EARLY BREEDING SEASON BEHAVIOR OF DOWNY WOODPECKERS

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The present report is one in a series on my studies of the year-round behavior of Downy Woodpeckers (Dendrocopos pubescens), done with an idea that it is only against a background of the total natural history of a species that selection pressures operative in its evolution are likely to be understood. My previous reports on D. pubescens have included winter and sexual differences in feeding, copulatory behavior as related to courtship, and a preliminary one on the entire breeding season that gives descriptions of the main vocalizations and displays (Kilham, 1962, 1970, 1974). Present observations, made in Lyme, New Hampshire between 1961 and 1974, supplement the 1962 report. Other accounts on the behavior of this species include those of Bent (1939), Staebler (1949), Lawrence (1967), and Short (1971), the last giving details of the displays of various species of the genus Dendrocopos, which in his terminology is called Picoides.

Although the various aspects of early breeding season behavior take place concurrently, for convenience I have divided them into: agonistic and territorial behavior as seen in winter and spring; types of drumming; courtship flights; the search for a nest site; and finally the dependence of successful courtship and nesting on an adequate environment.

AGONISTIC AND TERRITORIAL BEHAVIOR

Displacings.—The following descriptions of fall and winter interactions between the sexes are given by way of background to those seen in the early breeding season. Thus on 26 September 1968 a male displaced a female five times in 15 min, and a month later another male displaced a female four times in less than 10 min. These displacings, which continue during winter months and are often accompanied by the aggressive chrr note, do not always involve the seizure of a better feeding spot; often they appear as an assertion of male dominance, and this results in spacing out the sexes in relation to feeding (Kilham, 1970). Female Downies usually move away a short distance without appearing disturbed if displaced by their mate. On other occasions, I have seen female Downies react by holding strained, bill-forward poses, swinging under a limb as in combat, or opening their wings in a threat display to the male. Supplanting attacks of a somewhat similar nature are described by Short (1971) for the Nuttall's (D. nuttallii) and the Ladder-backed (D. scalaris) Woodpeckers.

The seeming hostility of male to female was reflected by the reaction of male B (MB) to his mate-to-be in mid-winter in a woodland swamp. MB nested with the same mate (FB) in 1971 and 1972 and remained on the breeding territory alone in the intervening winter. I never saw FB in the swamp at this time with exception of 29 January 1972, when she flew to within one m of MB. He swooped at her immediately, making check, check and chrr notes as he drove her away. This hostility was in contrast to the behavior of a nearby pair of Hairy Woodpeckers (D. villosus) that had started courtship in late December.

Territorial behavior.—If one accepts Noble's (1939) definition of territory as "any defended area," then four types of territorial behavior and hence territories are observable among Downy Woodpeckers. The first two, occurring mainly in fall and winter months, are exhibited by lone individuals of either sex. These types of territory are: 1, small areas with definite boundaries in some directions, in localities where feeding conditions are favorable (Kilham, 1970); 2, the area in close vicinity of a roost hole, a situation where females may drive off males as well as other females; 3, large areas claimed by a pair in the early breeding season; and 4, smaller areas around the nest hole.

The characteristics of last two types of territory are brought out in the examples of conflicts given below. Examples I and II (below) relate to early breeding season territories which, although hard to estimate, may be as large as 10 to 15 ha. Their main function, it would seem, is to provide an area where the members of a pair of Downies can search for nest stubs. Really suitable stubs are in short supply in most areas, and their scarcity appears to be an important limiting factor in breeding success, at least in New Hampshire. A fourth type of territorial behavior, appearing once a nest site is established, is defense of the area around it. This type, also noted by Lawrence (1967), is illustrated by Example III (below).

I. On 10 February 1968 male A and a rival fought on trunks of small saplings along their common border from 07:20 to 07:35. They were often within 18 cm of each other in bouts of bill-waving dances, as well as in intermittent pauses of resting in strained postures. The section of woods where the males fought was 50 m from where pair A nested the following May.

