AN ANALYSIS OF ACOUSTIC COMMUNICATION WITHIN THE SOCIAL SYSTEM OF DOWNY WOODPECKERS (*Picoides pubescens*)

DISSERTATION

Presented in Partial Fulfillment of the Requirements for the Degree Doctor of Philosophy in the Graduate School of The Ohio State University

By

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ABSTRACT

In contrast to many avian species, woodpeckers use both non-vocal and vocal signals for territorial advertisement. This use of two signals permitted investigation into whether downy woodpeckers (Picoides pubescens) encoded individual recognition cues within both vocal and non-vocal acoustic signals. There are three distinct long distance signals commonly used by downy woodpeckers throughout the breeding season: rattle calls, pik calls, and drums. The first two are vocal signals, the later non-vocal. Males and females used these signals at similar average rates for the entire breeding season (signals hour\(^{-1}\)), but females used drums at higher rates (drums hour\(^{-1}\)) earlier in the season than males. Individuals did not use drums as consistently as rattle or pik calls during the breeding season, which indicated drums may not be used often enough for neighbor recognition in the later part of the breeding season. Results of neighbor-stranger playback experiments indicated downy woodpeckers were able to recognize individuals by rattle and pik calls, but failed to express a differential behavioral response between neighbor and stranger drums. The data from this study indicated downy woodpeckers were able to recognize a neighbor’s vocal signals but did not differentiate between neighbors and strangers by the non-vocal drum.

Downy woodpeckers have been documented to raise their young in monogamous pairs. However, I observed at four of thirteen cavities a female downy woodpecker
helping a monogamous pair during the 1998-2001 breeding seasons, Kraus Woods, Delaware Co, OH. “Helper” females assisted the primary breeding pair by incubating eggs and delivering food to nestlings. “Helper” females used rattle calls and pik calls at lower rates during the breeding season than did primary breeding females. In addition, “helper” females did not use drums while assisting monogamous pairs, but did use drums if the monogamous pairs’ nest failed. An analysis of calls exchanged between helpers and mated pairs indicated that calls previously described for the species were exchanged during interactions with helper females; novel calls were not observed. I used multilocus minisatellite DNA fingerprinting to test for relatedness of individuals within groups. The average proportion of bands shared between females and “helpers” (0.22), was significantly less than the average proportion of bands shared between males and “helpers” (0.41). These proportions indicated that “helpers” were not first order relatives, but “helpers” were more related to the males they helped than the females. The proportion of bands shared between mates, and between males and non-mated, non-helper females was 0.15. Primary breeding females were present within the territory the previous year, but primary breeding males were not observed the previous year. Therefore it is unknown how “helper” females dispersed to an area where they were close to a territory of the related male.

I recorded and analyzed acoustic features of pik calls, rattle calls and drums from color banded downy woodpeckers during the 1998-2001 breeding seasons to test whether all three signals encoded individual recognition cues, and which variable(s) were responsible for encoding identity. I also tested whether the signals changed within or
between breeding seasons. Using discriminant function analysis, there was sufficient
variability between individuals to correctly classify individuals by their drum or pik calls,
but rattle calls had the highest correct classification of individuals. The frequency
characteristics of rattle calls varied between individuals, while the temporal characteristics
varied between breeding stages. The some of the frequency parameters of the rattle call
significantly changed between the two years sampled. I tested the responses of mates to
rattle calls to ascertain whether the changes within the rattle call between years were
perceived as differences in individual identity. The weaker response by mates to a mate’s
call of the previous year indicated changes in call characteristics between years did
change the how the calls were perceived by individuals.
I dedicate my dissertation to my husband Robert Stark, in appreciation of his enduring support of my academic endeavors.
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CHAPTER 1
INTRODUCTION

Communication is an essential component of a social system, as it facilitates the interactions between individuals. Encoding individual identity is not required for information to be conveyed, but knowing the identity of the signaler can aid a receiver in gauging the reliability of information. Although individual recognition cues can be encoded within different modalities of communication, many avian species live in habitats that favor auditory communication. Consequently, it is not surprising to find a multitude of examples of individual recognition by auditory cues among avian species (Falls 1982).

The characteristics of territorial signals that encode individual identity are used by territorial neighbors to evaluate the stability of established borders thereby reducing the number of aggressive encounters (Ydenberg et al. 1988). Brooks and Falls (1975) used playbacks of male song as a method of demonstrating that white-throated sparrows (Zonotrichia albicollis) were able to discriminate between territorial neighbors and strangers. Additional playback experiments of presenting the neighbor’s song from the opposite boundary confirmed that white-throated sparrows recognized individual neighbors, not just familiar from unfamiliar vocalizations. Since these initial studies, 25 out of 28 passerine species studied have demonstrated individual neighbor recognition by voice (Stoddard 1996).
Relative to passerines, there have been few studies of non-passerine species on the acoustic recognition of neighboring individuals (Falls and McNicholl 1979, Galeotti and Pavan 1993). Crusoe (1980) used appropriate and opposite boundary speaker placement experiments with the territorial call of male red-headed woodpeckers (Melanerpes erythrocephalus), and found that males were able to recognize individual territorial neighbors and mates acoustically by the territorial call. Therefore, although there are not as many studies of non-passerine species, the few studies done have indicated many avian species are able to acoustically recognize neighboring individuals using vocal territorial signals. However, studies on non-passerines which use calls to maintain a territory have not investigated whether non-territorial acoustic signals in a bird’s repertoire also encode individual identity.

Studies of acoustic recognition of same sex territorial neighbors have focused primarily on territorial males. One exception is the study of striped-backed wrens (Campylorhynchus nuchalis), which investigated the recognition of territorial neighbors by male-female pairs, but not females separately (Wiley and Wiley 1977). Although males are the primary producers of song, there are species in which females use song for territory maintenance (Beletsky, 1983a, Hoelzel 1986, Baptista et al. 1993). Therefore, if individual recognition is universal among birds, then females which use a song to maintain a territory should be capable of identifying their female neighbors by song.

Contrary to this prediction, a series of playback experiments with red-winged blackbirds (Agelaius phoeniceus) indicated that males distinguished between neighbor and stranger females (Beletsky 1983b), but females did not respond differently to neighbor and stranger females (Beletsky 1983c). However, Beletsky concluded that placement of the speaker at the center of the female’s territory during playback trials might have been the
reason for the lack of discrimination by females, since the speaker was not at the shared border between neighbors. This conclusion is consistent with evidence of male neighbor recognition, since male song sparrows also do not exhibit neighbor-stranger differential responses when songs are played from the territory center (Stoddard 1996).

A study of pied flycatchers (*Ficedula hypoleuca*, Lampe 1998) offers evidence that females may, when tested under similar conditions as males, recognize territory neighbors by song. Female pied flycatchers exhibited different responses to the songs of mates and those of neighboring or strange males. Experiments with female song sparrows (*Melospiza melodia*, O’Loghlen and Beecher 1999) and female dunnocks (*Prunella modularis*, Wiley et al. 1991) have also shown that females can recognize neighboring males by song. Therefore a lack of studies showing female recognition of territorial neighbors, as opposed to mates, is possibly due to females not using song as a territorial signal as often as males. An alternative hypothesis is that females may not exhibit differential responses because borders between neighboring females may not be as stable as those between neighboring males.

There are several characteristics of the communication signals used by woodpecker (*Picoides*) species that offer opportunities to test several hypotheses concerning recognition by sound. Female downy woodpeckers (*Picoides pubescens*) maintain territories and use the same vocal and non-vocal signals as males (Lawrence 1967, Winkler and Short 1978). This offers the opportunity to investigate whether females recognize individual neighbors acoustically in a manner similar to males. It is possible to test the recognition ability of females without the presence of males because both sexes maintain separate territories until choosing a nest site.
Another aspect of the communication system of woodpeckers permits testing whether a non-vocal territorial signal encodes information about individual identity. Woodpeckers maintain territories by using their bill to strike a resonant surface producing a species typical pulse pattern, termed drumming (Winkler and Short 1978). Theoretically, if a non-vocal signal functions to maintain territory boundaries, neighbors should be able to recognize one another by this signal, as the selection pressure for individual recognition should be similar as with vocal signals.

If rattle calls and drums serve as territorial signals then one or both might encode individual identity. The *Picoides* rattle call has been attributed the same functions as drumming and the two signals are considered functionally interchangeable (Lawrence 1967, Winkler and Short 1978). When used in conjunction, these two signals may function as a multiple display to maintain territories. If both signals have the same function, then only one signal may be needed to encode an individual’s identity. Therefore, drums may be used as an initial long distance signal, whereas rattle calls serve as the individual recognition signal to maintain a stable territorial boundary. The two signals used in this manner would be effective if both signals are highly localizable and therefore can be assessed as being produced by the same individual, despite one signal not containing information about the individual’s identity. If rattle calls and drums function in the proposed coupled manner, we would predict that only rattle calls encode information about individual identity.

Alternatively, rattle calls and drums could serve different functions. Drumming has been hypothesized to the function in territorial defense because of observations of downy woodpeckers using drums throughout the breeding season (Kilham 1962, Winkler and
However these observations were not made on banded populations, so an individual’s temporal pattern of signal use is not known. Therefore, drums may serve as only a mate attraction signal, which might not have the selection pressure favoring individual recognition. If downy woodpeckers drum most frequently during the beginning of the breeding season and once mated reduce or cease drumming, the drum would not serve as a reliable individual identifier for neighbors during the later part of the breeding season. This would not eliminate the possibility of mates identifying one another by drum as they may learn the difference between individuals before selecting a mate.

Downy woodpeckers mate and raise young in apparently monogamous pairs (Winkler et al. 1995). However, four pairs of downy woodpeckers breeding in Kraus Woods, Delaware Co. OH were observed to have a female helper. There were also breeding attempts observed between one of the female helpers and a neighboring male, so it is unknown whether all the eggs in the shared nest were those of one female. These four groups of three downy woodpeckers are unusual and provide an opportunity to investigate signals used between individuals during social encounters of non-mates. An analysis of the signals used by helpers during interactions with mated pairs offers the opportunity to investigate whether novel signals were used between group members or if signals already described for the species acoustic repertoire were used during these atypical interactions.

The following chapters summarize the results from investigating the communication system of Downy woodpeckers. Chapter 2 consists of results from monitoring the use of pik calls, rattle calls, and drums by downy woodpeckers during the breeding season. Also monitoring of male and female downy woodpeckers established
whether joint territories are maintained prior to selecting a nest site. Chapter 3 consists of the observations of a female downy woodpecker helping an apparently monogamous pair at four different nests. It also reports the results of tests of the genetic relatedness among helper groups. Chapter 4 then consists of playback experiments of individual recognition of territory neighbors and mates testing whether any of the acoustic signals are used for long distance individual recognition. Chapter 5 summarizes the statistical results of an acoustic analysis of the downy woodpecker “pik” call, “rattle” call and drum. Each signal was tested for differences between individuals, breeding stages and breeding years. This comprehensive analysis of the downy woodpecker acoustic communication system provides additional knowledge of how acoustic communication is involved in and facilitates social group interactions.
CHAPTER 2

A NATURAL HISTORY OF DOWNY WOODPECKERS IN CENTRAL OHIO

The ecology of woodpeckers has been well documented, as they are an integral component to understanding the dynamics of forest ecosystems (Mikusinski et al. 2001, Weikel and Hayes 1999, Eckhard 1997). Ecological studies often do not include detailed observations of territory dynamics or communication through the use of acoustic signals. Thus, there are only a few natural history studies which describe these aspects of downy woodpecker behavior. The natural history of downy woodpeckers is described primarily from naturalists’ observations of unbanded populations, with a few notable exceptions (Lawrence 1967, Jackson 1970, Mahan 1996). I will begin with an account of previous studies on the natural history of downy woodpeckers. Herein, I will address aspects that have not been included in previous studies of downy woodpeckers. The integration of observations from previous studies and results from this study will aid in clarifying aspects of the downy woodpecker’s territory dynamics and its use of long distance acoustic signals.

There is observational evidence that portions of the northern populations of downy woodpeckers are short distance migrants, but downy woodpeckers are non-migratory within Ohio (Short 1982). Individuals are solitary in winter and may often
defend foraging areas with high concentrations of insect infested trees (Travis 1977, Winkler et al. 1995). However, downy woodpeckers have not been observed to defend winter foraging areas in Ohio (Matthysen et al. 1993). Since a territory is an area an individual occupies and defends against intruders, downy woodpeckers are presumed not to maintain a winter territory. Instead, the area a downy woodpecker occupies during the winter is more correctly referred to as a home range. A home range is an area an individual lives within, and may or may not actively defend against intruders.

Matthysen (et. al., 1993) studied the social interactions of downy woodpeckers in Ohio during the winter months of December and January. They found that individual home ranges commonly overlapped by more than 50% during mid-winter, regardless of paired status or sex. During December and January, downy woodpeckers foraged within view of other conspecifics but did not exhibit behaviors associated with territorial defense. Downy woodpeckers were seen less often foraging close to same sex conspecifics, while they did forage close to opposite sex conspecifics more often than was expected by chance. However, Matthysen and colleagues did not observe any permanent pair bond associations between males and females. Based on the lack of territorial aggression and the degree of overlap between individual home ranges, they concluded there was no evidence that individual territories were maintained during the winter months. Although resident individuals may not maintain a territory during a portion of the winter, they are reported to occupy a restricted home range during this time of the year (Kilham 1962, Lawrence 1967).

Studies of home range use did not address the question of when males and females defend a breeding territory, and whether they defend a joint territory or separate
territories. There are only a few observational studies of the territory dynamics between males and females prior to nesting. Male and female downy woodpeckers in Massachusetts set up and maintained separate territories until a nest cavity was excavated (Kilham 1962). However, Lawrence (1967) observed in Ontario that male and female downy woodpeckers occupied separate “ranges” but jointly defended an area prior to the excavation of a nest cavity. These contradictory observations might be explained if downy woodpeckers employ two different strategies of home range use. The first pattern would be to set up a breeding territory within the boundary of the home range area used during the winter. If downy woodpeckers employ this pattern of home range use, an individual could share a territory with its mate or set up a breeding territory separately prior to the selection of a mate. The second pattern would be for an individual to use one area during the winter and then disperse at the beginning of the breeding season to a second separate area. After dispersal, an individual could either share a mate’s territory or establish a territory to attract a potential mate. If an individual employed the first type of home range use I would expect to observe conditions of either joint territorial defense or individual territories. However, if an individual employed the second type of home range use, I would expect defense of an individual territory at the onset of the breeding season. Once the individual established a territory, joint territorial defense would be expected after a mate was attracted.

Based on previous documentation (Lawrence 1967) and personal observations, resident downy woodpeckers begin exhibiting behaviors related to breeding during early February. However, breeding pairs do not select a nest cavity site until mid-April (Figure 2.1). The cavity site is primarily chosen by the female and a new nest cavity is excavated
each breeding season (Lawrence 1967, Kilham 1962). The cavity is excavated by both sexes, with the female spending slightly more time than the male excavating (Short 1982). During the cavity excavation phase and continuing for the remainder of the breeding season, the male and female defend a joint territory centered on the nest cavity (Lawrence 1967, Kilham 1962, Short 1982). The size of the joint territory varies, but is smaller than the area defended prior to the selection of a nest site (Kilham 1962, per. obs.) Males and females share parental duties, but the female reduces her effort during the latter portion of the breeding season once the chicks have fledged (Winker et al. 1995).

Downy woodpeckers use three signals for long distance communication during the breeding season. These communication signals can be classified into two categories: the vocal signals of rattle and pik calls, and a non-vocal mechanical signal, the drum. Rattle calls are a repeated series of call notes which vary in frequency within the call. These calls have been thought to function as an acoustic signal of aggression and announcement of the signaler's location and presence within a territory (Winkler and Short 1978). A pik call is a single vocal element (rather than a series of elements), and has been suggested to function as an acoustic signal of the sender's location, and is particularly used during changes in position (Kilham 1962, Short 1982). Woodpecker drums are a rapid, repetitive series of strikes with the bird's bill on a resonant surface, not associated with foraging or cavity excavation. The drum has been suggested to function in territory defense and as a mate attraction signal (Miller and Bock 1972, Winkler and Short 1978). Given the aggressive function attributed to the rattle call, it has been hypothesized to function similar to drums in territory defense (Lawrence 1967, Winker and Short 1978).
Short (1982) also hypothesized that rattle calls rather than drums were the woodpecker equivalent to passerine song, since they were more likely to encode markers for species and individual recognition.

Previous researchers (Kilham 1962, Lawrence 1967, Winker and Short 1978) have inferred the functions of the long distance signals from observations of when, and in what contexts, downy woodpeckers used acoustic signals during the breeding season. However, observations of seasonal use have differed between studies for both rattle calls and drums. Winkler and Short (1978) observed females using drums much less often than males, but males and females seemed to use rattle calls similarly during the year. Lawrence (1967) observed females using drums as often as males, but reported rattle calls were used only during the breeding season. Kilham’s (1983) observations of male and female seasonal drum use were similar to Lawrence’s (1967), but he reported rattle calls were also used in the non-breeding season.

