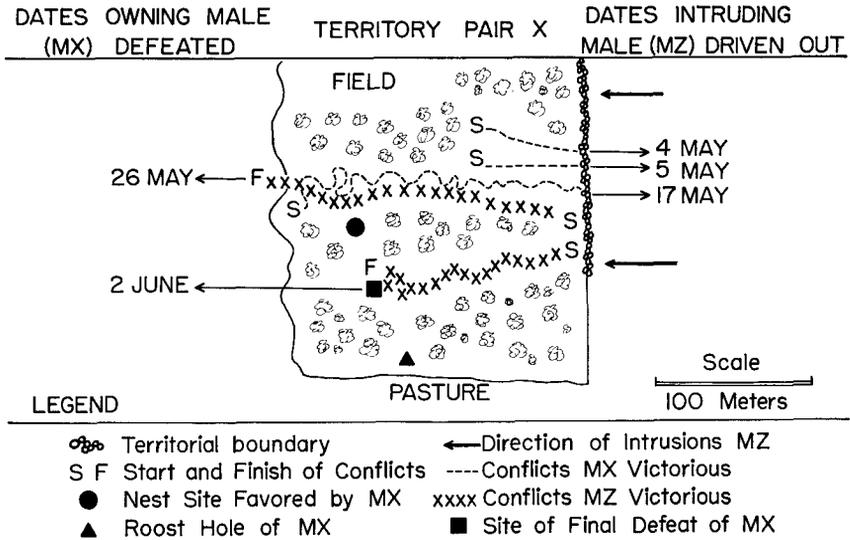


FIG. 4. Diagrammatic view of five invasions of intruding male Hairy Woodpecker MZ into territory of mated male MX, showing manner in which MX was ultimately defeated on his own territory in May and June, 1963.

17 May.—MX was resting as I watched him for 20 minutes in the center of his territory. He stretched himself out on a dead limb in a sunbath, with head back and wings relaxed, scratched his head directly (Kilham, 1959c), and preened. MZ interrupted these activities at 08:30 by appearing in woods below. I was thus present at the onset of a conflict which lasted for one hour. It involved a gamut of activities ranging from Bill-waving Dances and full-wing threat displays to bodily clashes with loss of feathers, all accompanied by occasional *wick-a-wick-a-wick* vocalizations. The two males appeared to be evenly balanced. It was only by a slight margin that MX drove his rival backward the way he had come (Fig. 4).

25 May.—This was an extraordinary day in which MX in one part of the wood and his mate FX in another carried on duets of drumming, answering each other with regularity at rates of about six times a minute. The duets began at 05:45 and were still continuing, off and on, at 19:45. FX tapped a number of times at a potential nest stub of poor quality. It appeared as if she were trying to get her mate to come and inspect it. If he started to approach, she would cease drumming and wait. The fact that he did not actually come gave an appearance of strained relations between the two. This was the final day that I observed efforts by either of them to find a possible nest site.

26 May.—The course of this encounter, which began at 09:30, was the reverse of that described for 17 May (Fig. 4), for MX was driven back to the center of his territory which he finally abandoned to his rival MZ.

2 June.—MX precipitated the final conflict observed when his drumming brought MZ to the boundary at 05:30. As on 26 May, MZ forced MX back to the center of Territory X. Much of the fighting was done close to the ground. MX had enough after a half hour for he worked to the bottom of a brush pile to hide, but MZ followed and a spasmodic

beating of wings accompanied this final clash of the two males. MZ came out after a few minutes, rapped on a dead branch, and flew off. MX did not appear until five minutes later. He gave a few Speaks and a Sputter, then flew in a direction away from that taken by MZ.

Comment.—One may ask why intruder MZ was able to defeat owning male MX on the latter's own territory and why MZ should have been so persistently aggressive. Conceivable answers to these questions lie in a combination of circumstances. If MZ had lost his mate, as appeared to be the case, a drive built up in months of courtship may have found outlet in destructive aggression, a situation which I have observed among woodpeckers in an aviary when efforts to nest finally broke down (Kilham 1959*a*, 1962).

The failure of MX to defend his territory rested on a different type of situation, ecological in nature. Thus a feature of the conflicts was that MX won encounters with MZ up until 25 May. On this date he and his mate FX had duets of drumming carried on in what to an observer was an agonizing fashion, over a day of 15 hours. After this time the two woodpeckers, MX and FX, made no further attempts to nest. Their pair bond had broken and from then on MX did not have the will to fight he had before. The psychological advantage now went to the intruder.

I might not have appreciated the ecologic background of this situation had I not been following the succession of forest trees in these woods, which were my own. Thus a combination of hurricanes and lumbering operations had provided a supply of stubs favorable to nesting woodpeckers in previous years. No living larger trees remained, however, which might die and keep adding to a supply of nest sites. The best stubs either rotted in time or their potential as nest sites waned. They gradually gave way to a succession of vigorous young trees offering no dead wood such as might be suitable for excavating. The environment had thus become depleted of a resource of crucial importance to nesting woodpeckers.