II. On 28 March 1971 in woods deep in snow, two male Downies fought in a prolonged conflict from 07:05 to 08:10, along a rough boundary line 20 m long. Features of this boundary encounter were 1, nearly all of the fighting was low down on small saplings; 2, one male might swoop down at the other, which was usually able to shift around the tree in time to avoid contact; 3, on one occasion one male seized the other, coming away with

a bill full of small feathers which stuck to his bill, as he did a bill-waving dance, and 4, a female remained in the vicinity, and the fighting became most intense when she came close to the contending males.

III. On 25 April 1965, I noticed two pairs of Downy Woodpeckers approaching each other at 06:30. The two males began fighting almost immediately. The conflict was brief, intense, and accompanied by little display. As it was fought close to a stub where one of the females had tapped briefly, it seemed probable that the two pairs of woodpeckers were contending for a potential nesting site. The owner male carried on exaggerated pecking and feeding displacement activities after his rival had left. Other accounts of the agonistic behavior of *D. pubescens* are given by Short (1971), Bent (1939), and Staebler (1949).

DRUMMING

The onset of breeding behavior is marked by drumming, as well as by territorial conflicts, that begin in mid or late winter. There is little that is sterotyped about the drumming of *D. pubescens*. It varies in rate with a bird's emotional intensity and in carrying power with the type of substrate, e.g. whether this be a hollow place, one of solid hardwood, or an indifferent one of no particular resonance. Both sexes drum, but females often do more drumming than males. The total amount of drumming varies with circumstances; a pair that has found a nest site early in the season drums relatively little, while a pair located in woods deficient in suitable stubs drums a great deal. Among types of drumming that are distinguishable in relation to circumstances are the following:

Mate-location.—This usually consists of only a few bursts, needed when the birds of a pair are feeding separately over a wide area, as they often are.

Dawn-rendezvous.—The efforts of a Downy Woodpecker to locate its mate at the start of a day can be prolonged, especially where roost holes are far apart. A female, for example, began drumming at 05:11 on 14 April at a rate of 18 bursts per min. Her mate came from his roost hole 3 min later and flew in her direction. He stopped on a dead pine to drum before reaching her, and she, after more drumming, then came closer to him.

Contact or contentment.—When Downy Woodpeckers are under no pressure to find a nest stub, either because it is early in the season or because they have already found one, one or the other of the pair, but particularly the female, may rest in the sun or some high dead limb, preening in a prolonged leisurely fashion and drumming in pauses in between. Such activities may, it would seem, promote the pair bond in relation to a particular locality.

Duetting.—Lawrence (1967) writes of reciprocal or answering drumming as occurring in March, at the onset of the breeding season. There are, how-

ever, two kinds of answering drumming. The first of these promotes the pair bond; when the affairs of a pair are going well, each bird drums, on occasions in unhurried fashion in response to the drumming of the other, with resting or preening in between.

The second type of duet drumming I refer to as a tug-of-war type. When relations between the members of a pair are disturbed, the male having preference for one nest stub and the female for another, each drums in an effort to entice the other to come and inspect the chosen site. Drumming can then be prolonged and the rate expressive of the intensity of the disagreement.

Displacement.—Downies, like Hairies and a number of other woodpeckers, drum as a displacement activity at the presence of an intruder, whether this be a conspecific or otherwise. The drumming is usually done where the woodpecker happens to be. On 11 April 1969, for example, a foreign female arrived in a territory, and was attacked by the female of the owner pair. The male did not participate in the conflict but immediately started to drum at a fast rate of 12–20 times a min.

Whisper.—When a nest excavation is on its way to completion, the members of pairs may respond to each other with low drumming; this appears to be expressive of a close pair bond. On 23 April a female, drumming close to a hole subsequently used for nesting, was answered in similar fashion by her mate in the woods nearby. Six days later I saw the reverse situation, with the male drumming by the nest cavity. Drumming softly, however, is not always a matter of a duet. A female near a completed nest cavity may occasionally drum in this manner wherever she happens to be.