Observations of a banded population (Mahan 1996) might provide a reason for these discrepancies between previous studies. Mahan used the observations of several individuals throughout the breeding season to estimate a seasonal pattern that was typical of a single individual. From these averaged results he concluded that males and females did not differ in their use of either drums or rattle calls. However, he was able to observe one male on consecutive observation periods over two months. This single male significantly changed his use of drums between months. Therefore, if individuals were monitored over the entire breeding season, and compared controlling for individual variation, the resulting seasonal pattern of signal use might be different from those based on a population average.
There are several aspects of male and female territory dynamics and use of long distance signals during the breeding season that remain unclear. To clarify the seasonal patterns of signal use I monitored the use of rattle calls, pik calls, and drums by individual male and female downy woodpeckers during six stages of the breeding season. Previous studies have established how males and females differ in their use of a home range and that both sexes forage together, but they have not addressed whether this tolerant foraging behavior was equivalent to joint territorial defense. To ascertain whether males and females defended separate or joint territories, I examined the spatial distribution of rattle calls and drums used within Kraus woods. These territory maps also reflected the seasonal changes in territory size that have been previously noted for other woodpecker species (Wiktander et al. 2001). To ascertain whether downy woodpeckers remain within their wintering territory during the breeding season or disperse to a separate area, I studied the choice of mates over three years. If males and females maintained separate territories but remained within their winter home ranges, I would expect them to choose mates from neighboring males and females. If males or females established a territory and then attracted mates that had dispersed from a separate overwintering area, I would expect them to choose non-neighboring individuals as mates.

Finally, I compared the seasonal patterns of signal use by downy woodpeckers to those of passerine species. If downy woodpeckers use each signal as hypothesized then I expected downy woodpeckers seasonal use patterns to be similar to those of song use observed in passerine species. Based on previous experiments with white-throated
sparrows (Zonotrichia albicollis, Falls 1987) testing the function of song, I expected a territorial signal to be used at high rates while territories were being established and then at low rates to maintain the territory for the rest of the breeding season.

If a signal served a mate attraction function I expected a seasonal pattern of peak use at either the beginning of the breeding season. A peak at the beginning of the breeding season would be similar to the use of song by reed warblers (Acrocephalus scirpaceus Catchpole 1973), which use their song initially to attract a mate and cease using song for the remainder of the breeding season. A signal that serves to attract a mate to a location within the territory (i.e. to the nest or site for copulation) would be used at high rates during the nest building and incubation stages. The use of a signal during stages when a female is most fertile would be similar to the use of song by mockingbirds (Mimus polyglottos, Logan 1983) and yellowhammers (Emberiza citrinella, Møller 1988). The particular function of a signal during these stages of the breeding season is not similar between species. Song use during the female fertile period can either serve a mate guarding function (Møller 1990) or have a stimulating effect on the reproductive cycle of the female (Logan et al. 1990). Although a peak in a signal's use during the female’s fertile cycle can not be used to differentiate a particular function, it would indicate the signal is used in contexts other than defense of a territory.

A final possible seasonal use pattern would be for a signal that served as both a mate attractant and territorial signal. I expected this type of signal to be used at higher rates during the beginning of the breeding season, and then at lower rates during the remainder of the breeding season. Since the signal would be serving as a mate attractant
it might also be used at a high rate during the nesting building stage or incubation stage. Without the increased rate during the nesting building stage, this pattern would be similar to the seasonal pattern use of a signal for only territorial defense. Therefore, to discern whether a signal served only a territorial function and not both territory and mate attraction functions, it was necessary to compare the signaling rates of individuals with mates and without mates. If the signal served an additional mate attraction function, I expected the rates of signal use by unmated individuals to be higher than those of mated individuals.

METHODS

STUDY AREA

This study was conducted within a 30 ha eastern deciduous forest, Kraus Wilderness Preserve, Delaware Co., OH (N 40° 11', W 83° 03', 30 ha). Downy woodpeckers were mist netted and color banded for individual identification from November through February, 1998-2000. Kraus Wilderness Preserve was used for monitoring signal and territory use during the 1998-2000 breeding seasons.

TERRITORIES AND BREEDING STATUS

The boundaries individuals defended from February to July (1998-2000) were mapped for fourteen males and eighteen females within the Kraus Wilderness Preserve study area. Individual territory boundaries were resolved by locations of drumming sites and rattle calls. The coordinates of rattle call and drum locations were mapped using a
Garmin GPSIII global positioning system. There were 14 females and 7 males over the 3 years of this study observed and banded at feeding stations, but they are not included in the analysis because they did not remain within the study area for more than two weeks. To ascertain whether males and females maintained a joint or a separate territory prior to nesting, the outer boundary of the area where an individual used rattle calls and drums was noted during three intervals of the breeding season; February to March, April to May, and June to July. Rattle calls were often given once before the bird changed location, so the unit of measure for estimating boundaries was a rattle call not a series of calls. However, drums were repeated multiple times from the same location. Therefore drums given in the same tree were categorized as a drumming bout. Locations of these drumming bouts were then to mapped along with locations of rattle calls and used to indicate the boundaries of individual territories. Once a cavity was excavated, both the male and female defended the site, so the nest site of a pair was included within the boundary of both individual territories. The two month long interval categories were used in order to include all birds that used a rattle call or drum within the study area, not just those that had successful nesting attempts. The two month intervals approximately corresponded to the following breeding stages based upon individuals that did acquire mates during the season: 1) During the interval of February to March individuals had not selected a permanent mate but might have begun foraging within a opposite sex neighbor’s area (corresponding the pre-mate selection and pre-nestling stages). 2) During the interval of April to May, cavity sites were selected and excavated and individuals without mates were exhibiting pronounced attempts at acquiring a mate (corresponding to the cavity excavation, incubation and the beginning of the nestling stage).
3) During the interval of June to July individuals engaged in a nesting attempt were completing the nestling stage and feeding post-fledged juveniles.

To describe the seasonal patterns of home range use by males and females the following aspects of each breeding attempt were noted: whether a mate was a neighbor or non-neighbor, whether an individual used the same territory in successive breeding seasons, whether individuals had the same mates between breeding seasons, whether the nest site was located within an area the male, female or both defended prior to excavation, and whether a breeding attempt was successful or unsuccessful. Whether a nest cavity was categorized as established within the male’s or female’s pre-nesting territory was dependent upon its location relative to the spatial pattern of signal use. If a pair established a nest cavity within 20 meters of a location where the male drummed or rattle called during the pre-nesting stage, then the nest site was categorized as within the male’s territory. If the nest cavity was within 20 meters where the female had previously used drums and rattle calls during the pre-nesting stage, but not the male, then the nest cavity was categorized as within the female’s territory. A border category was used for nest sites that were established in an area that was not within 20 meters of where either the male or female had used drums or rattle calls during the pre-nesting stage. A nesting attempt was categorized as successful if at least one nestling survived and fledged from the nest. A nesting attempt was categorized as unsuccessful if there were no fledglings produced after a cavity was excavated. If a pair did not finish the excavation of a cavity the breeding attempt was not included in the summary of successful and unsuccessful nesting attempts.
SEASONAL USE OF SIGNALS

To investigate whether use of the three acoustic signals differed throughout the breeding season, a total of twenty-eight downy woodpecker territories were monitored. Each territory was monitored twice a week on a bi-weekly schedule for three hours (8:00-11:00 a.m. EST) per day from February through June, 1998-2000. The numbers of drums, rattle calls, and pik calls used by the focal animal within the observation area during each three hour observation period were used to estimate an average signal use per hour. The average signal use per hour for each observation period was then used to determine a mean rate of use for pik calls, rattle calls and drums during six pre-defined breeding stages: pre-mate selection, pre-nesting, cavity excavation, incubation, nestling, and post-fledging of young.

The breeding stage of pre-mate selection was characterized by when an individual was seen foraging alone or associated with different individuals of the opposite sex during consecutive visits. The pre-nesting stage was characterized by when the focal individual was observed foraging during consecutive visits within the territory of the same individual of the opposite sex. During this stage males and females were considered mated but until a cavity site was chosen individuals had the chance to select another mate prior to nesting. The nest excavation stage was the observation period during which the focal individual was excavating a nest cavity. The period of incubation was from when the focal individual was no longer excavating a cavity to the first day I observed the parents feeding nestlings. The nestling stage included the period when the adults were delivering
food to the nestlings. The post-fledging stage began when the pair stopped returning to the cavity with food and continued for two weeks. For all individuals this period ended by the first week in July.

To test whether individuals that did not acquire a mate during the breeding season differed from those that did in their use of each signal, I compared the signaling rates of ten unmated males and females to those of the eighteen mated males and females. An individual was categorized as mated if they were engaged in a nesting attempt with another opposite sex conspecific and completed the excavation of a nest cavity. Individuals were categorized as unmated if they were not engaged in a nesting attempt or were observed with an opposite sex conspecific for less than two observation visits. The breeding stages compared (pre-nesting, nest excavation, and incubation) corresponded to the breeding status of individuals with mates. I used the calendar week when mated individuals began or ceased exhibiting behaviors characteristic of the breeding stage to estimate the delineations between categories for the unmated individuals. Therefore, individuals without mates did not exhibit the behaviors associated with the three stages. It was necessary to categorize the unmated individuals according to the breeding stages of the mated individuals to make comparisons between the groups. I compared three breeding stages only because none of the unmated individuals occupied territories during the pre-mate selection, nestling, or fledging young breeding stages. There were two individuals that had mates until the cavity excavation stage but lost their mates before the end of the cavity excavation stage. These individuals were included in the comparison as unmated for the cavity excavation and incubation stage.
I used a repeated measures multivariate analysis of variance to test for differences in mean signal use by males and females during the six breeding stages. Significant differences among means were compared using a Bonferroni correction for multiple comparisons. To satisfy the multivariate analysis of variance assumption of sphericity the data were normalized using a square root transformation. A Greenhouse-Geisser correction factor was used if sphericity could not be assumed. I identified differences in signal variables among breeding stages using ANOVA with a Bonferroni correction factor for multiple comparisons.

**BEHAVIORAL CONTEXTS OF SIGNAL USE**

Eight males and eight females were the subjects used to summarize the context each of the three signals were given in. I noted the context and signal used for each of the 10 individuals during ten of the monitoring periods in the 1998 and 1999 breeding seasons. Five observation periods occurred prior to the individual acquiring a mate and choosing a nest site and five were after the individual had chosen a nest site. There were six categories of contexts focusing on whether a conspecific individual was or was not within visual range when a signal was given. Spontaneous signals were defined as those given when no conspecific had given a signal 5 minutes prior and there were no other conspecifics within 20 meters of the focal individual. Mate signals were given when a mate or future mate was within 10 meters of the focal individual. Opposite sex neighbor signals were given when a neighbor of the opposite sex was within 10 meters of the focal individual. Same-sex neighbor signals were given when a neighbor of the same sex was within 10 meters of the focal individual. Long distance response signals were given when
a neighbor greater than 50 meters (not within visual range) gave a signal within 2 minutes of the focal individual’s response. Floater signals were given when a conspecific without a territory within Kraus woods was within 10 meters of the focal individual.

I used a multivariate analysis of variance to test for differences between males and females in the use of each signal during the six social contexts. The data were normalized using a square root transformation and a Greenhouse-Geisser factor for the correction of the degrees of freedom since equal variances could not be assumed. I used univariate analysis of variance tests using a Bonferroni correction for multiple comparisons to identify differences between social contexts.

RESULTS

TERRITORIES AND BREEDING STATUS

A total of eighteen males and twenty females remained within the study plot, Kraus woods, for more than two weeks during the months of January to July, 1998-2000. Nine males and nine females remained with a mate after the pre-nesting stage through the nestling stage. The spatial distribution of rattle calls and drums used by males and females, 1998-2000, are summarized in Figures 2.2, 2.3, and 2.4. The number of calls and drumming bouts varied for each individual, Table 2.1 and 2.2. The territory maps illustrate the outer boundary where individuals gave signals during each two month interval during the breeding season (February through March, April through May, and June through July). Individuals that were not observed to remain in the study plot during the following winter were also not observed after the second week in June. Males and
females used both drums and rattle calls within separate areas during the pre-mate selection stage, which was from mid-January to the end of February.

Although males and females began foraging within each others’ territories extensively during mid-February to mid-March, they gave rattle calls and drums within separate areas. Some males began to use rattle calls and drums within the area only the female had previously used drums and rattle calls in. This occurred during the cavity excavation stage and incubation stage during the month of April. Females within Kraus woods during February and March did not cross over male territory boundaries and begin signaling within an area where only a male had been previously using either rattle calls or drums. Females continued to use rattle calls near the nest cavity during the month of April. Individuals that used rattle calls and drums only within their mate’s territory were not observed to have a territory within Kraus woods prior to the selection of a nest site. The four males and one female that exhibited this pattern also did not remain within Kraus woods during the winter months.

Fifty percent of the nest cavities were located within the area where female used rattle calls and drums prior to the cavity excavation stage (Table 2.3). Sixty one percent of the males and 55% of the females choose a territorial neighbor as a mate. There were seventeen nesting attempts over three years, twelve of which were successful. Of the successful nesting attempts, 75% were between pairs that had previously been neighbors. Sixty one percent of females and 20% of the males remained within the same territory between years.
SEASONAL USE OF SIGNALS

MALES AND FEMALES: ALL BREEDING STAGES

The individuals included in the analysis of downy woodpecker signal use for six breeding stages remained within the study area from January through the month of June. These individuals acquired mates and completed a nesting attempt at least through the incubation stage. The average seasonal use of rattle calls and drums did not differ between males and females (Table 2.4; MANOVA: Wilks’ $\lambda = 0.007; \text{df} = 1, 16; P = 0.933$). The average seasonal pik call rate of males was lower than for females (MANOVA: Wilks’ $\lambda = 9.01; \text{df} = 1, 16; P = 0.008$). The average signal rate of all three signals differed between breeding stages (Figures 2.6C, 2.7C and 2.8C; MANOVA: Wilks’ $\lambda = 5.98; \text{df} = 15, 215.7; P < 0.001$).

RATTLE AND PIK CALLS

Males and females had similar average rattle call rates within each breeding stage (MANOVA: Wilks’ $\lambda = 6.7; \text{df} = 2.6, 41.6; P = 0.256$). Males and females had higher rattle call rates during the pre-nesting and cavity excavation stages, than during any of the other breeding stages (Figure 2.5C). The mean rattle call rate decreased constantly from the pre-mate selection stage through the nesting stage. Males and females increased their mean rate of rattle calls after the nesting stage to a level that was similar to rates
during the pre-mate selection and incubation stages (ANOVA Bonferroni correction: $F = 6.6$ and 12.8; df = 2.6, 80; $P < 0.05$). Males had a significantly lower seasonal average pik call rate than females, but the pik call rates within each breeding stage did not differ significantly between males and females (Figure 2.6C; ANOVA Bonferroni correction: $F = 1.1$; df = 5, 80; $P > 0.05$). Pik calls were used at a reduced mean rate during the post-fledging period relative to during the preceding five breeding periods (ANOVA Bonferroni correction: $F = 3.14$; df = 5, 80; $P < 0.05$).

DRUMS

The mean drum rates for males and females combined differed significantly between breeding stages (Figure 2.7C; MANOVA: Wilks’ $\lambda = 15.3$; df = 5, 80; $P < 0.001$). Males used drums at significantly higher rates during the cavity excavation and incubation stages than during other breeding stages (ANOVA Bonferroni: df = 5, 80; $P < 0.05$). Male drum rates were low during the pre-mate selection, pre-nesting, and nestling stages. Males began using drums during the post-fledging stage at rates similar to but lower than during the incubation stage (ANOVA Bonferroni: df = 5, 80; $P > 0.05$). Females drummed at significantly increased rates during the pre-mate selection, pre-nesting and cavity excavation stages than during any other stages (ANOVA Bonferroni correction: df = 5, 80; $P < 0.05$). The drum rates of females were then low for the remainder of the breeding season.
UNMATED AND MATED MALES AND FEMALES

Unmated individuals occupied territories during the pre-nesting, cavity excavation, and incubation stages of neighboring mated birds. Eight of the unmated individuals were not observed within a territory during the pre-mate selection, nestling, and post-fledging stages. Therefore, their signal use only during the pre-nesting, cavity excavation, and incubation stages was compared to that of mated males and females. There were five unmated males and only two acquired mates after the incubation stage while other conspecifics were feeding chicks.

There were no significant differences between males and females in rate of drums (ANOVA Bonferroni correction: F = 1.68; df = 1,24; P = 0.197), rattle calls (ANOVA Bonferroni correction: F = 0.421; df = 1, 24; P = 0.421), or pik calls (ANOVA Bonferroni correction F = 0.819; df = 1, 24; P = 0.447) across all breeding stages irrespective of whether an individual was mated or unmated. Partitioning by breeding status revealed unmated and mated males and females differed in their average rattle call rates (Figure 2.5 A and B; ANOVA Bonferroni correction F = 9.5; df = 2, 48; P <0.001) pik call rates (Figure 2.6 A and B; ANOVA Bonferroni correction F = 8.2; df = 2, 48; P = 0.001) and drum rates (Figure 2.7 A and B; ANOVA Bonferroni correction F= 12.16; df = 2, 48; P < 0.001) within breeding stages. For unmated birds, there was a significant difference in the average drum rate (ANOVA Bonferroni: F = 7.11; df = 2, 48; P = 0.034), rattle call rate (ANOVA Bonferroni: F = 5.55; df = 2, 48; P = 0.01) and pik call rate (ANOVA Bonferroni: F = 8.87; df = 2, 48; P = 0.001) between the three breeding stages.

Although both unmated males and females increased their rates of rattle calls during the period mated individuals were excavating cavities or incubating eggs, the
increase was not significant (ANOVA pairwise comparisons Bonferroni correction: df = 11, 72; P > 0.05). Mated females decreased their rattle call rates during incubation, but not significantly from previous breeding stages (ANOVA pairwise Bonferroni correction: df = 11, 72; P = 0.902). Mated males also decreased their rattle call rates during incubation but not significantly lower than those rates of use during pre-nesting or cavity excavation (ANOVA pairwise Bonferroni correction: df = 11, 72; P > 0.05). Unmated individuals had lower pik calls rates than mated individuals for all three breeding stages (MANOVA: Wilks’ λ = 8.28; df 3, 22; P = 0.001). Unmated males and females increase their pik call rates by period mated individuals began incubating eggs, but not significantly from the rates during the pre-mate selection stage (ANOVA pairwise Bonferroni correction: df = 11, 72; P > 0.05).