My first appreciation of this depletion of habitat came from observations of Pair A of Yellow-bellied Sapsuckers (*Sphyrapicus varius*) which had nested in the same area of woodland (Fig. 4) in 1958 (Kilham, 1962). Pair A failed to nest in the following year, however, when efforts to find a suitable tree were unsuccessful. An end result was that the male sapsucker with no nest to attend to in May and June flew around and around his territorial borders seeking to precipitate conflicts with males of four neighboring pairs, then occupied in raising young. Pair A of the sapsuckers and Pair X of Hairy Woodpeckers might have been able to nest had the birds moved elsewhere. Both species, however, remained attached to their territories.

INTERSPECIFIC CONFLICT

Interspecific competition is rarely observable in nature. A series of encounters between Pair F of Hairy Woodpeckers and a male Yellow-bellied Sapsucker observed in April 1963, however, revealed that competition exists between these two species for a crucial resource; for optimal nesting both require living trees with rotten centers of identical diameters. This idea, first suggested by the interspecific encounters, has been substantiated in continuing observations. A second point of interest about the conflicts was the insight given into the fighting potential of the male as compared with that of the female Hairy Woodpecker in the breeding season.

The members of Pair F had been excavating a nest hole 15 meters up in a hop hornbeam (*Ostrya virginiana*) in Lyme when the male sapsucker began excavating a hole 75 centimeters above. The sapsucker had appeared in the area three days before and had inspected the hornbeam. Female F paid little attention to this initial intrusion as she rested before her excavation. The intruder began an excavation of his own on the following day. By this time he was more aggressive and able to drive the female Hairy Woodpecker away. The main conflicts came on 21 April. I had begun watching the female of *D. villosus* at 06:30, when the sapsucker arrived and attacked her at her excavation. Both birds fell grappling to the ground. They lay there momentarily, and when the two had reascended the tree trunk, the woodpecker renewed the conflict, thus precipitating a second episode of grappling and fall. The female Hairy Woodpecker was beaten in this encounter. The male sapsucker pursued her from tree to tree, then returned to inspect her excavation unmolested. He finally left for a round of drumming on various trees. FF remained at a spot 70 feet away for the next 15 minutes, preening in a nervous manner and making an unusual number of *jeek* notes as if disturbed. Meanwhile her mate, who had been absent during the conflict, arrived at the nest excavation. He tapped at the entrance as if trying to get her to return, but she remained at a distance. The Yellow-bellied Sapsucker now returned to the hornbeam and immediately swooped on the male Hairy Woodpecker hitting him so forcefully that the two fell grappling to the ground where they remained clutching for nearly a minute. On this occasion the male Hairy Woodpecker was decidedly the victor. He chased the sapsucker away so effectively that the intruder did not return nor did its incipient nest excavation become any larger.

DISCUSSION

Hairy Woodpeckers are birds of marked individuality living, in New Hampshire, in woodlands which are forever changing due to lumbering, diseases and other factors; to nest successfully under such circumstances

requires close adaptation not only to environment but also between the two members of a breeding pair. Cooperation comes to be of the closest kind, once a nest site has been selected and excavation begun. It develops progressively in the early breeding season when two types of activity engender social bonds. One type relates to courtship in which Hairy Woodpeckers display, even in February when woods are deep in snow, by exchanges of intimate notes, pseudo-coition, and activities about a symbolic nest hole and the other type, to agonistic encounters with rival pairs. This latter behavior takes place between January and March. A schematic view of these events is that if the male is new the female attracts him by her drumming or presence to sections of the territorial border where he is likely to encounter the male of the neighboring pair. He may flee from initial conflicts. As he gains familiarity with his new territory and mate, however, encounters with rival males become rituals serving a number of functions. A male Hairy Woodpecker, for example, has superabundant energy and aggressiveness in the early morning of a favorable day, and this might well be directed against his mate were it not channeled off in ritualized conflicts with rival males. Hence the energy serves to strengthen rather than weaken the pair bond, as may happen under conditions in an aviary where no rival is present. Males with energy to expend may enjoy doing so. A conflicting desire to flee has not been apparent in encounters observed. In fact an analogy which came to mind in watching the woodpeckers was rather of a vigorous tennis match in which both male contestants were satisfied with the boundary (the net) staying where it was, and both were driven on by the presence of their mates who attended the performance, but back at a distance and without direct participation (Fig. 3). If the actual displays continued for an hour, both males might show signs of fatigue. Now one and now the other, might start pecking as if desirous to start feeding, which was natural, since neither male may have fed since emerging from its roost hole at dawn. Sometimes a female would incite her mate to attack his rival by coming closer and giving vocalizations. This in turn initiated a further bout of displays. The suggestion was that these encounters were joint enterprises. The females became aroused sexually by attending them as well as the males by the contesting, as was evidenced when a female assumed a coition pose crosswise on a limb at the moment her mate flew from an encounter. Copulation may take place in such circumstances, within seconds. This close association of agonistic and sexual behavior is also observable among Pileated Woodpeckers (*Dryocopus pileatus*) as described elsewhere (Kilham, 1959b).