Copulatory.—Downies of either sex, but chiefly the male, may drum when ready for copulation, thus attracting its mate from a distance. This is one of a number of types of drumming also noted for *D. villosus* (Kilham, 1966).

Territorial.—Drumming from a high place may have a function in proclaiming territory. Drumming of this type can, as a side effect, attract rivals and precipitate conflicts, thus possibly, hastening, settlements of territorial disputes before the time of actual nesting.

Downies, like other species of woodpeckers, have drum trees (such as the hard wood at the top of a dead maple) that have special resonance. A male Downy may ascend such a place, trying successive spots with a few bursts on each, extracting a variety of sounds, some flat, some deep, and others loud and sharp, the effect being like the playing of a xylophone. It should be emphasized that some types of drumming, as for example in conflicts or of the whisper type, may be done on places of indifferent resonance wherever the Downy happens to be.

Some pairs of Downies, and particularly those that have no potential or

actual nest site on which to center activities, resort to one particular drum tree as a rendezvous, as though a center of some sort were needed for the pair bond. Lawrence (1967) cites the example of one male that came to such a tree for three years. I have noted three such headquarter trees. On one of these the female, arriving in response to the male's drumming, started drumming three m below him in an irregular duet. From this and comparable experiences with other pairs, it would seem that males can attract females to headquarter trees.

SEARCH FOR A NEST SITE

Downies, as in woodpeckers such as the Yellow-bellied Sapsucker (*Sphyrapicus varius*) (Kilham, 1971), appear to have a search image of an optimal nest site. This image appears, in New Hampshire, to be the broken off, dead top of a living tree. Both sexes search for nest sites as is brought out below:

- I. On 24 April a female moved slowly over the broken top of an old butternut (*Juglans cinerea*), giving an occasional burst of drumming and percussing here and there. After 5 min she tapped briefly near the top of the tree as her mate flew to her. She left as he arrived. He then inspected the stub and left.
- II. On 20 April a male Downy drummed on the top of an aspen stub for 3 min, then took a bill-forward pose on seeing his mate. He then moved to the rear of the stub, tapped a few times, and flew off in a ruffle flight (Kilham, 1962) as she arrived.

The above examples illustrate a spectrum of behavior that I have observed at over 30 potential nest sites. Either the male or the female locates a potential nesting stub and then drums for its mate. As the mate approaches, the bird on the stub taps briefly and leaves. The drumming and the tapping are not always in pure form, for sometimes they are intermixed. The arriving bird inspects the stub superficially or more thoroughly percussing as it goes. It may take a number of such inspecting visits before a stub is accepted or rejected. The longer the second Downy spends on the stub, especially if it remains on it to preen in a leisurely fashion, the more likely that it is interested in it as a nest site. Whether the female or the male is taking the lead is difficult to say because an observer never knows for certain that he has seen the whole sequence of events.

COURTSHIP FLIGHTS

These fluttering or gliding displays are alike and are used in the same ways in *D. pubescens* and *D. villosus* (Kilham, 1962, 1966). Table 1 summarizes 33 flights observed for *D. pubescens* in the breeding season. The majority were by males and appeared to strengthen attachment to an actual

TABLE 1
SUMMARY OF 33 COURTSHIP FLIGHTS OF DOWNY WOODPECKERS WITH CONTEXTS
IN WHICH THEY TOOK PLACE

Phase of breeding and dates of observations (inclusive)	Partner displaying	Direction of flights	Number of observations
Drumming; search for nest site	F	To tree where M feeding	1
(15 Feb2 Apr.)	\mathbf{M}	To tree where F feeding	
		(no displacing)	1
	\mathbf{M}	From a potential nest stub	2
	F	To M by a potential nest stub	1
	M	From drum place as F came to	it 1
Triangle conflicts	M	To vicinity F-F conflict	2
(17 Feb.–16 Apr.)	F	To vicinity M-M conflict	1
	F	F-F conflict, M nearby	5
Excavation of nest; copulation (27 Apr24 May)	M	To hole, F probably nearby	9
	\mathbf{M}	To F; pre-copulatory	7
	M	From hole as F came to it	1
Incubation (11 May)	M	To F; pre-copulatory	1
Late nestling (14 June)	M	M & F by hole. M flew off	1