During the pre-nesting stage, mated and unmated males and females had similar drum rates (ANOVA Bonferroni correction: F = 2.10; df = 3, 22; P = 0.127). While excavating cavities, mated females had drum rates similar to those of unmated females (ANOVA pairwise Bonferroni correction: df = 11, 72; P = 0.87). However, when mated females began incubating eggs they decreased their drum rates and females without mates continued using drums at significantly higher rates (ANOVA pairwise Bonferroni correction: df = 11, 72; P = 0.002). Both mated males and unmated males used drums during the cavity excavation stage but mated males used them at a significantly higher rate (ANOVA pairwise Bonferroni correction: df = 11, 72; P = 0.033). While mated males were sharing incubation duties with their mates, unmated males significantly increased their drum rates to a level similar to that of mated males during cavity excavation (ANOVA pairwise Bonferroni correction: df = 11, 72; P = 0.032).
The social contexts during which signals were used are summarized in Figure 2.8. The number of calls and drum bouts varied among eight males and eight females monitored during the 1998 and 1999 breeding seasons (Table 2.5). Male and female downy woodpeckers used pik calls less often when either same- or opposite-sex neighbors were within 10 meters than during any other social context (ANOVA Post-hoc Bonferroni: F = 18.2; df = 5, 108; P < 0.01). Females used pik calls less than males when a mate or future mate was within 10 meters (ANOVA Post-hoc Bonferroni: F = 9.13; df = 1, 108; P < 0.05). Rattle calls were used less often when individuals of the same sex were within 10 meters than during other contexts (ANOVA Post-hoc Bonferroni: F = 22.5; df = 5, 108; P < 0.01). However, males and females used rattle calls more often when floaters of the same sex were within 10 meters than when neighbors were close to the focal individual. Females used rattle calls more often than males when a neighbor either called from a distance greater than 50 meters or when a same sex neighbor was within 10 meters of the focal female (ANOVA Post-hoc Bonferroni: F = 9.08; df = 1, 108; P < 0.05). Drums were primarily used spontaneously and when a mate or future mate was within 10 meters (ANOVA Post-hoc Bonferroni: F = 12.01; df = 5, 108; P < 0.01). Drums were also used in response to a neighbor greater than 20 meters away and out of visual range of the focal individual. Males used drums spontaneously more often than females (ANOVA Post-hoc Bonferroni: F = 3.44; df = 1, 108; P < 0.05). Females used drums more often when a floater of the same sex or a neighbor of the opposite sex was within 10 meters. Both used drums when a mate or future mate was within 10 meters. In addition,
males and females used drums at similar rates in response to an unseen neighbor but did not use drums when a same sex neighbor was within 10 meters.

SEASONAL SIGNAL USE SUMMARY

Males and females used each signal at similar seasonal rates. The pik call was used by both males and females at a consistent rate throughout the breeding season, and unmated individuals used the pik call less often than mated individuals. Rattle calls were used at lower rates by unmated individuals. Individuals used rattle calls at higher rates during pre-nesting and cavity excavation than other breeding stages. Rattle call rates then decreased during incubation and nestling. After the nestling stage rattle calls were used at slightly increased rates during post-fledging.

Males and females had similar patterns of seasonal rattle call rates. Females used rattle calls at slightly higher rates than males during the breeding season, except for the post-fledging stage. Males and females had similar seasonal drum rates, but differed in which breeding stages rates were decreased or increased. Females used drums at the highest rate during the pre-mate selection stage. Females decreased their use of drums during the pre-nesting and cavity excavation stages and rarely used drums during the incubation or nestling stage. Females then slightly increased their drum rates during the post-fledging stage. Males had a seasonal drum use pattern opposite to that of females. Males used drums at very low rates during the pre-mate selection stage and not at all during the pre-nesting stage. Males then significantly increased their drum rates during cavity excavation and incubation stages. Like females, males greatly reduced their use of
drums during the nestling stage and then began using drums at a moderate rate during the post-fledging stage.

DISCUSSION

TERRITORIES AND BREEDING STATUS

Lawrence (1967) suggested that males and females foraged together during the winter because they maintained a joint territory. If males and females defend a joint territory year round, I expected to observe males and females that foraged together to also actively defend the same restricted area against other conspecific intruders. This prediction was not supported either by observations of Matthysen (et al. 1993) or those of this study. Although most pairs observed foraging together that were later mates during the breeding season, 38% of the nesting attempts (both successful and unsuccessful) were with non-neighbors. This pattern of mate choice is consistent with the prediction that downy woodpeckers occupy an area during the winter and then disperse to a separate area during the breeding season. Although this pattern involved a minority of the nesting pairs, it provides evidence that not all individuals maintained a joint territory with a mate prior to choosing a cavity site.

In Kraus woods, males and females defended separate areas prior to choosing a cavity site. The spatial distributions where rattle calls and drums were produced by males and females did not overlap prior the excavation of a cavity. Despite the fact that 29% of the nest cavities were located between a male and female’s territory, there were no observations of joint defense prior to selecting the site. It is unclear which one of the pair
might have defended the area between the two territories. Therefore, there is not enough evidence to conclude joint territorial defense prior to choosing a cavity site. Instead, results of this study indicated that males and females maintained a joint territory only after a nest site was selected.

I observed downy woodpecker males and females within Kraus woods foraging within close proximity to one another during the winter, which was similar to the social structure described by MatthySEN (et. al., 1993). There were more downy woodpeckers within Kraus woods during the winter months than during the breeding season. Although some individuals dispersed from the area after the breeding season, there was an influx of new individuals during the autumn. If downy woodpeckers had maintained territories in the winter I expected to observe aggressive encounters or a reduction in territory size, given an increased density of conspecifics. Contrary to this expectation, I did not observe any territorial displays or aggression until late February for the 1999 and 2000 seasons. During the 1998 season there were occasional female-female aggressive encounters during late January to early February, but these were only during two monitoring visits. Therefore, the onset of territorial behaviors was on consistent but did not occur early in the winter, during December. The individuals observed within Kraus woods only during the winter months were transients and did not forage in any particular area of the study plot for more than two weeks.

Individual downy woodpeckers occupied restricted areas during the winter (from November to February) but did not aggressively exclude occasional floaters and neighbors from foraging areas. Since I did not monitor which cavities each individual used, I can not exclude the possibility that downy woodpeckers defended overnight
cavities, as described by Kilham (1962). Downy woodpeckers did not express overt territorial behaviors during the winter until late February and occasionally several weeks earlier. These observations agreed with a previous study of downy woodpeckers in Ohio (Matthysen et al. 1993). However, despite the lack of observable territorial exclusion during part of the winter, 66% of the females and 36% of males occupied the same restricted area within Kraus woods through multiple years.

How individuals were able to maintain dominance within an area was not part of this investigation. However, there are aspects of downy woodpecker behavior that might account for the lack of overt territorial defense during portions of the winter. Conspecifics of the opposite sex may be tolerated when trespassing because they do not pose the same degree of competition for resources as a same-sex individual. Males and females while foraging together have been noted to partition the available food resources (Ligon 1968). Yet, the partitioning of foraging substrates is not equal; males use supplanting attacks to exclude females from preferred foraging substrates (Peters and Grubb 1983). Females should avoid mixed-sex foraging to minimize being excluded from preferred foraging substrates (Kilham 1962). Counter to this prediction females tolerate mixed-sex foraging situations during latter part of the winter (Lawrence 1967, Travis 1977). One possible reason females allow trespassing by an opposite-sex conspecific during late winter might be to facilitate the selection of a mate for the subsequent breeding season. The downy woodpeckers in Kraus woods often selected as mates individuals that occupied an adjacent territory during the winter months; 61% of the
males and 55% of the females mated with a neighboring individual. Given 75% of the
successful nests belonged to pairs that had been previous neighbors, this preference for a
neighbor resulted in greater nesting success.

Preference for neighbors as mates might explain the tolerance of an opposite-sex
conspecific, but not the lack of aggression towards a trespassing same-sex conspecific. 
During the winter, there were more same-sex conspecifics foraging within the Kraus
woods study area than during the successive breeding season. Downy woodpeckers have
other alternative behaviors for establishing dominance that do not require the use of
territorial vocalizations or ritualized visual displays. An individual might exclude same-
sex trespassers in the same manner as they exclude opposite-sex conspecifics. For
instance, males maintain foraging dominance over females by supplanting attacks only
after the female has strayed onto a male preferred foraging substrate (Ligon 1968).
Therefore physical attacks would not be observed unless a trespasser foraged on the
preferred substrate of the dominant individual.

Alternatively, downy woodpeckers might not exhibit overt territorial behavior
because dominance within an area was established the previous autumn. Downy
woodpeckers have been observed to have aggressive encounters between dominant and
subordinate individuals during the fall (Selander 1966). Individuals that had maintained
a territory within Kraus woods during the breeding season seemed dominant to those that
had just arrived for the winter. The dominant status of the resident bird was apparent
when a transient individual would delay approaching a feeder if there was a dominant
individual also approaching the feeder. A transient individual would also leave a feeding
station when approached by an individual that occupied the territory during the previous
breeding season. Given the limitations of my observations, further studies of downy woodpecker social dynamics would be necessary to test whether downy woodpeckers use an alternate method of territorial maintenance during the winter. Although it is possible downy woodpeckers might maintain a territory during the winter without overt aggressive behavior, it is not clear if the maintenance of a winter territory is necessary for an individual to effectively establish a breeding territory the following spring.

**SIGNAL CONTEXT AND FUNCTION**

The functions of signals in downy woodpeckers are difficult to compare with those for most passerine species because patterns of territory establishment and defense differ greatly between these groups. Fifty percent of the nest cavities in Kraus woods were located within an area the female defended prior to the selection of a mate. For these nests males had to move to the territory of a female, which is generally not the case for passerine species for which the function of song has been tested. In fact, only 21% of the nest cavities within Kraus woods were within areas the male had defended prior to selecting a mate. This strongly contrasted with the passerine pattern in which males attract females by defending an area with suitable habitat for a nest site (Baker 2001). In order for comparisons to be made between downy woodpecker and temperate passerine species, the confounding variable of male location must be taken into account. When male breeding status is examined independently from male location the similarities in patterns of signal use between the two taxa can shed light on the function of all three downy woodpecker signals.
RATTLE CALL

As did Kilham (1962) and Winkler and Short (1978), I observed males and females using rattle calls prior to the onset of the breeding season. Pre-mate selection was characterized by individuals foraging with conspecifics, but not maintaining a recurrent foraging association with one bird of the opposite sex. The downy woodpeckers in Kraus woods did not exhibit associated reproductive activities, such as aggressive displays and extended foraging associations with opposite-sex conspecific individuals, until late February and continued through early March. This time interval corresponded with the pre-nesting stage of the breeding season. Individuals had their highest rates of rattle calls during the pre-nesting and cavity excavation stages.

The seasonal pattern of the use of rattle calls by male and female downy woodpeckers in this study was comparable to the use of song by white-throated sparrows (Zonotrichia albicollis, Falls 1987). Both species used an acoustic signal at high rates during the onset of the breeding season, when territories are being established. An additional similarity between the two species was that both signals were then used consistently at lower levels until the end of the breeding season. Experiments using speakers to replace territorial males provided evidence that white-throated sparrows use song to repel rival males which resulted in the maintenance of territory boundaries (Falls 1987). The similarity in seasonal patterns of signal use between the signals used by downy woodpeckers and white-throated sparrows is preliminary evidence that woodpecker rattle calls may serve at a minimum, in the establishment and maintenance of a territory.

The use of rattle calls and the use of song are not entirely similar between the two species, however. Both male and female downy woodpeckers use rattle calls, but only

Although the seasonal patterns of singing vary among species, song is most common in periods of high female-female competition, typically within a territorial context (Levin 1996, Henry and Hausberger 2001, Elekonich 2000). Female downy woodpeckers use the same bill wave displays during female-female aggressive encounters that males use during male-male encounters (Kilham 1962, Winker and Short 1978). These female-female aggressive encounters occur more often during the pre-mate selection and pre-nesting stages (Kilham 1962, Lawrence 1967). Additionally, females in Kraus woods used rattle calls at rates similar to males during the pre-mate selection stage and at higher rates during the pre-nesting stage.

Downy woodpeckers rattle calls were used in a variety of social contexts. Both males and females used rattle calls less often when a same-sex conspecific was within ten meters than when at greater than 50 meters. The low rates for the contexts when individuals were within 10 meters of a conspecific were likely due to the use of aggressive displays and other vocalizations at distances less than ten meters. Downy woodpeckers fight with same sex-conspecifics by using a ritualized bill wave display and low amplitude chirr calls (Winker and Short 1978, Lawrence 1967). Rattle calls were given before and after encounters between same-sex conspecifics, but chirr calls were used when the individuals were in close proximity.

Rattle calls were not only used during intra-sexual contexts; males and females also gave rattle calls spontaneously and when opposite-sex neighbors or mates were within ten meters. The use of rattle calls in close proximity to a mate does not necessarily
mean these calls were used for inter-sexual communication. Levin (1996) found that when female bay wrens (*Thryothorus nigricapillus*) engaged in duets with mates, they were using song in the context of intra-sexual aggression. Downy woodpeckers might also use rattle calls in an intra-sexual context and the presence of the mate was incidental to the use of the call. Further experiments testing how males and females respond to rattle calls would be required to conclude whether rattle calls are used differently for intra-sexual and inter-sexual communication.

There are no previous studies that suggest males and females maintain territorial borders against an opposite-sex neighbor by the use of rattle calls. I did not observe any males or females engaging in territorial displays with an opposite-sex neighbor. Instead, encounters with between opposite-sex neighbors were characterized by three types of responses; individuals moved away from one another, foraged within a ten meter area without any visible aggressive behaviors, or one individual displaced the other from a substrate by using a supplanting attack. Although supplanting attacks were usually a male displacing a female (Kilham 1962, Ligon 1968, Peters and Grubb 1983), there were occasions when females displaced males. Since rattle calls were used while opposite-sex conspecifics were close by, they were likely used for inter-sexual communication. However, this study does not provide evidence sufficient to determine whether individuals respond similarly to rattle calls of opposite- and same-sex neighbors.

Since rattle calls were used at high rates at the onset of the breeding season they might have also served to attract a mate and then be used at lower levels to maintain a territory for the remainder of the breeding season. Experiments with great tits *Parus major* (Krebs et. al. 1981) provided evidence of song function based on comparing the rates of
song use by individuals with and without mates. Great tits were observed to significantly increase their use of song after their mate was removed from the territory. So, if mate attraction were an additional function of rattle calls, then they would be expected to be used at higher rates by unmated individuals than individuals with a mate. Although unmated male and female downy woodpeckers had lower rattle call rates than mated males and females, they maintained a territory until early April. Therefore, the lower rattle call rate by unmated male and female downy woodpeckers is not consistent with the prediction of a mate attraction function.

PIK CALLS

In downy woodpeckers, pik calls were used differently by each sex. The use of pik calls by both males and females did not display a seasonal pattern that would be expected for signals that are used in territorial defense. In females, the highest rate of pik call use was during the nesting stage. This high call rate during the nesting stage was usually during interactions with other species of cavity nesting birds that were close to the nest cavity. Female downy woodpeckers also used pik calls at higher rates during the pre-mate selection and pre-nesting stages. Female use of pik calls at high rates during the pre-breeding season would be consistent with a mate attraction function. However, contrary to predictions for a mate attractant signal, unmated females did not use pik calls at higher rates than mated females. Male downy woodpeckers used pik calls at a constant rate throughout the breeding season; males only reduced their use of pik calls during the
post-fledging stage when they were feeding chicks that were outside the nest cavity. Therefore, the seasonal use of pik calls by males was not consistent with expected patterns for either a territorial or mate attraction signal.

Winker and Short (1978) proposed that pik calls serve an alarm function during situations of disturbance, such as the presence of a predator. Support for this hypothesis was evident from observations of females using pik calls at high rates during the nestling stage and using pik calls less often when within ten meters of a mate. If another species of bird or terrestrial predator approached the nest, females used pik calls at high rates which resulted in the male approaching the cavity site and aiding in defense of the nest (unpubl. data). Pik calls were also given when same-sex floaters or opposite-sex neighbors were within ten meters when the focal individual was foraging outside its territorial area. Pik calls were usually used during these interactions during changes in location and did not result in aggressive interactions between birds. Therefore, the use of pik calls was consistent with the proposed function of individuals using these calls to signal a change in their location (Lawrence 1967, Winker and Short 1982). Thus, the social contexts in which pik calls were used by individuals were consistent with the functions proposed by previous studies.

DRUMS

The use of drums by male downy woodpeckers was not similar to the use of song by the majority of passerine species. Male passerines, whether they use their song for mate attraction or territorial establishment, begin singing prior to acquiring a mate. For example, sedge warblers (Aerocephalus schoenobaenus) and reed warblers (A. scirpaceus) both
sing prior to obtaining a mate. The difference between the two species in their song function is that sedge warblers stop singing after acquiring a mate, while reed warblers continue to sing after acquiring a mate (Catchpole 1973). Therefore, the difference between a song functioning as a mate attraction signal and a territorial signal is the timing of the cessation of use not in the beginning of use. Of the male downy woodpeckers I studied, 61% did not begin drumming until after selecting a mate and locating a nest site.

The pattern of drum use by male downy woodpeckers was similar to the mid-breeding season use of song by mockingbirds (Mimus polyglottos, Logan 1983) and yellowhammers (Emberiza citrinella, Møller 1988); both passerine species increased their song rates during the nest building and incubation stages, when the female was most fertile. Downy woodpeckers in Kraus woods began laying eggs after the cavity was excavated during late April and early May. This period of female fertility corresponded to the male’s peak drumming rate. Although this study did not investigate whether male downy woodpecker drums serve the mate guarding function of yellowhammer song or the female reproductive stimulation function of mockingbird song, male downy woodpeckers used drums during a reproductively fertile stage for females.