Other aspects of the lives of Hairy Woodpeckers may also serve to obviate male aggressiveness. Among these are occupation of territories in the fall by the females who establish boundaries to some extent in conflicts with other

females. The female is thus on familiar ground by the onset of the breeding season in mid-winter, a circumstance giving her a psychological advantage counteracting male dominance, at least initially. And again, in later months when members of a pair feed together in woodlands, sexual differences in feeding behavior may further serve to forestall male aggressiveness arising from dominance at food situations. It should also be emphasized that Hairy Woodpeckers are mated for life. Familiarity with mate and terrain thus acquired may further contribute to the intimate pair bond characteristic of *D. villosus* but not of all woodpeckers (Heinroth and Heinroth, 1958, Kilham, 1966b).

Agonistic behavior among Hairy Woodpeckers is a constructive force under usual circumstances. It may, however, become destructive in situations which are abnormal or unbalanced, such as loss of a mate or tenacity to habitat which has become depleted of some essential requirement. Illustrations given of this situation were (1) the persistent territorial invasions of an unmated male Hairy Woodpecker (MZ) and his ultimate defeat of a mated male (MX), as described from Tamworth in May, 1963 (Fig. 4), and (2) the excessively aggressive behavior of a male sapsucker which had failed to nest successfully in the same area in a previous year (Kilham, 1962).

In conclusion I would agree with Hinde (1956) that "the ways in which territorial fighting is specialized" may vary with each species. The balance of selective forces for Hairy Woodpeckers, occupying large, ill-defined territories with comparatively little competitive pressure, may be quite different than that for colonial-nesting species such as gulls (Tinbergen, 1960). This may explain why I have not noted displacement activity, and the simultaneous arousal of the tendency to attack and a tendency to flee, as being features of their agonistic behavior.

SUMMARY

The agonistic behavior of Hairy Woodpeckers in relation to courtship and territory takes place on favorable days in winter when neighboring males, attended by their mates, seek encounters along a section of territorial borders held in common. Occasions when pre-copulatory behavior followed conflicts within seconds suggested that both sexes were aroused by such conflicts, even though the females did not participate directly. The greater aggressiveness of the males was revealed in other types of conflict in spring. Thus a male took the lead in driving an unmated female intruder from his breeding territory and in an interspecific encounter in April, a male Hairy Woodpecker defeated, whereas his mate was defeated by, a male Yellow-bellied Sapsucker. An unusual series of conflicts were observed in May in which an unmated male intruder finally defeated a mated male in the latter's own territory. This abnormal situation appeared related to the fact that the mated pair remained attached to a territory in which suitable nest trees were no longer available. A situation was observed in the case of a mated male, who appeared to have no territorial sense and took little interest in either agonistic or courtship activities, yet nested successfully later on. Hairy Wood-

peckers have large, often ill-defined territories in New Hampshire. What is surprising is the degree of individuality shown in their agonistic and other behavior. They appear able to develop close, intimate pair bonds under a wide variety of circumstances.

LITERATURE CITED

- HEINROTH, O., AND K. HEINROTH. 1958. The birds. Univ. Michigan Press, Ann Arbor.
- HINDE, R. A. 1956. The biological significance of the territories of birds. *Ibis*, 98:340-369.
- KILHAM, L. 1959a. Early reproductive behavior of flickers. *Wilson Bull.*, 71:323-336.
- KILHAM, L. 1959b. Behavior and methods of communication of Pileated Woodpeckers. *Condor*, 61:377-387.
- KILHAM, L. 1959c. Head-scratching and wing-stretching of woodpeckers. *Auk*, 76:527-528.
- KILHAM, L. 1960. Courtship and territorial behavior of Hairy Woodpeckers. *Auk*, 77:259-270.
- KILHAM, L. 1962. Breeding behavior of Yellow-bellied Sapsuckers. *Auk*, 79:31-43.
- KILHAM, L. 1965. Differences in feeding behavior of male and female Hairy Woodpeckers. *Wilson Bull.*, 77:134-145.
- KILHAM, L. 1966a. Reproductive behavior of Hairy Woodpeckers. I. Pair formation and courtship. *Wilson Bull.*, 78:251-265.
- KILHAM, L. 1966b. Nesting activities of Black-backed Woodpeckers. *Condor*, 68:308-310.
- KILHAM, L. 1968. Reproductive behavior of Hairy Woodpeckers. II. Nesting and Habitat. *Wilson Bull.*, 80:286-305.
- SKUTCH, A. F. 1955. The Hairy Woodpecker in Central America. *Wilson Bull.*, 67:25-32.
- TINBERGEN, N. 1960. Comparative studies of the behavior of gulls (Laridae: A progress report). *Behaviour*, 15:1-70.

DEPARTMENT OF MICROBIOLOGY, DARTMOUTH MEDICAL SCHOOL, HANOVER,
NEW HAMPSHIRE, 23 MARCH 1967.