or potential nest site. As described elsewhere (Kilham, 1974), Downies copulate close to excavations. Many of the courtship flights, from the nest hole to the branches were copulations took place, were to the female and were precopulatory in nature. They ceased, with one exception, at the time of incubation. Downies may experience a recrudescence of breeding behavior at the end of the nestling period and this may explain the courtship flight then. The courtship flights of females, when two of them were fighting for a single male, stimulated a high pitch of emotion. The fact that I never saw these displays in territorial conflicts of a male against a male or a female against a female, made it seem likely that the displays, in the triangular contests, were sexual in nature.

DEPENDENCE OF SUCCESSFUL COURTSHIP ON AN ADEQUATE ENVIRONMENT

Successful breeding depends on a habitat that offers what is needed. Nothing is more striking than the differences between the way in which a pair of Downies that has found a good nest site goes about nesting and the behavior of a pair that tries one potential nest site after another, finding all inadequate. Good nest stubs are nearly always in short supply. When an adequate site is lacking, the pair bond breaks down and the male begins

a period of prolonged drummings, seemingly in an effort to get his mate to return. These contrasting situations, one representing breeding success and the other failure, are brought out in the histories of pairs A and B below. The behavior of pair A was noteworthy in presenting in almost classic fashion the main forms of courtship observable in *D. pubescens*.

History of pair A.—The territory of pair A appeared favorable for nesting in a number of aspects. One was that it included paper birches that furnished a winter food supply (Kilham, 1970), and this permitted the members of the pair to stay more or less together in winter months. Signs of a pair bond were evident as early as 11 January 1968, when I saw the two birds feeding only 15 cm apart. When the male flew, the female followed. A week later the female persisted in staying in the vicinity of the male, in spite of his supplanting attacks; on 4 February he flew to her in floating, courtship flight. Seemingly uncertain of his intentions this early in the season, she faced him with bill pointed straight forward, as if to meet an attack. As the winter and spring of 1968 were unusually cold, this early onset of breeding behavior was certainly not attributable to mild weather.

On 17 February the Downies were together from 06:50 to 07:15. Male A (MA) drummed briefly and his mate, moving up a potential nest stub, gave a series of loud, single taps, and drum-taps near the top.

On 11 March when MA alighted on the dead top of a live red maple (Acer rubrum) that was to become the nest stub in May, he was displaced by FA in a reversal of the usual dominance. FA then rested, preening in leisurely fashion. That the stub was regarded as a nest site, although no excavating had been done, was evident on 30 March when the two Downies attacked a female Hairy Woodpecker that came close. In these attacks the female Downy was more persistent and aggressive than the male.

A variety of other behavior at this time indicated closeness of courtship. On both 30 and 31 March, for example, MA flew across the open swamp from the nest stub with wings held in a V, as he tilted from side to side in courtship flight, and later FA preened in leisurely fashion close to the stub while MA rested motionless. On 6 April MA and FA had a drumming duet, one answering the other in unhurried fashion.

I witnessed copulations of pair A by their maple stub on 2 May, and by 8 June the young were ready to leave the nest. This pair thus had had an exceptionally early start on their nesting and were able to fledge the young about 2 weeks ahead of most pairs that I have watched in New Hampshire. This earlier breeding of resident as compared to a migratory pair of Downies is also described by Lawrence (1967).

Breakdown of breeding behavior.—In 1968 two pairs (including B) of Downy Woodpeckers nested successfully in a wood of 15 or more ha. In the

following year, I sought to follow the breeding behavior of these two from its earliest onset through to the time the young were fledged. Neither pair proved able to establish a nest. From following the birds through April into May it was apparent that they had inspected every possible site; in the young woods growing up after lumbering some years before, however, there were no dead stubs of the right type remaining.