Unmated males had a different seasonal pattern of drum use than did mated males. Unmated males began using drums at low rates during the pre-nesting stage and increased to a higher drum rate than mated males during the incubation stage. This increased use of drums by unmated males was consistent with the prediction that drums serve as a mate attraction signal, although it is unclear why these males waited until the incubation stage. Given that drums are used within the territory, it is not possible to
discount the use of drums in the maintenance of a territory. However, males did not use drums during any intra-sexual contexts, which would be expected if drums served a territorial function.

In contrast to males, female downy woodpeckers used drums at high rates prior to the onset of the breeding season. This pre-breeding seasonal use by female downy woodpeckers is similar to the use of song by some female passerine species that use song during the pre-breeding season in the context of intra-sexual aggression (Baptista et al. 1993, Elekonich 2000, Henry and Hausberger 2001). However, female downy woodpeckers used drums in inter-sexual contexts, when mates or opposite-sex neighbors were within ten meters. The number of drum bouts when a same sex-floater was within ten meters was significantly less than the number of drum bouts during any of the inter-sexual contexts. Furthermore, unmated female downy woodpeckers drummed at higher rates than mated females. The unmated females continued to drum during the incubation phase when mated female downy woodpeckers had ceased using drums. Female downy woodpeckers began using drums before selecting a mate and prior to observations of aggressive interactions between females. Although this evidence is consistent with the prediction that female drums serve a mate attraction function, females that acquired mates during the pre-mate selection stage continued to use drums during the pre-nesting and cavity excavation stages. Therefore, female drums may serve a territorial function as well.

The Picoides rattle call has been attributed a similar function as the drum (Lawrence 1967, Winker and Short 1978). Although both signals were used during the breeding season, the downy woodpeckers I studied had differing patterns of signal use for
rattle calls and drums between breeding stages. The difference in the patterns of their use indicated these two signals had different functions. The drums of males were not used to deter rival males when initially establishing a territory, since males did not begin using drums until after a cavity site was selected. In addition, males that remained within the same territory through the following winter did not continue using drums after the nesting stage.

Although the males I studied in Ohio did not use drums to maintain a territory prior to selecting a mate, previous studies have reported male downy woodpeckers using drums during the pre-nesting stage (Lawrence 1967, Kilham 1962, Winker and Short 1978). In light of these observations I do not reject the hypothesis that male downy woodpecker drums might use drums for territorial defense. It is unclear how drums might serve a territorial function, given they are not used consistently throughout the breeding season. The use of drums by downy woodpeckers most resembles that of the fee-bee song of black-capped chickadees (Poecile atricapilla). The fee-bee song has been postulated to function as a means of locating a rival, and attracting that rival to a site for exchange of ritualized displays, rather than as a means of repelling an individual from a fixed boundary (Dixon and Stefanski 1970). Further investigation is required to test whether an overall function of attracting individuals, rather than repelling males and attracting females, can be attributed to drums.
Figure 2.1. Breeding stages of non-migratory downy woodpeckers based on data from Lawrence, 1967. The period when males and females occupy the same territory was based upon when nest sites were selected to when nestlings fledged.
Figure 2.2. Locations and temporal use of rattle calls and drums by male and female downy woodpeckers within Kraus Wilderness Preserve during the 1998 breeding season. February and March were during the pre-mate selection and pre-nesting stages, April and May were during the cavity excavation, incubation, and nesting stages, and June and July were during the later part of the nestling stage and the post-fledging stage. The number of rattle calls and drums represented by either an x or circled x varied for each individual. The x and circled x represent the outer boundary limit where an individual used either a rattle call or drum. The sample sizes for each individual included all rattles and drum bouts used to map the outer boundaries for all of the breeding stages are in Table 2.1. If there are no markers for a call or drum (either an x or encircled x) representing a two month interval, then there were no rattle calls or drums heard within the territory during those months excluded.
Figure 2.3. Locations and temporal use of rattle calls and drums by male and female downy woodpeckers within Kraus Wilderness Preserve during the 1999 breeding season. February and March were during the pre-mate selection and pre-nesting stages, April and May were during the cavity excavation, incubation, and nesting stages, and June and July were during the later part of the nesting stage and the post-fledging stage. The number of rattle calls and drums used among individuals are in Table 2.1 and are represented by either an x or circled x. The x and encircled x represent the outer boundary limit where an individual used either a rattle call or drum.
Figure 2.4. Locations and seasonal use of rattle calls and drums by male and female downy woodpeckers within Kraus Wilderness Preserve during the 2000 breeding season. February and March were during the pre-mate selection and pre-nesting stages, April and May were during the cavity excavation, incubation, and nesting stages, and June and July were during the later part of the nestling stage and the post-fledging stage. The number of rattle calls and drums for each individual are in Table 2.2. The x and circled x represent the outer boundary limit where an individual used either a rattle call or drum.
Figure 2.5. Downy woodpeckers rattle call rates during the breeding season (means ± S.E.). A. Unmated and mated female rattle call rates during three of the breeding stages, N=5 and N=9. B. Unmated and mated males rattle call rates during three stages of the breeding season, N=5, and N=9. C. The rattle call rates for males and females that had successful nesting attempts and remained within the study plot during all six breeding stages, N=9, N=9. These are the same nine males and females represented as mated in graphs A and B.
Figure 2.6. Downy woodpeckers pik call rates during the breeding season (means ± S.E.). A. Unmated and mated female pik call rates during three of the breeding stages, N=5 and N=9. B. Unmated and mated males pik call rates during three stages of the breeding season, N=5, and N=9. C. The pik call rates for males and females that had successful nesting attempts and remained within the study plot during all six breeding stages, N=9, N=9. These are the same nine males and females represented as mated in graphs A and B.
Figure 2.7. Downy woodpeckers drumming rates during the breeding season (means ± S.E.). A). Unmated and mated female drum rates during three breeding stages, N=5 and N=9. B). Unmated and mated males drum rates during three breeding stages, N=5, and N=9. C). The drum rates for males and females that had successful nesting attempts and remained within the study plot during all six breeding stages, N=9, N=9. These are the same males and females represented as mated in graphs A and B.
Figure 2.8. The number of times per individual (Means ± S.E.) and the context of when long distance signals were used by male and female downy woodpeckers. A square root transformation was used to normalize the data. Eight males and eight females were monitored for a total of ten observation periods during the 1998 and 1999 breeding seasons.

- $P < 0.05$, crosses denote statistically significant differences from the social contexts without the cross.
- $P < 0.05$, diamonds denote statistically significant differences between males and females for a social context.
<table>
<thead>
<tr>
<th>Year</th>
<th>Individual</th>
<th>Sex</th>
<th>First Date</th>
<th>Last Date</th>
<th>Rattle calls</th>
<th>Drums</th>
<th>Nesting Attempt</th>
</tr>
</thead>
<tbody>
<tr>
<td>1998</td>
<td>GMY</td>
<td>female</td>
<td>07/25/98</td>
<td>continued</td>
<td>4</td>
<td>5</td>
<td>none</td>
</tr>
<tr>
<td></td>
<td>YG</td>
<td>female</td>
<td>01/28/98</td>
<td>continued</td>
<td>12</td>
<td>8</td>
<td>successful</td>
</tr>
<tr>
<td></td>
<td>GG</td>
<td>female</td>
<td>01/29/98</td>
<td>continued</td>
<td>2</td>
<td></td>
<td>unsuccessful</td>
</tr>
<tr>
<td></td>
<td>YGO</td>
<td>male</td>
<td>02/25/98</td>
<td>06/12/98</td>
<td></td>
<td>5</td>
<td>successful</td>
</tr>
<tr>
<td></td>
<td>YGG</td>
<td>male</td>
<td>03/11/98</td>
<td>06/09/98</td>
<td>13</td>
<td>6</td>
<td>successful</td>
</tr>
<tr>
<td></td>
<td>YGY</td>
<td>female</td>
<td>02/25/98</td>
<td>continued</td>
<td>8</td>
<td>5</td>
<td>successful</td>
</tr>
<tr>
<td></td>
<td>MM</td>
<td>male</td>
<td>02/19/98</td>
<td>continued</td>
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<td>4</td>
<td>successful</td>
</tr>
<tr>
<td></td>
<td>GY</td>
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<td>01/20/98</td>
<td>03/28/98</td>
<td></td>
<td>7</td>
<td>unsuccessful</td>
</tr>
<tr>
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<td>female</td>
<td>01/29/98</td>
<td>continued</td>
<td>10</td>
<td>9</td>
<td>off study plot</td>
</tr>
<tr>
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<td>YO</td>
<td>male</td>
<td>02/07/98</td>
<td>03/23/98</td>
<td></td>
<td>2</td>
<td>unsuccessful</td>
</tr>
<tr>
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<td>BBG</td>
<td>male</td>
<td>04/18/98</td>
<td>continued</td>
<td></td>
<td>7</td>
<td>unsuccessful</td>
</tr>
<tr>
<td></td>
<td>OM</td>
<td>female</td>
<td>02/08/98</td>
<td>continued</td>
<td>14</td>
<td>4</td>
<td>successful</td>
</tr>
<tr>
<td>1999</td>
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<td>02/27/99</td>
<td>continued</td>
<td>5</td>
<td>6</td>
<td>none</td>
</tr>
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<td></td>
<td>YG</td>
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<td>01/20/98</td>
<td>continued</td>
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<td>3</td>
<td>successful</td>
</tr>
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<td>05/23/99</td>
<td>continued</td>
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<td>unsuccessful</td>
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<tr>
<td></td>
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<td>06/07/99</td>
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<td>7</td>
<td>successful</td>
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<td></td>
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<td>07/03/99</td>
<td>continued</td>
<td>13</td>
<td>4</td>
<td>successful</td>
</tr>
<tr>
<td></td>
<td>YO</td>
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<td>04/02/99</td>
<td>continued</td>
<td>4</td>
<td>2</td>
<td>off study plot</td>
</tr>
<tr>
<td></td>
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<td>male</td>
<td>06/11/99</td>
<td>continued</td>
<td>8</td>
<td>9</td>
<td>successful</td>
</tr>
<tr>
<td></td>
<td>OM</td>
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<td>06/11/99</td>
<td>continued</td>
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<td>3</td>
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</tr>
<tr>
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<td>06/05/99</td>
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<td>3</td>
<td>successful</td>
</tr>
<tr>
<td></td>
<td>BR</td>
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<td>07/05/99</td>
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<tr>
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<td>03/02/99</td>
<td>continued</td>
<td>0</td>
<td>5</td>
<td>unsuccessful</td>
</tr>
<tr>
<td></td>
<td>BG</td>
<td>female</td>
<td>01/12/99</td>
<td>06/03/99</td>
<td>8</td>
<td>7</td>
<td>unsuccessful</td>
</tr>
<tr>
<td></td>
<td>RRB</td>
<td>female</td>
<td>04/14/99</td>
<td>continued</td>
<td>14</td>
<td>6</td>
<td>successful</td>
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<td>UB&lt;sup&gt;a&lt;/sup&gt;</td>
<td>male</td>
<td>03/13/99</td>
<td>05/03/99</td>
<td>6</td>
<td>7</td>
<td>unsuccessful</td>
</tr>
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</table>

Table 2.1. Summary information about individual downy woodpeckers represented in the territory maps, Figures 2.2-2.3. The individual codes are based upon the band color combinations attached to the tarsometatarsus. The first date refers to when the individual was captured and banded or observed within the territory area. The last date refers to the date the bird was no longer observed within the study plot and did not return on any subsequent date. The continued category designates the individual was observed to remain within the territory area until the last date listed in a subsequent year. The rattle call and drum bout categories are the sample sizes of each signal used to estimate the outer boundaries in Figures 2.2 and 2.3.

<sup>a</sup> The individual was not captured or color banded.
<table>
<thead>
<tr>
<th>Year</th>
<th>Individual</th>
<th>Sex</th>
<th>First Date</th>
<th>Last Date</th>
<th>Rattle calls</th>
<th>Drums</th>
<th>Nesting Attempt</th>
</tr>
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<td>continued</td>
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<tr>
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<td>OP</td>
<td>male</td>
<td>02/27/00</td>
<td>continued</td>
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<td>5</td>
<td>successful</td>
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<tr>
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<td>9</td>
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<tr>
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<td>male</td>
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<td>05/28/00</td>
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<td>7</td>
<td>unsuccessful</td>
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<tr>
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<td>6</td>
<td>4</td>
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<tr>
<td></td>
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<td>5</td>
<td>successful</td>
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<td>unsuccessful</td>
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<tr>
<td></td>
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<td>continued</td>
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<td>6</td>
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<td>unsuccessful</td>
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<tr>
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<td>05/28/00</td>
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Table 2.2. Continued from Table 2.2, summary information of downy woodpecker territory map data, Figure 2.4. The first date refers to when the individual was captured and banded or observed within the territory area. The last date refers to the date the bird was no longer observed within the study plot and did not return on any subsequent date. The continued category designates the individual was observed to remain within the territory area until the last date listed in a subsequent year. The rattle call and drum bout categories are the sample sizes of each signal used to estimate the outer boundaries in Figure 2.4.
Table 2.3. Summary of male and female downy woodpecker nesting attempts in relation to territory defense and choice of mate within Kraus Wilderness Preserve for 1998-2000. A breeding attempt was categorized as successful if chicks survived through the nesting stage. A breeding attempt was categorized as unsuccessful if either the male or female were not observed to feed chicks or abandoned the areas prior to the nesting stage. Percentages were based upon the total observed individuals, 18 males and 20 females. The not all category counts represent different birds since some individuals occupied the same territory in subsequent years.

<table>
<thead>
<tr>
<th></th>
<th>Year</th>
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<th>1999</th>
<th>2000</th>
<th>% total of same sex</th>
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<td></td>
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<td>Total observed</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
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<tr>
<td>with neighbor mate</td>
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<td></td>
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<td>50</td>
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<tr>
<td>with non-neighbor mate</td>
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<td>same territory second year</td>
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<td>6</td>
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<tr>
<td>same mate from the previous year</td>
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<td></td>
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<td></td>
</tr>
<tr>
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<td>5</td>
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<td>within a pre-nesting territory</td>
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<td>7</td>
<td>4</td>
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<tr>
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<td>5</td>
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<td>6</td>
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<td>13</td>
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Kraus Wilderness Preserve
<table>
<thead>
<tr>
<th>Number of breeding stages</th>
<th>Three&lt;sup&gt;a&lt;/sup&gt;</th>
<th></th>
<th></th>
<th>Six&lt;sup&gt;b&lt;/sup&gt;</th>
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<tbody>
<tr>
<td>Signal Used</td>
<td>Rattle Call</td>
<td>Pik Call</td>
<td>Drum</td>
<td>Rattle Call</td>
<td>Pik Call</td>
<td>Drum</td>
</tr>
<tr>
<td>Mated</td>
<td>All</td>
<td>1.28 ± 0.08</td>
<td>3.89 ± 0.23</td>
<td>3.27 ± 0.48</td>
<td>1.04 ± 0.08</td>
<td>3.92 ± 0.10</td>
</tr>
<tr>
<td></td>
<td>Males</td>
<td>1.14 ± 0.12</td>
<td>7.72 ± 0.32</td>
<td>4.53 ± 0.68</td>
<td>0.50 ± 0.16</td>
<td>3.50 ± 0.26</td>
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<td>Females</td>
<td>1.43 ± 0.12</td>
<td>4.07 ± 0.32</td>
<td>2.01 ± 0.68</td>
<td>0.81 ± 0.14</td>
<td>4.30 ± 0.26</td>
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<tr>
<td>Unmated</td>
<td>All</td>
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<td>0.61 ± 0.31</td>
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<td>Males</td>
<td>0.19 ± 0.16</td>
<td>0.78 ± 0.43</td>
<td>4.55 ± 0.91</td>
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<tr>
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<td>Females</td>
<td>0.19 ± 0.16</td>
<td>0.44 ± 0.43</td>
<td>5.48 ± 0.91</td>
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Table 2.4. **Mean ± S.E. (signals / hour) breeding season signal use for mated N= 18 and unmated downy woodpeckers N=10.**

<sup>a</sup> mean for breeding stages mate-selection, cavity excavation, and incubation.

<sup>b</sup> mean for breeding stages pre-mate selection, mate-selection, cavity excavation, incubation, nesting, and post-fledging.
<table>
<thead>
<tr>
<th>Sex of focal Individual</th>
<th>Context</th>
<th>No. of Pli calls</th>
<th>No. of Rattle calls</th>
<th>No. of Drum bouts</th>
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<td>female</td>
<td>spontaneous</td>
<td>15</td>
<td>46</td>
<td>23</td>
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<td></td>
<td>neighbor unknown sex &gt; 50 m</td>
<td>4</td>
<td>100</td>
<td>24</td>
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<tr>
<td></td>
<td>neighbor same sex &lt; 10m</td>
<td>36</td>
<td>33</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>floater same sex conspecific &lt; 10m</td>
<td>0</td>
<td>56</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>neighbor opposite sex &lt; 10m</td>
<td>60</td>
<td>40</td>
<td>15</td>
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<td>30</td>
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<td>male</td>
<td>spontaneous</td>
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<tr>
<td></td>
<td>response &gt; 20 m</td>
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</tr>
<tr>
<td></td>
<td>neighbor &lt; 10m</td>
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<td>51</td>
<td>0</td>
</tr>
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<td></td>
<td>floater &lt; 10m</td>
<td>0</td>
<td>8</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>non-mate opposite sex</td>
<td>25</td>
<td>0</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td>mate or future mate &lt; 10m</td>
<td>174</td>
<td>138</td>
<td>132</td>
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</table>

Table 2.5. Female and Male downy woodpecker calls and drum bouts during different contexts N=8, N=8. The individuals were monitored during the 1998 and 1999 breeding seasons. The means for each context are summarized in Figure 2.8.
CHAPTER 3

OBSERVATIONS OF “HELPER” FEMALES AT DOWNY WOOPECKER NESTS

A nest helper is a reproductively mature individual that does not engage in its own reproductive effort and instead assists others in the care of young. Cooperative breeding occurs within avian social systems when this alloparental behavior is adaptive for helpers (Ligon and Stacey 1991, Brown 1978, Emlen and Vehrencamp 1983). This reproductive strategy is uncommon among birds, occurring in only 220 of approximately 9000 species (Stacey and Koenig 1990). However, there is no expected delineation along a continuum, from rare to normal occurrence, of helpers within a population that predicts when cooperative breeding will persist as a favorable reproductive strategy (Stacey and Koenig 1990). Presumably, the conditions favoring such behavior should be similar whether helpers are common or rare within a population.

Helping behavior within avian social systems is not distinctive to cooperative breeding, and consequently it can occur under conditions that are not consistent with the predictions based on the dynamics of a cooperative system (Jamieson 1991). There are interspecific and intraspecific examples of individuals feeding other pairs’ nestlings or fledged chicks (Shy 1982, Gill and Krannitz 1997, Trombino 2000, Hoag 2000). These instances of helping are postulated to be misdirected responses to the stimulus of begging chicks (Jamieson and Craig 1987). Presumably, these individuals are misdirecting their
parental response of provisioning young in a non-adaptive effort, as the helpers do not benefit from this behavior. Although misdirected parental efforts would not be favored to persist within a population, the stimulus response of feeding nestlings is maintained as a consequence of the selection for parental care of altricial young (Jamieson 1989). Thus, helpers might be observed within a population even though the population is not subject to conditions favorable for the maintenance of cooperative breeding as a reproductive strategy.

Kin selection is one hypothetical mechanism for the selection of helpers within a cooperatively breeding system (Emlen and Wrege 1988). Theoretically, the helper receives the indirect benefit of inclusive fitness, given it assists relatives during the breeding season. Consequently, given the indirect fitness benefits, helpers are expected to favor aiding relatives over helping non-relatives. However, helpers can receive direct benefits to their own fitness by helping; therefore kin selection is a sufficient but not necessary component of a cooperative breeding system (Clutton-Brock 2002, Magrath and Whittingham 1997, Dunn et al. 1995).

The kin selection hypothesis only explains who helpers assist, not the conditions that would lead an individual to forgo its own reproductive effort. Gaining indirect fitness would not be beneficial if an individual could have gained direct fitness by successfully producing its own offspring. Emlen (1982) identified two ecological conditions under which helping others with their reproduction would impart direct benefits to the helper. First, if environmental conditions are unpredictable and harsh, then an inexperienced bird might not be able to reproduce and would benefit by delaying dispersal and aiding in the care of siblings. Similarly, if there is limited breeding habitat available and
competition is high, then an inexperienced individual would benefit by delaying
reproduction until a breeding territory is either available or inherited.

Identifying members within a group is an important factor which leads to the
formation of reciprocal cooperation and stability among social groups (Trivers 1971,
Wilson 1975). Vocalizations are a primary way in which birds communicate with other
individuals. Conspecifics are presumed to have the ability to recognize and decode the
pertinent information within these signals, and this system of signal recognition is critical
in establishing and maintaining social systems. Most helpers are philopatric young that
have remained in the parents’ territory and aid in raising siblings (Stacey and Koenig
1990). As an individual benefits more from helping related individuals, many
cooperatively breeding species exhibit specialized social recognition vocalizations (Price
1999). Furthermore, helpers often suppress their own species’ territorial signals and
behaviors that would threaten the dominance of the breeding pair. For example,
cooperatively breeding red-cockaded woodpeckers, *Picoides borealis*, have vocalizations
specialized for use between social group members and helpers do not use aggressive
territorial calls (Jackson 1994).

Downy woodpeckers have been documented to raise their young in monogamous
pairs (Kilham 1962, Lawrence 1967, Winker and Short 1978). Both male and female
contribute equally to parental care, with decreased nestling survival in the absence of a
mate (Kilham 1983). Woodpecker defense of the breeding territory against conspecifics is
strictly intrasexual (Short 1982). Territorial intruders are challenged and the fights
proceed from vocalizations to an exchange of ritualized wing spreads and bill wave
displays. Interspecific helpers have been observed for other picid species (Shy 1982), but
intraspecific helpers have not been reported to occur in downy woodpeckers. Thus my observation of a second female aiding a breeding pair at four out of thirteen nests during the 1998 through the 2001 breeding seasons was a novel occurrence in downy woodpeckers. As these nest helpers might have represented instances of misdirected parental care in response to a feeding stimulus (Jamieson and Craig 1987), I investigated whether these trios exhibited characteristics predicted to favor cooperative group formation. Furthermore, I used DNA fingerprint analysis to test whether the helper females were related to the pair they helped. By monitoring the use of long distance signals by territorial females to those of the female helpers I was able to compare whether the helper females exhibited a lack of aggressive behavior while assisting on other territories. The extent of assistance the helpers provided was documented by the amount of time spent with or at the nest cavity and the intervals between visits feeding the nestlings.

METHODS

STUDY AREA

This investigation was conducted at Kraus Wilderness Preserve, Delaware Co., OH (N 40° 11', W 83° 03') from November through July 1998-2001. Downy woodpeckers were mist netted and color banded to enable individual identification during November through March. This contiguous 30 ha preserve, owned by Ohio Wesleyan University, is dominated by beech (Fagus sp.), maple (Acer sp.), and oak (Quercus sp.) trees common to eastern deciduous forests.
SIGNAL USE RATES & NEST MONITORING

To investigate whether use of long distance signals differed between primary breeding females and those females that helped nesting pairs, a total of thirteen downy woodpecker territories were monitored. Each territory was monitored twice a week on a bi-weekly schedule for three hours (8:00-11:00 a.m. EST) from February through June, 1998-2000. The number of drums, rattle calls, and pik calls used by the female downy woodpecker within the observation area during each observation period were used to ascertain an average signal use per hour. The average signal use was then used to determine a mean rate of use for pik calls, rattle calls and drums during six stages of the breeding cycle: pre-mate selection, mate selection, nest excavation, incubation, nesting, and post-fledging of young.

I monitored the nests with helpers (N=4) and a subset of the total nests without helpers (N=5) during the cavity excavation, incubation and nesting stages. I calculated the average duration spent within the nest and the average interval between food deliveries to the nestlings for the primary male, primary female and helper female. I used an analysis of variance to test for differences between primary breeders with helpers and without helpers and whether female helpers differed from primary females.

I used a repeated measures multivariate analysis of variance to test for differences in mean signal use by males and females during the six breeding stages. Significant differences among means were compared using a Bonferroni correction for multiple comparisons. To satisfy the multivariate analysis of variance assumption of sphericity, the data were normalized using a square root transformation. A Greenhouse-Geisser
correction factor was used if sphericity could not be assumed. I identified differences among breeding stages using ANOVA with a Bonferroni correction factor for multiple comparisons.

Winkler and Short (1978) cataloged the vocalizations typically given by downy woodpeckers during the breeding season. I monitored the use of long distance signals and categorized each vocalization given during social interactions between helpers and primary breeders for three of the trios. Vocalizations were then digitized using signal analysis software (Engineering Design 2001) and the spectrograms were visually matched to spectrograms of previously described vocalization to signal categories (Winker and Short 1978). I compared the vocalizations exchanged between trios to ascertain if these individuals were using vocalizations different from other known downy woodpecker vocalizations.

DNA FINGERPRINTING

To examine whether the helpers were young from a previous year of the nesting pair, blood samples were taken from all adults involved with nests observed to have helpers. A nesting pair without a helper was also included for comparison. DNA fingerprints from twelve individuals were used to ascertain the relatedness between the breeding pair and the helper. I compared three groups with a helper and primary breeding pair forming a trio at the same nest. Although there was another group with a helper during the study, they were not included in the analysis because there were no blood samples from the female helper. The fourth group compared was among a
polygynous group of a male and two females with separate nest cavities. The polygynous females did not aid in feeding each others young and therefore neither was categorized as a “helper” for the comparison.

I used a Jeffreys’ multilocus minisatellite probe 33.15 (Jeffreys et al. 1985 a, b) to create a DNA fingerprint of each individual. DNA was extracted from 50 ml blood samples mixed with lysis buffer (Longmire et al. 1988). DNA samples (~ 5mg) were digested with 7.5x excess restriction enzyme Hae III at 37 °C for 4 hours. The DNA fragments were separated through a 0.8% agarose gel at 20V for ~65 hours, transferred to nylon by Southern blot in 10 x SSC buffer, and fixed by UV crosslinking. The nylon filter was hybridized at 65 °C by the addition of Jeffreys’ multilocus minisatellite probe 33.15. Filters were washed at 62 °C in 1.5 X SSC, 0.1% SDS, and exposed to x-ray film at -20 °C for several days. I estimated the band-sharing coefficient (x) for each individual on the same gel where \( x = \frac{2S}{(2S + A + B)} \). I tested for a correlation between higher band-sharing coefficients between primary breeders and helper females versus non-helper dyads using a Mantel test.

RESULTS

SIGNAL USE MONITORING

Helper females used pik calls, rattle calls and drums at lower rates than primary breeding females (MANOVA, Wilk’s \( \lambda_{3,9} = 78.3, \ P < 0.001 \), Figure 3.1). There were no significant differences for either the helper females or the primary breeding females in the rates of rattle calls and pik calls among breeding stages (MANOVA, Wilk’s \( \lambda_{3,5} = 1.5 \).
and 0.591, $P > 0.20$). There was a significant interaction between the breeding stages and breeding status of individuals in drum usage (MANOVA, Wilk’s $\lambda_{5,55} = 4.5$, $P = 0.002$). Primary breeding females differed from helpers in which breeding stage drums were used at increased rates. Primary breeding females used drums at significantly higher rates during the pre-mate selection stage than during any other stage (Figure 3.1B; ANOVA: Bonferroni correction $F_{1,66} = 4.5$, $P < 0.05$). The drumming rates during the pre-nesting, cavity excavation and post-fledging stages were similar and significantly higher than drum rates during the incubation and nesting stages (ANOVA: Bonferroni correction $F_{1,66} = 4.5$, $P < 0.05$).

Although two of the helper females used drums during the breeding season there was no significant difference between the rates of drums used between breeding stages (ANOVA: Bonferroni correction $df = 11, 66$, $P > 0.05$). One female that assisted a neighboring pair used drums during the pre-mate selection stage, but not within the border of either primary breeder. The female helper that used drums during incubation and nesting phases used them after the primary breeder’s nest failed. She also used drums and rattle calls within a restricted area outside the borders of the primary breeding pairs’ territory.

A number of vocal signals were given during social interactions between the helper female and both primary breeders. However, helper females did not use rattle calls during encounters with either the primary male or female. The mutter and chatter calls were used during close encounters while individuals were on the same tree or branch, between individuals. All vocalizations except one “mutter” call were
unaccompanied by visual displays (Table 3.1). The one display observed with “mutter”
calls from the primary breeders was given during a group (3 individuals) wing-spread
display.

NEST MONITORING

There was a significant effect of breeding status on the duration at or within the
nest cavity (ANOVA: $F_{4,246} = 37.1$, $P < 0.001$, Figure 3.2). Females with helpers,
females without helpers, and males without helpers spent more time at or within the nest
cavity incubating eggs than males with helpers or the female helpers. The males with
helpers also spent more time at or within the cavity than the helper females (ANOVA:
Bonferroni correction for pairwise comparisons $P < 0.05$). Helper females did not aid
with cavity excavation. Helper females had significantly shorter incubation durations,
and greater intervals between feedings, than both the primary males and females.

Breeding status had a significant effect on the intervals between feeding visits (ANOVA: $F_{1,93} = 39.5$, $P < 0.01$, Figure 3.2). Helper females had significantly longer intervals
between feeding visits than the primary breeding males and females. The males and
females with helpers had similar intervals of feeding visits as the males and females
without helpers (ANOVA: Bonferroni correction for pairwise comparisons $P < 0.05$).

DNA FINGERPRINTS

I used multilocus minisatellite DNA fingerprinting to test for relatedness between
individuals within groups. Genetic analysis of the cooperative breeding groups indicated
that the helper females and primary breeding males had a higher band sharing coefficient
than did helper females and primary breeding females (Figure 3.3). The average proportion of bands shared between females and helpers was 0.22, and the average proportion of bands shared between males and helpers was 0.41. The proportion of bands shared between mates, and between males and non-mated, non-helper females was 0.15. The proportions indicated that helpers were not first order relatives. There was a correlation between the degree of band-sharing and whether the dyad of comparison included a helper female (Mantel: $r = 0.45, P=0.003$). Helper females were more related to the pair they were assisting than they were to other pairs within Kraus Wilderness Preserve. There was a positive correlation between the proportion of bands shared and the degree of relatedness between the helper female and the primary breeding male (Mantel: $r = 0.78, P = 0.0002$). There was no correlation between the proportions of bands shared between the helper female and the primary female (Mantel: $r = 0.36, P = 0.137$). Thus, helper females were more closely related to the primary males than to the primary females they were assisting. The primary males and helper females at two of the nests had not been seen occupying the territories of the primary breeding female the previous year. There were two nests with female helpers the first year of the study, so it is unknown if those helpers or primary males were occupants of the territory the previous year.

DISCUSSION

Downy woodpeckers normally breed in socially monogamous pairs (Bent 1939, Winkler et al. 1995). To date, there have been no reports in the literature documenting helpers or cooperative breeding in this species. As this study did not investigate whether
the second female at the nest produced any young, I will refer to them as “helpers”, since there is a possibility that they did not produce any young. This investigation noted female “helpers” in 31% of active breeding cavities (N=13) over four years. “Helpers” at the cavity did not significantly influence the breeding biology of both males and females during the nesting and feeding chicks stage of the breeding cycle. There was a significant difference between primary breeders and female “helpers” in the duration spent at or within the cavity and the interval between feedings. However, there was no difference in the duration and interval between feedings for primary breeding females at nests with “helpers” versus nests without “helpers”. Males with “helpers” also did not differ from males without “helpers” for both duration and interval between feedings. However, there was a trend for both males and females to spend less time within the nest cavity and more time between feeding visits at nests with “helpers”.

Only female downy woodpeckers were observed helping apparently monogamous breeding pairs. This is an unusual sex bias, as most cooperative breeding species have male helpers (Emlen and Verencamp 1983). Genetic analysis indicated that helpers were not first order relatives of either primary breeder. Many vertebrate cooperative breeding systems arise when juveniles are retained on the natal territory and assist parents in successive breeding attempts (Brown 1987). The strategy observed in this investigation was rare, since there was no evidence of male philopatry. “Helper” females were not retained juveniles from the previous year because they were not related to the primary breeding female. During pre-breeding season monitoring the primary breeding females were the only occupants of territories, “helper” females only appeared later in the season. In all cases, the primary breeding male changed nest cavities between years.
while the female did not. The monitoring of dispersal movements was not included in this study, so it is possible that the “helper” female dispersed to the breeding territory with the primary breeding male.

Breeding attempts were observed between one female “helper” and a neighboring territorial male (not the primary breeding male), so it is unknown whether all the eggs in the shared nest were those of primary breeding female. However, there were no copulation attempts observed between “helpers” and the primary breeding male. It is possible that these helpers were reproductively active and adding additional eggs to the clutch (i.e. egg dumping). If this were the case these would have been occurrences of polygyny. The “helper” females may have been caring for their own young, while aiding the “primary” breeding female with her young. Although that would make this a form of “helping” behavior, it would not be misdirected parental care or cooperative breeding.

Females observed helping were present prior to and during incubation, minimizing the possibility of these cases being observations of misdirected parental care. However, this can not be entirely discounted, as there were indications that the helper females had failed in their own breeding attempts. One of the “helper” females had started a nest cavity with a male prior to helping the neighboring breeding pair. None of the “helpers” were observed to be successful primary breeders in subsequent breeding seasons. Results indicated that “helpers” did not have much of an effect on the primary breeder’s parental behaviors in regards to feeding of chicks. Still, the additional feeding may have had secondary benefits for the mated pair. “Helpers” may not have increased the feeding rates at nests, but may have reduced the workload of one or both of the primary breeders. This decreased workload on the primary breeders may secondarily
have increased the success of the breeding attempt in a number of ways, including increased vigilance or antipredator defense of the cavity (Rabenold 1984, Austad and Rabenold 1985). This study did not measure the number of fledglings per nest or the causes of nest failures, therefore I can not conclude whether “helpers” had an effect on the reproductive success of the pair they helped.

Finally, I monitored the signal use of all individuals at these nests, to ascertain whether the vocal and non-vocal signals differed significantly among group members. The signals used by primary breeding individuals during interactions with helper females were species typical and previously described by Winkler and Short (1978). However, the absence of visual displays, which normally accompany these vocalizations, indicated these vocal signals were not used in an aggressive context. Both primary breeders differed significantly in their signal use from “helpers”, especially in the use of rattle calls. This vocalization has been implicated as the primary signal for territorial establishment and defense (Short 1982), and was only observed being given by the primary breeders in the social groups studied here. Thus, female ““helpers”” were never observed acoustically challenging the primary breeding female for the territory over the course of this investigation.