The members of the pair B exhibited the usual signs of courtship and a developing pair bond in April 1969. In absence of any nest site or potential one, the male often drummed and preened on a slanting maple, his head-quarter tree; it was there that he met his mate at dawn. There was a dead stub nearby, obviously inadequate for nesting, but on 14 May MB and FB both flew to it in courtship flight. This was the last I saw of the two together. The behavior of MB showed a change on the following day. He was resting on the slanting maple in the early morning with feathers fluffed out, head drawn in, while looking about restlessly. His mate did not appear then, or on the following day, when he began the prolonged drumming that was to last well into June.

DISCUSSION

Points from the foregoing reports needing comment are the nature of the bill-waving dances, of the courtship flights, and of the dominance relations between members of pairs.

Bill-waving dances.—The dances of both D. villosus and D. pubescens, when performed in persistent fashion, have always, in my experience (Kilham, 1959, 1962, 1966, 1969), been used in territorial conflicts of male against male and female against female. Bill-waving can be used against non-specific intruders, such as Starlings (Sturnus vulgaris), by a nest hole, but then only briefly. It is confusing, therefore, that some authors have regarded the dances as courtship. F. H. Allen in Bent (1939) gives good descriptions of the dances of both villosus and pubescens, yet refers to the woodpeckers as courting when admitting that he was unable to identify the sexes. Identification of the sexes is indeed not always easy. The head-back position involved in the dances compresses the males' red nuchal patches, making them less visible; this is a situation one would hardly expect if the dances were sexual in nature. Staebler (1949) also misconstrues the nature of the dances by referring to bill-waving between two males in the fall as being courtship. This is a use of the term that lies outside of all usual definitions (Thomson, 1964). A male Downy may attack an intruding female Downy, and vice versa. In such situations, which are usually by nest (Kilham, 1974) or roost hole, the attacks are direct with little display.

A question is why two male Downies should face each other, in a small stretch of woods in March, in bouts of bill-waving that may go on for over an hour. Several answers are conceivable. One is that the boundary being new, neither male has a psychological advantage over the other. Under these circumstances each might fight equally hard in any direct conflict, and this could lead to injury. By holding their weapons, i.e. their bills, upward and back in a position ineffective for striking blows, the rivals are able to face each other in a ritualized conflict that is relatively harmless. A second point is that the prolonged nature of these conflicts may have value in imprinting; that is in forcing each male to become very well-acquainted with that small bit of woods where the prolonged conflict occurred.

Courtship flights.—I have interpreted the aerial displays of *D. pubescens* as courtship, and this appears to be that also of Lawrence (1967), whose few descriptions (op. cit.:59, 77) fit in with the observations given in Table 1. Pynnönen (1939) describes similar flights in the Greater (*D. major*) and Lesser (*D. minor*) Spotted Woodpeckers. He also links these with courtship, regarding them as expressive of high excitment. Short (1971), on the other hand, takes an opposite point of view and regards "flutter aerial displays" as being clearly agonistic. His observations are different from mine as regards contexts, and I am not sure whether we are following the same criteria or observing the same phenomena.

In relation to possible agonistic components to courtship flights there are three points that should be made, one being that occasionally a Hairy (Kilham, 1966) or a Downy Woodpecker (and usually a male) may hold its wings out in a position of full threat display when about to alight close to a rival. These short displays seem to me to be purely agonistic and unrelated to the more prolonged fluttering or gliding flights used in courtship. A second point is that courtship flights can occur in the context of two females or two males fighting in the presence of the mate of one of them. Sexual emotion can be intense at these times, as shown by the copulations that may take place with both Hairy (Kilham, 1969) and Pileated (*Dryocopus pileatus*) (Kilham, 1959) Woodpeckers under the same circumstances. It is as if the emotion built up by agonistic were directly transferable to sexual behavior.

A third point is that in some cases courtship displays appear to have been derived from what were originally threat or agonistic displays. By this derivation, displays that relate entirely to courtship in one species may still have a hostile connotation in some related species. An excellent review of this subject is given by Andrew (1961). Although he deals with passerines, much of what he reviews may apply to some picine displays as well. I am not sure that the courtship flights of *D. pubescens* or *D. villosus* have any such derivation. They would seem, on the contrary, simply to be a normal

activity (i.e. flying), carried out in an exaggerated manner, a phenomena discussed by Lorenz (1970) for geese and, amusingly, for man.