Although “helpers” in this population were documented over three years, there is little evidence that this is a stable reproductive strategy within this population of downy woodpeckers. Little is known concerning dispersal within this species. Therefore, it remains unknown how the “helper” females dispersed to an area where they were close to
a related male, when neither was present within the study plot the previous year. In addition, there was no indication from the results of this investigation how the “helper” female might have identified the primary breeding male as kin. Finally, the conditions favoring helping within this population were not identified, leaving clear avenues for future research.
Figure 3.1. Mean rates ± S.E. of signals used by primary breeding females with and without helpers (N = 9) and mean rates of signals used ± S.E. by females who assisted other breeding pairs (N=4). A). Primary and helper female woodpecker rates of rattle call use during six breeding stages. B). Primary and helper female woodpecker rates of pik call use during six breeding stages. C). Primary and helper female woodpecker rates of drum use during six breeding stages. These are the same mated females represented in Figures 2.5, 2.6, and 2.7.
Figure 3.2. Mean ± S.E. of durations at the entrance or within the nest cavity and between food deliveries to the nestlings. There were four nests with helpers and five nests without helpers observed during the 1998 to the 2001 breeding season. The rates of food delivery were recorded only during the nesting stage. A female or male with helper was the primary breeding individual. A female or male without a helper was a neighboring breeding pair.
Figure 3.3. Results of multilocus minisatellite DNA fingerprinting. The groups compared were: F/F = females and other non-helper females, M/M = males and other breeding males, M/F = males and non-helper females, Mates = primary breeding male and female, F/H = females and helper females, and M/H = males and helper females.
Table 3.1. Vocalizations used by trios while a helper was within 20 meters, N= 3 trios.

<table>
<thead>
<tr>
<th>Individual</th>
<th>no. of interactions</th>
<th>pik</th>
<th>rattle</th>
<th>kweeks</th>
<th>mutter&lt;sup&gt;a&lt;/sup&gt;</th>
<th>chatter</th>
</tr>
</thead>
<tbody>
<tr>
<td>Primary breeding female</td>
<td>15</td>
<td>45</td>
<td>35</td>
<td>20</td>
<td>13</td>
<td>20</td>
</tr>
<tr>
<td>Primary breeding male</td>
<td>10</td>
<td>20</td>
<td>20</td>
<td>0</td>
<td>6</td>
<td>6</td>
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<tr>
<td>Helper female</td>
<td>25</td>
<td>45</td>
<td>0</td>
<td>6</td>
<td>13</td>
<td>20</td>
</tr>
</tbody>
</table>

<sup>a</sup> All vocalizations except one “mutter” call were unaccompanied by visual displays. The one display observed with “mutter” calls from the primary breeders was given during a group (3 individuals) wing-spread display.
CHAPTER 4
ACOUSTIC INDIVIDUAL RECOGNITION IN DOWNY WOODPECKERS

The characteristics of avian long distance acoustic signals are subject to a wide variety of selection pressures. Theoretically, there are selective pressures on birds to differentiate between neighbors and territorial intruders in order to minimize unnecessary repetitive aggressive encounters during the breeding season (Ydenberg et al. 1988). Individual recognition of territory neighbors by song for males has been well documented in the scientific literature (Falls 1982, Baker 2001). There have been few studies which have tested for recognition of female territory neighbors by females (Levin 1996, Cooney and Cockburn 1995). However, birds use song for both territorial defense and mate attraction (Catchpole and Slater 1995, Ratcliffe and Otter 1996). There are several examples of females identifying individual males by song (Wiley et al. 1991, Lampe and Slagsvold 1998, O’Loghlen and Beecher 1999). These studies indicate that although a female may not use song to identify female territory neighbors, they do use song to individual recognize males.

There are two general strategies birds can use to communicate information between individuals of the opposite- or same-sex over long distances: either the same signal can be used to communicate with either sexes, or one signal can be used for
interactions with same sex individuals, such as neighbors, and another a signal used for inter-sexual interactions, such as mates. It is not unexpected, given the variety of signals used by birds, that reproductive partners often recognize one another by signals which are not exchanged between territorial neighbors, and vice versa. For example, female American goldfinches recognize the flight calls of mates but this vocalization is not individually recognizable by neighboring males (Mundinger 1970).

As previously stated, song has been demonstrated to serve a territorial function. Yet birds have an acoustic repertoire that includes the use of other vocalizations, calls, within the territorial boundary. These calls may potentially serve a secondary territorial function (Kroodsma and Byers 1991). In non-song birds that defend territories in a manner similar to song birds, neighbors have been found to recognize each other by territorial calls (Prum 1998, Galeotti and Pavan 1993, Falls and McNicholl 1979, Rebbeck et al. 2001). These investigations indicated that the primary territorial call encoded individual identity pertinent to neighbors within the population. However, these studies did not test whether other calls in the repertoire encoded information about individual identity.

There are several characteristics of the communication signals used by woodpeckers, *Picoides* species, which offer opportunities to clarify aspects of recognition of individual identity by sound. Female downy woodpeckers (*Picoides pubescens*) maintain territories and use the same vocal and non-vocal signals as males (Lawrence 1967, Winkler and Short 1978). This offers the opportunity to investigate whether females recognize individual territorial neighbors acoustically. It is possible to test the recognition
ability of females separately from males because both sexes maintain separate territories until they pair for the breeding season.

There are three signals used by downy woodpeckers for long distance communication during the breeding season. These signals can be classified into two categories: rattle and pik calls are both vocal signals, whereas drums are a non-vocal mechanical acoustic signal. Rattle calls are a repeated series of variable call notes and have been suggested to play a role in territorial defense (Winkler and Short 1978). In contrast, pik calls are a single vocal element (rather than a series of elements), and have been noted to correlate with the motivational state of individuals while simultaneously functioning as a location call (Kilham 1962, Short 1982). Woodpecker drums are a rapid, repetitive series of strikes of the bird’s bill on a resonant surface that are not associated with foraging or cavity excavation. Drumming appears to play a role in territorial and reproductive behaviors (Miller and Bock 1972, Winkler and Short 1978). Since rattle calls, pik calls, and drums are used during the breeding season within a territory, each signal is theoretically subject to the selection pressure to encode individual identity. Therefore, it is possible to test if all long distance signals used during a breeding season communicate individual identity.

Previous research has shown that red-headed woodpeckers, *Melanerpes erythrocephalus*, encode cues to individual identity within their territorial calls (Crusoe 1980), and that acoustic variation within northern flicker, *Colaptes auratus*, territorial calls can be used to statistically identify individuals (Duncan 1990). Drums have been shown to encode species identity (Dodenhoff et al. 2001, Stark et al. 1998), but there are no
studies demonstrating whether woodpeckers identify individuals by their drums. If a non-vocal signal functions to maintain territory boundaries, neighbors should be able to recognize one another by this signal, as the advantages to individual recognition should be similar to those for vocal signals. However, if a signal serves primarily as a mate attractant, and only secondarily in territory defense, then it might not be favored to encode individual identity but still might encode of species information, or signaler quality.

I analyzed the behavioral responses to playbacks of three different long distance signals performed by neighbors and strangers. Given that downy woodpeckers are reported to use both rattle calls and drums for territoriality, analysis of behavioral responses allowed investigation of whether individual recognition cues were encoded in both types of territorial signals. In addition, analysis of behavioral responses to pik calls tested whether woodpeckers encode individual identity within other call non-territorial calls.

METHODS

STUDY AREA

This study was conducted within a 30 ha tract of eastern deciduous forest, Kraus Wilderness Preserve, Delaware Co., OH (N 40° 11’, W 83° 03’, 30 ha). Downy woodpeckers were mist netted and color banded from December through March, 1999-2001 for individual identification. Playback experiments with territory neighbors were
conducted during February 1999 and 2000, prior to the breeding seasons. The playback experiments with mated pairs were conducted in April during the 2000 and 2001 breeding seasons.

INDIVIDUAL RECOGNITION

I used neighbor-stranger (N:S) playback experiments to test whether 12 female and 8 male downy woodpeckers differed in their responses to territory neighbors versus non-familiar (stranger) individuals. Signals were recorded using a Sony TCD5 Pro II and Sennheiser ME 67-K6P microphone, and digitized using SIGNAL 3.1 (Engineering Design 1999). Field recorded signals were bandpass filtered, recorded onto cassette tapes, and repeated at set intervals for a total duration of 2 minutes: Rattle calls were repeated at rate of 3 per minute, pik calls at a rate of 6 per minute. Playback tapes of drums retained the inter-drum intervals of the individual bird recorded because the inter-drum interval has been hypothesized to encode individual information (Winker and Short 1978). Rattle calls were presented at a rate greater than the population average of 1.28 ± 0.08 per hour (Chapter 2) because this rate was too low to elicit responses during the seven minute playback trial. Although three rattle calls per minute was not a natural rate for this population, all focal birds were presented with the same rattle call rate during all playback trials. Signals of paired neighbor-stranger recordings were standardized to the same root mean square amplitude of the two signals. Neighbor-stranger signal pairs were also matched for sex differences; a male neighbor signal was played with a male stranger signal. This standardization of sex was also done for female recordings. This
does not mean that I matched the playback signal to the sex of the focal individual; if a female had a male neighbor then the playback signal was a recording of the male neighbor and a recording of a stranger male. Of the twenty dyads of neighbor-stranger playbacks, twelve were same-sex neighbors and eight were opposite-sex neighbors. No male-female pairs were used if they were mates later in the breeding season. Therefore, all male-female pairs included in the analyses involved non-mates.

Neighbors were defined as individuals that shared a territory border with the focal bird; strangers were classified as individuals that were separated from the focal bird by a minimum of 3 territories. Focal birds were presented with neighbor and stranger (N:S) stimuli in random order, in a balanced pairwise design. Each playback trial had a different pair of neighbor and stranger signals. I conducted three types of playback experiments; N:S rattle call, N:S pik call, N:S drum, where the speaker was placed within 5 meters along the territorial border shared between the focal bird and neighbor. A fourth playback experiment presented the N:S rattle call from the border opposite the shared border between neighboring individuals. There was an interval of at least 1 hour between the presentation of neighbor and stranger stimuli to minimize behavioral carry-over from the previous stimulus. The same focal individual was used for one experiment per day. Therefore, each focal individual required four days to complete all four experiments with a rattle call at the shared border and opposite border, a pik call, and a drum. These days were not consecutive but were completed before the individual selected a mate. All paired comparison trials with a neighbor and stranger stimulus were completed within 3 hours on the same day.
Playback trials consisted of three periods: a 5 minute pre-stimulus observation, a 2 minute stimulus presentation, and a 5 minute post-stimulus period. Playback experiments were conducted if the focal bird was not engaged in a social interaction with a conspecific, and was not observed drumming or calling during the five minute pre-stimulus period. Six variables were used to measure the behavioral response during the 2 minute stimulus and the 5 minute post-stimulus period: pik call rate, rattle call rate, drum rate, closest approach to the speaker, duration within five meters of the speaker, and latency to first response. I used a principal components analysis to reduce the six correlated variables to two independent component scores. I compared principal component scores with an eigenvalues greater than 1.0 in Wilcoxon signed rank comparisons (McGregor 1992). I used a Kruskal-Wallis test to detect differences between male and female responses. Mann-Whitney U tests were then used in a post-hoc analysis to detect which male and female responses were different. The responses to signals from opposite- and same-sex neighbor-strangers were compared using a Mann-Whitney U test.

MATE RECOGNITION

Mate recognition experiments were conducted with eight established pairs. The playback experiments were conducted while the male and female were excavating a nest cavity. Prior to the playback trials, the mate was either observed foraging outside the area for the playback experiment or removed (i.e., captured and restrained under permit) from the territory to avoid interfering with the focal individual. Three stimuli, the mate’s acoustic signal, a stranger’s acoustic signal, and a neighbor heterospecific (hairy
woodpecker, *P. villosus*) were played during a trial. An interval of one hour elapsed before another stimulus was played to the focal bird. I conducted three experiments that differed in the stimulus played, a rattle call, a pik call, or a drum. I conducted one experiment per day with each focal individual. Although each bird was not tested with a rattle call, pik call, and drum on consecutive days, no more than two days elapsed between experiments with the same focal bird. The mate that was restrained was not used for any trials the day it was restrained. Each focal bird required three days to complete experimental trials with all three stimuli, a rattle call, a pik call, and a drum. The playback protocol was identical to the neighbor recognition experiments. The behavioral response variables were also the same as those used in the neighbor recognition experiments, with the addition of the variable chatter call rate. The chatter call rate was added to mate recognition playbacks because it is a call given in response to the presence of a mate (Winkler and Short 1978). Principal components scores were compared using Friedman’s method for randomized blocks. I used a Wilcoxon signed-rank test as a post hoc test to identify which responses differed between the three signals. Finally, I used a Kruskal Wallis test to ascertain whether males and females differed in their responses to a mate or stranger rattle call, pik call and drum.
RESULTS

INDIVIDUAL RECOGNITION OF TERRITORIAL NEIGHBORS

The neighbor-stranger playback experiments were conducted with twelve female and eight male downy woodpeckers. The first and second principal components explained 35% and 30% of the variation in the data set, respectively (Table 4.1). The first principal component was correlated with the bird's response once it arrived at the speaker location (i.e., drum rate, closest approach, and duration within 5 m of the speaker), while the second principal component was correlated with variables that measured the bird's response while moving towards the speaker location (i.e., pik call rate, rattle call rate, and latency to first response). I employed the first and second principal component scores in Wilcoxon signed rank comparisons; the third principal component was not used in further analysis since the eigenvalue was less than 1.0.

RATTLE CALLS

Both males and females gave significantly stronger responses to playback of stranger rattle calls than they did to neighbor rattle calls (Table 4.2). The first principal component represents a strong response in an increased drum rate, a longer duration within 10 m of the speaker, and a closer approach to the speaker (Figure 4.1). The responses to same sex neighbors did not differ from those to an opposite sex neighbor (Table 4.2). However, as measured by both PC1 and PC2, male and female responses to rattle calls differed. Males did not use drums, but females did use drums in response to
the rattle calls ($P < 0.05$, Figure 4.2). The trend for male and female responses to opposite sex and same-sex neighbors indicated that males did not use drums in response to either male or female rattle calls. Whereas females used drums in response to the rattle calls of female neighbors and strangers, and also neighboring males, they did not drum in response to male strangers (Figure 4.2).

There was a significant difference between the response to a neighbor’s rattle call from the correct border and a neighbor’s rattle call from the opposite border for principal component 1 (Table 4.2): individuals responded to a neighbor’s rattle call from the opposite border with higher rates of drumming and closer approaches to the speaker. In addition, responses were similar to a neighbor’s rattle call and a stranger’s rattle call both from the neighbor’s opposite border (Table 4.2). The difference in response to a neighbor’s rattle call from the correct border versus the opposite border was similar for males and females on both principal component 1 and 2 (Table 4.2). Response to a same-sex or opposite-sex neighbor rattle call from the correct border were similar for both the first and second principal components (Table 4.2).

PIK CALLS

Downy woodpeckers made a stronger response to playback of neighbor pik calls than to stranger pik calls, as measured by principal component 1 (Table 4.2). Individuals remained within 10 meters of the speaker longer and approached closer to the speaker during playback trials with a neighbor pik call than when a stranger pik call was played (Figure 4.3). Responses to opposite- and same-sex neighbors and strangers were similar
(Table 4.2). Males and females responded similarly to pik calls (Table 4.2). Pik calls and rattle calls were given in response to playbacks of pik calls; drums were never used in response to a pik call.

**DRUMS**

Individual responses to the drums of a neighbor were similar to the responses to the drums of a stranger (Table 4.2, Figure 4.4). Individuals also took more than one minute to first respond to drums, approached within 8 meters of the speaker, and spent approximately five minutes within 10 meters of the speaker. The responses to opposite sex and same sex drums were similar (Table 4.2). Furthermore, males and females responded similarly to drums of neighbors and strangers (Table 4.2).

**IN INDIVIDUAL RECOGNITION BETWEEN MATES**

The mate-stranger playback experiments were conducted with eight female and eight male downy woodpeckers. The seven correlated response variables were reduced to three principal components (Table 4.3); the fourth principal component was not used in further analysis since the eigenvalue was less than 1.0. The behavioral measures of drum rate, closest approach to the speaker and duration within 5 meters of the speaker were correlated with the first principal component. The second principal component was highly correlated for the variables of latency of response, pik call rate, and rattle call rate than the first and third principal component. The third principal component was highly correlated with higher a lower drum rate and a higher chatter call rate.

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RATTLE CALLS

The behavioral responses to rattle calls of a mate differed from those to a stranger rattle call or a hairy woodpecker rattle call (Table 4.4). Individuals did not respond with drums to the heterospecific rattle call. Rattle calls and pik calls were given at lower rates and the latency to respond to a hairy woodpecker was greater than those responses to a downy woodpecker rattle call. Furthermore, there was a significant difference in the responses to a mate’s and stranger’s rattle call for both the first and second principal components. Individual’s responded to spent longer within 5 m of the speaker, and a slightly higher rate of drumming to a mate’s rattle call than to a stranger’s rattle call, (Figure 4.5). The response of chatter calls, given only in response to a mate’s rattle call, contributed to the significant difference in the third component (Figure 4.6). Males and females responded similarly to rattle calls whether they were from a mate or a stranger (Table 4.4).

PIK CALLS

In response to a mate’s pik call, individuals approached closer to the speaker location than they did in response to a stranger’s pik call, as measured by principal component 1 (Table 4.4, Figure 4.7.). The responses to the control heterospecific pik call were weaker than for either a mate or stranger downy woodpecker pik call (Table 4.4). Male and female responses to pik calls were similar (Table 4.4); drums were not given in
response to pik calls (Figure 4.7). Pik calls were given at a higher rate than rattle calls in response to either a mate or stranger pik call, but chatter calls were never given in response to a pik call (Figure 4.6).

DRUMS

The responses to the control heterospecific drum were weaker than responses to either a mate or stranger downy woodpecker drums (Table 4.4). However, the responses to a mate’s drum were similar to the response to a stranger’s drum (Table 4.3). Male and female responses to drums did not differ significantly (Table 4.4): individuals responded to drums with rattle calls, pik calls, and drums (Figure 4.8). Both males and females gave chatter calls in response to a mate’s and a stranger’s drum (Figure 4.6). Individuals approached on average within approximately six meters of the speaker, and remained an average of five minutes within five meters of the playback speaker.

DISCUSSION

The results from both the neighbor-stranger and mate-stranger playback experiments demonstrated that downy woodpeckers were able to recognize individuals by both types of vocal signals, but did not express a differential behavioral response to drums. Thus, downy woodpeckers were able to use vocal, but not non-vocal signals to recognize individuals. The differential response to rattle calls is consistent with previous research on woodpeckers that demonstrated males identified territory neighbors and females identified mates by their vocal territorial signal (Crusoe 1980). However, the
results of this investigation showed females identified both male and female neighbors by their territorial vocal signal, which had not been shown previously. Responses by both males and females to opposite-sex territorial neighbors were similar to the responses to a same-sex neighbor. A similar response by an individual to a same-sex and opposite-sex neighbor would not be expected, since territories are usually maintained between conspecifics of the same sex. Therefore, if males and females response to opposite-sex neighbors territorially, then downy woodpeckers defend territories against both male and female neighbors.

Pik calls have been reported to be an acoustic response to disturbances by an intruder or to signal the bird’s “state of alarm” (Short 1982). In addition, another postulated function of pik calls was to signal the sender’s location, since they were used frequently during changes in location (Kilham 1962, Short 1982). The use of pik calls to convey of individual identity between territorial neighbors was evidence that they served additional functions other than conveying an alarmed state. The use of pik calls was similar to the use of rattle calls; both were used between territorial neighbors and in response to opposite-sex and same-sex individuals. This similarity between pik calls and rattle calls is evidence that both signals aid in territory defense. Rattle calls appeared to signal a higher level of aggression than pik calls, as they were used at higher rates in response to strangers and same-sex individuals. So, rattle calls were likely the primary acoustic signal for territorial establishment and maintenance. Thus, pik calls are an example of an acoustic signal functioning as a secondary territorial signal. Although the use of two signals for territorial defense would allow for males and females to use different
signals for territorial defense, results from this investigation did not support this hypothesis. The difference between the uses of each signal could be a gauge for the level of aggression conveyed, rather than one call being used for territorial defense and the other used to maintain contact between individuals.

The drums of woodpeckers have been hypothesized to function as a territorial defense and mate attraction signal (Miller and Bock 1972, Winkler and Short 1978). However, results from this study indicated that neighboring individuals could not differentiate between familiar and unfamiliar individuals by drum. Since previous research has demonstrated species that use territorial signals are favored to encode individual information (Becker 1982, Falls 1982), it is unlikely drums served as a primary territorial signal. Drums may serve a function other than territorial defense, and therefore are not exposed to selection pressures favoring individual recognition. If drums serve only to advertise mating status, or synchronize the breeding cycle within pairs, then the encoding of individual cues may not be favored. These hypotheses are not implausible, as many species have been noted to duet with drums (Wilkins and Ritchison 1999, Kilham 1962). Alternatively, drums could be a highly aggressive signal, and dictate that a territorial individual respond equally to both neighbor and stranger individuals. Given mates respond similarly to drum from both males and females, only the mate attraction hypothesis appears to be supported by the results of this investigation.

The possibility that drums serve as a mate attraction signal without encoding individual information used by receivers, leads to a number of questions concerning their use within this communication system. If drums served primarily as a mate attractant, a
differential response to mate versus stranger drums would not be expected if drums served as an indicator of mate quality; an aspect of signal communication that would result in variation between signals of individuals (Catchpole 1982). Finally, drums may only have an attractant quality, with males and females using this signal differently to manipulate potential receivers. These questions were beyond the scope of this investigation and remain to be studied.

There are several aspects of reproductive behavior that female downy woodpeckers share in common with species that have been found to recognize individual female territory neighbors. Female downy woodpeckers defend their territories against same-sex conspecifics with the similar displays and vocalizations as those used by males. Although they do not actively maintain territories all year, they establish a territory separate from males prior to the breeding season. However, female downy woodpeckers were different from most other avian species where the female maintains a territory, in that their responses to female and male neighbors were similar. For example, female striped-back wrens (Campylorhynchus nuchalis) and spotted antbirds (Hylophylax naevioides) both exhibited less of an aggressive response to male song versus female song (Levin 1996, Bard et al., 2002).

Individual responses were similar to all three long distance signals from an opposite sex or same sex individual. In addition, none of the long distance signals were used primarily in response to either opposite sex or same sex individuals. The equality of responses to opposite sex and same sex individuals indicated that the use of multiple long distance signals by down woodpeckers was not a method of segregating communication.
between territorial neighbors and mates. However, the signals potentially convey different meanings, since the responses of males and females to rattle calls were not similar: males did not drum in response to rattle calls, while females did.
Figure 4.1. Behavioral responses of the focal individual (N=20) and principal component scores for playback experiments with territorial neighbor rattle calls. 
A). principal component score one for neighbor/stranger playbacks with rattle calls.  
B). drum rate response to neighbor/stranger signals.  
C). closest approach to the speaker during playback.  
D). duration spent within 5 meters of the speaker during the playback trial.  
E). principal component score two for neighbor/stranger playbacks with rattle calls.  
F). pik call rate in response to playbacks of neighbor/stranger rattle calls.  
G). rattle call rate in response to playbacks of neighbor/stranger rattle calls.  
H). latency to first response to playbacks of neighbor/stranger rattle calls.
Figure 4.2. Behavioral responses of male (N=8) and female (N=12) downy woodpeckers and principal component scores for playback experiments with territorial neighbor rattle calls. A), principal component score one for neighbor/stranger playbacks with rattle calls. B), drum rate response to neighbor/stranger signals. C), closest approach to the speaker during playback. D), duration spent within 5 meters of the speaker during the playback trial. E), principal component score two for neighbor/stranger playbacks with rattle calls. F), pik call rate in response to playbacks of neighbor/stranger rattle calls. G), rattle call rate in response to playbacks of neighbor/stranger rattle calls. H), latency to first response to playbacks of neighbor/stranger rattle calls.
Figure 4.3. Behavioral responses of focal individuals (N=20) and principal component scores for experiments playing territorial neighbor pik calls. A), principal component score one for playbacks with pik calls. B), drum rate response to neighbor/stranger pik calls. C), closest approach to the speaker during playback trials. D), duration spent within 5 meters of the speaker during the playback trial. E), principal component score two for neighbor/stranger playbacks with pik calls. F), pik call rate in response to playbacks of neighbor/stranger pik calls. G), rattle call rate in response to playbacks of neighbor/stranger pik calls. H), latency to first response to playbacks of neighbor/stranger pik calls.
Figure 4.6. Behavioral responses of the focal individual (N= 16) and principal component scores for playback experiments with mate, stranger and Hairy woodpecker rattle calls, pik calls, and drums. A), principal component score three for playbacks with rattle calls. B), chatter call rate in response playback. C), principal component score three for playbacks with pik calls. D), chatter call rate in response playback of pik calls. E), principal component score three for playbacks with drums. F), chatter call rate in response playbacks of drums.
Figure 4.8. Behavioral responses of the focal individual (N = 16) and principal component scores for playback experiments with mate, stranger and Hairy woodpecker drums. A), principal component score one for playbacks with drums. B), drum rate response playback of drums. C), closest approach to the speaker during playback. D), duration spent within 5 meters of the speaker during the playback trial. E), principal component score two for playbacks with drums. F), pik call rate in response to playbacks of drums. G), rattle call rate in response to playbacks of drums. H), latency to first response to playbacks of drums.
**Behavioral Response** | **PC1 (35%)** | **PC2 (30%)**
--- | --- | ---
Drum rate | 0.728 | -0.184
Closest approach to the speaker | -0.613 | -0.496
Duration of time within 5m of the speaker | 0.893 | 0.129
Pik call rate | -0.345 | 0.633
Rattle call rate | 0.289 | 0.692
Latency to first response | 0.434 | -0.617

* variability in original variables correlated with principal component

Table 4.1. Results of the principal components extraction and the correlation coefficients of the original response variables of the playback experiments with territory neighbors.
<table>
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<tr>
<th></th>
<th>Neighbor PC 1</th>
<th>Stranger PC 2</th>
<th>Male response PC 1</th>
<th>Female response PC 2</th>
<th>Same sex PC 1</th>
<th>Opposite sex neighbor PC 2</th>
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<tr>
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</tbody>
</table>

Table 4.2. Summary results of the comparisons for the differences in response to neighbor and stranger rattle calls, pik calls and drums. PC 1 = first principal component PC 2 = second principal component. Wilcoxon signed rank tests with a Bonferroni correction for multiple comparisons, experiment-wise error of 0.05. The comparisons tested whether responses differed between neighbor and stranger stimuli. The males-females comparison tested whether how males responded to all playbacks (neighbor and stranger) differed from the way females responded. The intersexual-intrasexual comparison tested whether responses to a same sex neighbor and stranger differed from the responses to an opposite sex neighbor and stranger.

* Wilcoxon signed rank test significant at $P < 0.05$. 

Table 4.3. Results of the principal components extraction and the correlation coefficients of the original response variables of the playback experiments with paired males and females.
<table>
<thead>
<tr>
<th>Signal</th>
<th>Comparison</th>
<th>PC 1</th>
<th>PC2</th>
<th>PC3</th>
</tr>
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<td>Rattle</td>
<td>mate-stranger-Hairy</td>
<td>$P &lt; 0.001^*$</td>
<td>$df = 2, \chi^2 = 25.25$</td>
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<td></td>
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<tr>
<td></td>
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<td>$P &lt; 0.05^*$</td>
<td>$P &lt; 0.05^*$</td>
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<tr>
<td></td>
<td>stranger-Hairy</td>
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<td>$P &gt; 0.05$</td>
<td>$P &lt; 0.05^*$</td>
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<td>male-female responses</td>
<td>$P = 0.341$</td>
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<td>$Z = -0.410$</td>
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<tr>
<td>Pik</td>
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<td>$P = 0.009^*$</td>
<td>$df = 2, \chi^2 = 9.5$</td>
<td>$P = 0.015$</td>
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<tr>
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<td>mate-Hairy</td>
<td>$P &lt; 0.05^*$</td>
<td>$df = 2, \chi^2 = 0.167$</td>
<td>$P = 0.835$</td>
</tr>
<tr>
<td></td>
<td>stranger-Hairy</td>
<td>$P &lt; 0.05^*$</td>
<td>$df = 2, \chi^2 = 0.187$</td>
<td>$P = 0.187$</td>
</tr>
<tr>
<td></td>
<td>male-female responses</td>
<td>$P = 0.160$</td>
<td>$Z = -1.43$</td>
<td>$P = 0.977$</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>$Z = -0.38$</td>
<td>$P = 0.887$</td>
</tr>
<tr>
<td></td>
<td></td>
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<td>$Z = -0.73$</td>
<td></td>
</tr>
<tr>
<td>Drum</td>
<td>mate-stranger-Hairy</td>
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<td>$df = 2, \chi^2 = 18.67$</td>
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<tr>
<td></td>
<td>mate-Hairy</td>
<td>$P &lt; 0.05^*$</td>
<td>$df = 2, \chi^2 = 0.187$</td>
<td>$P = 0.835$</td>
</tr>
<tr>
<td></td>
<td>stranger-Hairy</td>
<td>$P &lt; 0.05^*$</td>
<td>$df = 2, \chi^2 = 0.187$</td>
<td>$P = 0.835$</td>
</tr>
<tr>
<td></td>
<td>male-female responses</td>
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<td></td>
<td></td>
<td>$Z = -0.115$</td>
<td>$P = 0.932$</td>
</tr>
</tbody>
</table>

Table 4.4. Results of Friedman tests compared the responses to playbacks of mate, stranger and Hairy woodpecker signals, N= 8 males and N= 8 females. The significant differences between paired comparisons within each signal experiment were compared using a Wilcoxon signed rank test with a Bonferroni correction for multiple comparisons. Male and female comparisons combined responses to both mate and stranger trials and were compared using a Mann-Whitney U test.

* Test was significant at $P = 0.05$ level.
The study of characteristics that encode individual identity in avian acoustic signals has become an area of active research over the past two decades (Baker 2001). Passerines have been shown to identify individuals by song (Catchpole and Slater 1995, Baker 2001), while research on colonial seabirds indicated that markers for individual identity are also encoded in calls (Tschanz 1968, Bretagnolle 1996). Birds encode individual identity in their vocal signals in both temporal and spectral features. In all cases, markers for individual identity are encoded in signal features that vary more between than within individuals (Falls 1982).

Woodpeckers have been noted to use a number of different signals for long distance communication during the breeding season. Vocal signals in woodpeckers are generally species-specific (Winker et al. 1995), while a non-vocal signal, drumming has been documented as apparently lacking species typical features (Stark et al. 1998). However, in sympatry, drums are generally identifiable to species, due to divergence in signal characteristics (Dodenhoff et al. 2001). Research on *Melanerpes erythrocephalus* woodpeckers indicated they encode individual cues within their territorial calls (Crusoe 1980), and the cues encoded within *Colaptes auratus* territorial calls could be used to statistically identify individuals (Duncan 1990).
In downy woodpeckers (*Picoides pubescens*), there are three types of signals used for communication over long distances (Winker and Short 1978). Rattle and pik calls are vocal signals that have been implicated as important in a variety of territorial and reproductive contexts (Lawrence 1967, Kilham 1983, Short 1982), while the drum is a non-vocal signal that is also important in these encounters (Wilkins and Ritchison 1999). In downy woodpeckers, rattle calls are a series of repeated variable call notes while pik calls consist of a single vocal element. Downy woodpecker drums are a repetitive series of strikes produced by the bird’s bill on a resonant substrate.

As previously stated, all three types of signals are used by downy woodpeckers for long-distance communication. Each signal used over long distances for territorial maintenance or mate attraction should be subject to selection pressures to encode individual identity. Yet, whether individual markers are encoded within all three long-distance acoustic signals used by downy woodpeckers is unknown. Furthermore, if markers exist, the parameters encoding individual information within each signal have not been documented.

The signal parameters encoding individual identity should be consistent within a breeding season to facilitate recognition of territorial neighbors. Yet there have been no studies on woodpeckers to determine the stability of their vocalizations or drums over time. Signals may be stable both within and between breeding seasons, highly variable within and between breeding seasons or vary with the age of the bird. The latter possibility need not imply that woodpeckers learn their vocalizations or use auditory feedback for normal species-typical signal development. In this chapter, I investigated
whether there was plasticity observed in either of the two vocal signals or within drums of known individuals both within and between breeding seasons.

METHODS

STUDY AREA

This investigation was conducted at Kraus Wilderness Preserve, Delaware Co., OH (N 40° 11', W 83° 03') from November through July 1998-2001. Downy woodpeckers were mist-netted and color-banded with unique combinations during the winter months of November through February, which allowed for identification of known individuals during successive encounters.

EQUIPMENT AND ACOUSTIC ANALYSES

Drums and vocalizations of 8 male and 12 female downy woodpeckers were recorded with a Sony TCD 5 Pro II audio-cassette recorder with a Sennheiser ME67-K6P and an Auditechnica 815r microphone connected to a Denecke PS-1 phantom power source. Three signal types were analyzed for characteristics that might encode individual identity. Signals were digitized and analyzed using Signal 3.1 (Engineering Design 1999). A rattle call contained a series of notes each resembling a pik call. The notes varied in frequency within the call (Figure 3.1). The parameters I measured were selected to represent characteristics of the entire rattle call and the patterns of duration and frequency changes between the notes within a call. The parameters that represented the entire call were the call duration (sec), the call average inter-note interval (sec), the call
average note duration (sec), and the call average note frequency at maximum amplitude (Hz). The call was sectioned into quartiles and measurements from each quartile were used to represent the changes between quartiles within the call. The average quartile note duration (sec), and average quartile frequency was measured for each of the four sections of the rattle call. A pik call was a single note with an increase in frequency at the beginning and a decrease at the end of the call (Figure 5.2A). In pik calls, I measured the call duration (sec), duration of the frequency rise (upsweep, sec), duration of the peak frequency (sec), duration of the frequency fall (down sweep, sec), and four frequency measurements (Hz): lowest frequency of the upsweep, highest frequency of the upsweep, frequency at the “level” portion within the call (termed the level frequency), and the lowest frequency of the down sweep. A drum was a series of strikes against the wood that produced a series of beats (Figure 5.2B). I measured the variables of cadence (strikes sec\(^{-1}\)), drum duration (sec), average drum inter-strike interval (sec), average drum strike duration (sec), and average drum strike frequency at maximum amplitude (Hz).

The breeding season was subdivided into pre-mated and mated stages: a pre-mated bird had not selected a mate for the breeding season, while a mated individual had begun foraging with the same opposite-sex conspecific during two consecutive monitoring visits. The signals from twelve females and eight males were used for all of the acoustic analyses. The number of rattle and pik calls averaged to represent each individual averaged (± S.D.) 7 ± 5 calls for the pre-mated stage, 9 ± 4 calls for the mated stage and 16 ± 4 calls for comparisons between two years. The drums during one bout were averaged and the bout averages were used for statistical analysis. A drum bout was defined as a series of drums given from the same location. The number of drum bouts
used to represent an individual in the statistical analysis averaged (± S.D.) 25 ± 10 drum bouts. The number of drum bouts used to represent the pre-mated stage averaged (± S.D.) 10±4 drum bouts and the mated stage was 2±12 drum bouts. The low sample sizes for drum bouts during the mated stage were for females, since mated females rarely drum.

I used a multivariate repeated measures analysis of variance to test for differences between breeding stages and two breeding years within each type of signal. To test for which variables might encode individual identity I used a multivariate analysis of variance. I used a Mauchly’s test for sphericity of the variance-covariance matrix. A Greenhouse-Geisser correction factor was used if sphericity could not be assumed. Significant differences among means were compared using a Bonferroni correction for multiple comparisons. Then, I used a discriminant function analysis to test if signals could be correctly classified to individual identity based on the selected variables for each type of signal.