Sexual dominance.—That female Downy as well as Hairy Woodpeckers occasionally take the lead in breeding behavior is a subject worth more attention than it has received. Lawrence (1967) recognizes the problem and states that the male of D. villosus is dominant in nesting, while a reversal of roles in favor of the female exists in D. pubescens. Drawing upon other experience, it appears to me that females of both species occasionally take the lead, either temporarily or for longer periods, although this is not the usual situation. In Maryland, for example, I encountered a female of D. villosus (Kilham, 1960) that did an extraordinary amount of drumming in winter months in attracting a male to her territory; I also encountered a somewhat similar situation, of milder degree, in New Hampshire (Kilham, 1969). Among Downies, males do by far the larger part of the excavation of nest holes as described both by Lawrence (1967) and Kilham (1974). Yet in an earlier set of observations (Kilham, 1962), I encountered several females that did the larger share. This reversed situation was also noted by Shelly who, as quoted in Bent (1939), wrote that of "a number of nests observed I have never known the male Downy to assist in excavating."

A possible explanation of these departures is that the dominance relations between members of pairs of Downy Woodpeckers represent something of a "see-saw." As long as males continue to exert dominance, females remain subordinate. Various factors may lead to a temporary or longer-lasting reversal of dominance. These are matters needing further study. From observations on woodpeckers of a number of species, including some that were hand-raised and kept in an aviary (Kilham, ms), it seems that females have a drive to assume male behavior, but are kept from doing so by the dominance of their mates. This situation is described by Lorenz (1970) in his classic paper on "The role of the companion in the bird's world." In terms of survival value, increased female dominance in Downies means that, whenever the male does less of an activity such as excavating, his mate will fill in and do more.

Temporary reversals of dominance may be encountered in most pairs of Downy Woodpeckers. One instance noted in March in the present study was where the female of pair A drove her mate from what was to become the nest site in May. No two pairs of this species, however, will ever be found to behave exactly alike. Individuality, prior experience in nesting, and environmental factors can all lead to a diversification of behavior, particularly in the early breeding season.

A final point is the seeming hostility that exists between members of pairs of *D. pubescens* early in the breeding season. This hostility may relate to

feeding habits. Downies generally appear to have a difficult time finding prey in winter months, judging by the hours spent foraging (Kilham, 1970). Intrapair hostility, stemming largely from the male, may serve to separate members of a feeding pair in the early spring as well as winter. This situation prevents the formation of a close pair bond in March and early April. What brings the members of a pair to the close association needed for nesting is the possession of an adequate nest site that will serve as a center for courtship activities and, eventually for copulations, which almost always take place in its vicinity (Kilham, 1974).

SUMMARY

Male and female Downy Woodpeckers remain separate during winter months, when supplanting attacks by the male keep the two spaced out in relation to feeding. Early breeding behavior usually begins in March in New Hampshire and is marked by prolonged territorial conflicts, accompanied by bill-waving dances between males. Drumming, of which a number of types are described, serves to bring the two sexes together as well as having a territorial function. Signs of an increasing bond between members of pairs are that the two travel together at times in foraging, the female tolerating supplanting attacks by the male, and that when the male flies the female follows. Either member of a pair may percuss a stub to determine its suitability for the excavation of a nest, then drum or tap to attract its mate.

Once a nest stub is found, signs of increasing harmony between the members of pairs are leisurely preening, one of the pair resting motionless in the presence of the other, duets of drumming, courtship flights, and joint defense of the nest stub against potential competitors. When no adequate nest site can be found, the pair bond breaks down, the female leaving while the male remains in the territory, carrying on prolonged drumming over many weeks. Dominance by the male partner, occasional reversals of dominance where the female takes the lead, the nature of the bill waving dance, and courtship flights are discussed.

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