PLAYBACK EXPERIMENTS

I tested whether the variation within an individual’s rattle call between breeding stages or years affected individual recognition. For this analysis, playback tapes of rattle calls were made from field recordings of the known individual using Signal 3.1. Playbacks were conducted in a randomized balanced design. Prior to presentation of the stimulus, the focal bird was observed for five minutes to ensure that the target individual was not currently engaged in territorial, acoustic, or reproductive displays. Playback trials consisted of three intervals; a 5 minute pre-stimulus observation, a 2 minute stimulus
presentation, and a 5 minute post-stimulus presentation. The speaker was placed approximately 30 meters from the nest cavity and oriented in the direction the birds flew during visits to the nest cavity while excavating the nest. The focal bird of this playback design was the current mate of the individual that the playback rattle calls were recorded from; therefore, all experimental playback calls were recorded from the focal bird’s mate. Prior to the playback trials, the mate was either observed foraging outside the area or removed (i.e., captured and restrained under permit) from the territory to avoid interfering with the focal individual. Trials were conducted in the morning when the mate was likely to be foraging outside the playback experiment area. A minimum of one hour passed between each of the four trials with each focal bird. If the mate returned within the hour interval I waited until the mate had left to begin the next trial.

Four signals were played to the focal bird: the rattle call of a current neighbor (i.e., control), the rattle call of their current mate recorded from the previous year, the rattle call of their current mate recorded prior to mate selection, and that of the current mate after pairing. A total of four male and four female focal birds were tested. Of the eight mated pairs, three were mated during both years the rattle calls were recorded.

I measured seven behavioral responses to the playback stimuli: the latency to first response (sec), closest approach to the speaker (m), duration spent within 5m of the playback speaker, and the calling rates (in sec) of pik, rattle, and chatter (i.e., mate greeting call, Winkler and Short 1978) calls, along with the drum rate. I extracted the first, second, and third principal component scores (eigenvalue > 1.0) and tested for
significant differences in behavioral response to signals using Freidman’s tests. I tested for differences between paired playback responses with a Wilcoxon signed rank test with Bonferroni correction for multiple comparisons.

RESULTS

ACOUSTIC ANALYSES

Analysis of rattle calls, pik calls, and drums using a repeated measures analysis of variance indicated numerous significant differences in each signal attributable to the factors of individuals, breeding stages, and years. Rattle calls differed significantly among individuals in frequency characteristics for all four quartile sections of the rattle call and average rattle call frequency at maximum amplitude (MANOVA: $F = 752.35, df = 19, 132, P < 0.001$). The rattle call temporal characteristics of call duration, average note duration, and the 1st, 2nd, and 4th quartile in note duration were significantly longer during the pre-mated than during the mated breeding stages (Figures 5.3 and 5.4; MANOVA repeated measures: $F = 188.7, df = 7, 12, P < 0.001$). Rattle call frequency measures were significantly lower (1st, 2nd, and 3rd frequency quartile and average frequency) during the second year (Figure 5.5; MANOVA repeated measures: $F = 32.2, df = 7, 12, P < 0.001$). The differences in rattle calls between the two breeding years are illustrated in figure 5.6. Male rattle calls were lower in frequency than females, except for the 4th quartile section of the call (Figure 5.7, MANOVA repeated measures: $F = 242.2, df = 7, 12, P < 0.001$).
Pik calls of individual downy woodpeckers were similar in the duration of the upsweep frequency (MANOVA: $F = 1.03$, df = 19, 132, $P = 0.424$) and the lowest frequency of the down sweep (MANOVA: $F = 1.97$, df = 19, 132, $P = 0.64$). The pik calls differed between individuals in the call duration, duration of the peak frequency, duration of the down sweep, lowest frequency of the up-sweep, highest frequency of the up-sweep, and the frequency at the “level” portion (Figures 5.8 and 5.9, ANOVA Bonferroni correction for multiple comparisons: $P < 0.05$). Pik calls decreased significantly in the lowest frequencies of both the upsweep and down sweep after the pre-mated stage (MANOVA repeated measures: $F = 5.11$, df = 7, 12, $P = 0.006$, figure 5.9). Sex differences were found in all frequency measurements except the lowest frequency of the down-sweep, with males having lower call frequencies than females throughout the call (MANOVA repeated measures: $F = 30.97$, df = 7, 19, $P < 0.001$). Although male calls were lower in frequency than females, both sexes had similar decreases in the lowest frequency of the upsweep and down-sweep frequency (MANOVA repeated measures Bonferroni correction: $F = 1.407$, df = 7, 12, $P = 0.282$). Controlling for breeding stage, pik calls differed between breeding years in lowest frequency of the upsweep and the lowest frequency of the down sweep (Figure 5.9, MANOVA repeated measures Bonferroni correction: $F = 8.698$; df = 8, 9; $P < 0.05$).

Drums varied in interstrike interval and frequency at maximum amplitude (MANOVA: $F = 8.26$, df = 19, 132; $P < 0.001$) between individuals. During the pre-mated breeding stage drum duration was longer and frequency at maximum amplitude was higher than during the mated breeding stages (figure 5.10, MANOVA repeated measures Bonferroni correction: $F = 3.475$; df = 7, 12; $P < 0.05$). The drum average
inter-strike interval, drum average strike duration and drum duration was longer during the first year sampled than during the second year sampled (Figure 5.10, MANOVA repeated measures Bonferroni correction; $F = 5.6; \text{df} = 8, 9; P < 0.005$). There were no significant differences between the drums of male and female downy woodpeckers (MANOVA repeated measures; $F = 1.37; \text{df} = 7, 12; P = 0.281$). In drums, cadence (i.e., strikes sec$^{-1}$) was similar between breeding seasons and between years (MANOVA repeated measures $F = 1.45; \text{df} = 7, 12; P = 0.159$).

Classification by a discriminant function analysis indicated there was sufficient variation in the acoustic variables to classify individuals by either pik calls (50% error rate) or drum (33% error rate). However, rattle calls were individually identifiable 95% of the time (i.e., 5% error rate). The percent of pik calls rattle calls and drums correctly classified were greater than the 5% correct classification expected by chance for twenty individuals. In pik calls, the total duration, highest frequency of the upsweep and lowest frequency of the downsweep were highly correlated ($r \geq 0.6$) with the eight discriminant functions used for classification of the twenty birds. The average drum strike duration, average drum inter-strike interval, drum total duration, and the average drum frequency at maximum amplitude were all highly correlated ($r \geq 0.6$) to the six discriminant functions. The thirteen discriminant functions used to classify rattle calls were highly correlated ($r \geq 0.6$) with the parameters of average inter-note interval, call duration, and the average frequencies of the first and second call quartiles.
PLAYBACK EXPERIMENT

The behavioral responses to playback rattle calls correlated (correlation coefficient ≥ |0.5|) with PC1 included the latency to first response, the closest approach to the speaker, and the duration spent within 5m of the speaker. The rattle call rate, drum rate, and chatter call rate were highly correlated (correlation coefficient ≥ |0.5|) with PC2. There were significant differences in behavioral response by the local bird to the four different rattle calls for both PC1 and PC2 (Friedman tests: PC1; $\chi^2 = 8.70$, df=3, $P = 0.034$, PC2; $\chi^2 = 10.65$, df=3, $P = 0.014$). For principal component one (PC1), significant differences were found between the responses to rattle calls of neighbors versus post-mated second year rattle calls of their current mate (figure 5.11A, Wilcoxon signed ranks test Bonferroni correction; $P < 0.05$). The behavioral responses (PC2) to both the second year pre-mated and post-mated rattle calls differed from the responses to both the rattle calls of neighbors and the first year rattle call of their mate. Responses to a rattle call recorded during the current (2nd) year call prior to mating did not differ from the responses a rattle call recorded during the current (2nd) year after mating for PC2. Mate responses were similar for PC2 to the rattle call of a current year neighbor and a rattle call recorded from their mate the previous (1st) year (Figure 5.11B Wilcoxon signed ranks test Bonferroni correction $P< 0.05$). The response variable that differed most between playback of 1st year and 2nd year rattle calls was probably the chatter call rate (Table 5.1). Thus, the calls within a breeding year were perceived by mates as similar, but calls recorded during a previous year were perceived as different from the current year’s call.
DISCUSSION

Signals that are used by individuals to establish and maintain a territory are hypothesized to encode both species and individual information (Falls 1982, Becker 1982). If the vocal or non-vocal signals of downy woodpeckers encode individual identity, then sufficient variation should be observed within the patterns of each acoustic signal to allow for accurate classification of individuals (Falls 1982). The pik call and drum did have sufficient variation to identify individuals more than would be expected by chance. However, of the three signals analyzed in this investigation, the rattle call appeared to vary the most among individual downy woodpeckers. The frequency components of rattle calls were sufficient for distinguishing individuals within the population. Temporal characteristics also varied between breeding stages, but this did not affect the responses of mates to rattles during the same breeding year. Therefore, since all three signals are used for long distance communication, downy woodpeckers should favor identifying individuals by rattle calls over either pik calls or drums.

Given that acoustic signals are used for both communication between potential mates and territorial rivals, it is difficult to ascertain the selective pressures that favor the encoding of information pertinent to receivers. It is not unexpected, given the variety of signals used by birds, that each signal may be encoded with diverse information targeted for different individuals in the population. For example, reproductive partners often recognize one another by signals which are not exchanged between territorial neighbors; female American goldfinches (*Carduelis tristis*) recognize the flight calls of mates but this vocalization is not individually recognized by neighboring males (Mundinger 1970).
Another example, the chatter call of woodpeckers, is only given between mates and not between other members of the population (Winkler and Short 1978). Therefore, the variation within pik calls and drums might be sufficient to identify a single individual from all other unfamiliar individuals.

The first and second average quartile frequencies of rattle calls differed between breeding years. Both of these frequency parameters were different between individuals and therefore might encode individual identity. Playbacks with mated pairs revealed the changes in frequency between years had an effect on how the rattle call was perceived by mates. Mates did give the greeting chatter call in response to rattle calls recorded during the same year but not to calls recorded during the preceding breeding year. Thus, the changes within the rattle call between breeding seasons were perceived differently by the bird’s mate. The changes in the average frequency of the first and second quartile of the rattle call increased the signal’s complexity. Though this may be anecdotal evidence that individuals change their calls in order to differentiate themselves from conspecifics, an alternative hypothesis is that this change represents maturation in vocal development. Individuals that changed their rattle calls may have greater vocal control of their signals in successive years.

The sample size of individuals surviving within the study area beyond two years was too low for any conclusions about the extent to which rattle calls remained stable after two years. Bald eagle chatter calls significantly changed between years but have not been tested whether calls given during subsequent years were perceived as different calls (Eakle et. al. 1989). The individual features of eagle owl (Bubo bubo) hoot calls have been shown to remain stable between breeding years (Lengagne 2001). Further investigation of
the ontogeny of downy woodpecker rattle calls would be necessary before social influences on vocal performance such as those observed in long-tailed manakins (Chiroxipha linearis, Trainer et al. 2002) can be addressed. If this change is correlated to age, which was not directly tested in this study, then the rattle call could be a way in which individuals may gauge the age of potential mates or strangers vocalizing in the area. The relative difference between the note frequencies within a rattle call may be an honest indicator of an individual’s age and by extrapolation, experience. If the pattern of frequency changes between notes within a rattle call indicates age, further research is required to ascertain if this information is used by individuals.
Figure 5.1. Signal characteristics measured for a rattle call. A). The four measures that represented aspects of the entire signal; 1. the length of the arrow denotes the call duration (sec) 2. average inter-note interval (sec) 3. average note duration (sec) 4. the dot denotes the frequency at maximum amplitude for one note. The average note frequency at maximum amplitude (Hz) was calculated by adding the frequencies at maximum amplitude for all notes and dividing by the number of notes. B). The quartile measures that represented segments of the rattle call. The average note duration and average frequency at maximum amplitude was measured within each quartile of the rattle call. The 1st, 2nd, and 3rd quartiles contained the same number of notes, but the 4th quartile varied in the number of notes used for the average. The 4th quartile contained four to six notes and varied with the total number of notes within the call.
Figure 5.2. Signal characteristics measured for a pik call and a drum.

A). The parameters that represented the frequency aspects of the call are denoted with circles; 1. lowest frequency of the upsweep, 2. highest frequency of the upsweep, 3. frequency at the “level” portion within the call (level frequency), and 4. lowest frequency of the down sweep. The parameters that represented the temporal aspects of the pik call are denoted by a double arrow; 5. call duration (msec), 6. duration of the frequency rise (upsweep, msec), 7. duration of the peak frequency (msec), and 8. duration of the frequency fall (down sweep, msec). 

B). A drum is composed of a series of strikes and a 1 denotes the first strike. The parameters that represented a drum were; cadence (strikes per second) within one drum, 2. the drum duration (msec), 3. the interstrike interval (msec), 4. the strike duration (msec), and 5. the strike frequency at maximum amplitude (Hz).
Figure 5.3. Means ± S.E. of rattle call parameters for twenty downy woodpeckers. A). The duration of a rattle call (msec). B). The average duration of a note within the rattle call (msec). C). The average inter-note interval of a rattle call (msec). D). The average note frequency for the entire rattle call (Hz).
Figure 5.4. Means of rattle call parameters for twenty downy woodpeckers. A). The average note duration (msec) of the first rattle call quartile. B). The average note duration of the second quartile of a rattle call (msec). C). The average note duration of the third quartile of a rattle call (msec). D). The average note duration of the fourth quartile of the rattle call (msec).
Figure 5.5. Means of rattle call parameters twenty downy woodpeckers. A). The average note frequency (Hz) of the first rattle call quartile. B). The average note frequency (Hz) of the second quartile of a rattle call. C). The average note frequency (Hz) of the third quartile of a rattle call. D). The average note frequency (Hz) of the fourth quartile of the rattle call.
Figure 5.6. Sonagrams representing changes in an individual rattle call between breeding years. A. A rattle call recorded during the first year. There is a pattern of consistency in note frequency through the first half of the call. A change in the note frequency does not occur until the second portion of the rattle call. B. A rattle call from the same individual during the next breeding season. The call from the second year has a change in the note frequency during the second quartile section of the call and then again in the third quartile section.
Figure 5.7. Means ± S.E. of rattle call parameters for twelve female and eight male downy woodpeckers. A). The average note frequency (Hz) of the first rattle call quartile. B). The average note frequency (Hz) of the second rattle call quartile. C). The average note frequency (Hz) of the third rattle call quartile. D). The average note frequency (Hz) of the fourth rattle call quartile.
Figure 5.8. Means ± S.E. of pik call parameters for twenty downy woodpeckers. A). The duration of a pik call (msec). B). The duration of the frequency up-sweep (msec). C). The duration of the peak “level” frequency (msec). D). The duration of the frequency down-sweep (msec).
Figure 5.9. Means ± S.E. of pik call parameters for twenty downy woodpeckers. A). The lowest frequency of the up-sweep (Hz). B). The highest frequency of the up-sweep (Hz). C). The peak “level” frequency (Hz). D). The lowest frequency of the down-sweep (Hz). The parameters for year one are illustrated first for each category of pre-mated and mated.
Figure 5.10. Means ± S.E. of drum parameters for twenty downy woodpeckers. A). The duration of a drum (msec). B). The cadence (strikes sec⁻¹) of a drum. C). The inter-strike interval (msec). D). The strike duration (msec) E). The strike frequency at maximum amplitude (Hz).
Figure 5.11. The principal component scores representing the behavioral responses to four different rattle calls, N = 8 individuals. 
A). Principal component one represents temporal and distance behavioral responses, latency to first response, the closest approach to the speaker, and the duration spent within 5m of the speaker. B). Principal component two represents the acoustic behavioral responses, rattle call rate, drum rate, and chatter call rate.
Table 5.1. Mean ± S.D. responses to playback experiments with mated pairs which tested whether changes in rattle call characteristics effect individual recognition. The control was the rattle call of same sex neighbor.

<table>
<thead>
<tr>
<th>Signal Type</th>
<th>Latency of response</th>
<th>Pik (calls/min)</th>
<th>Rattle (calls/min)</th>
</tr>
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<tbody>
<tr>
<td>Control</td>
<td>95.38 ± 82.81</td>
<td>3.46 ± 8.71</td>
<td>0.20 ± 0.17</td>
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<tr>
<td>First Year call</td>
<td>95.38 ± 52.27</td>
<td>0.73 ± 0.94</td>
<td>0.23 ± 0.11</td>
</tr>
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<td>Pre-mated 2nd Year call</td>
<td>92.00 ± 52.52</td>
<td>0.80 ± 1.17</td>
<td>0.16 ± 0.12</td>
</tr>
<tr>
<td>Post-mated 2nd Year Call</td>
<td>97.25 ± 60.60</td>
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<td>0.19 ± 0.17</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>Drum (drums/min)</th>
<th>Chatter (calls/min)</th>
<th>closest approach</th>
<th>Duration with 5 m</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>0.02 ± 0.05</td>
<td>0.00 ± 0.00</td>
<td>8.27 ± 5.06</td>
<td>48.63 ± 65.76</td>
</tr>
<tr>
<td>First Year call</td>
<td>0.00 ± 0.00</td>
<td>0.18 ± 0.27</td>
<td>8.75 ± 3.54</td>
<td>69.00 ± 99.73</td>
</tr>
<tr>
<td>Pre-mated 2nd Year call</td>
<td>0.07 ± 0.20</td>
<td>0.52 ± 0.27</td>
<td>7.50 ± 3.78</td>
<td>167.50 ± 161.85</td>
</tr>
<tr>
<td>Post-mated 2nd Year Call</td>
<td>0.04 ± 0.10</td>
<td>0.43 ± 0.15</td>
<td>5.63 ± 1.77</td>
<td>131.13 ± 81.02</td>
</tr>
</tbody>
</table>
LIST OF REFERENCES


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