INDIVIDUAL AND INTERSEXUAL VARIATION IN ALARM CALLS OF THE WHITE-TAILED HAWK[1]

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Although variation in bird vocalizations is well-studied (Marler 1960, Beer 1970, Jellis 1977, Falls 1982, Brown and Farabaugh 1991), few falconiforms have been intensively examined. The White-tailed Hawk (*Buteo albicaudatus*), however, exhibits remarkable patterns of intersexual as well as individual variation (Farquhar 1986) not previously identified in this species (Brandt *in* Bent 1937, Stevenson and Meitzen 1946, Slud 1964, Snyder and Snyder 1991). Hereafter referred to as alarm calls in White-tailed Hawks, these loud vocalizations are given in the context of potential danger such as when their territory has been intruded by mate or food competitors, nest predators, or humans. In Falconiformes, alarm calls (also known as territorial calls) generally are considered to be their typical calls, and are commonly quoted in the literature as those which identify the species (Brown and Amadon 1968, Cramp and Simmons 1980). White-tailed Hawks of both sexes emit alarm calls throughout the year, without associated aggressive behavior or seasonal call variation (Farquhar 1986; Farquhar, unpubl. data). In this report I quantitatively examine individual and intersexual variation in vocalizations of the White-tailed Hawk.

METHODS

I recorded calls from six of the ten resident breeding adults at the Attwater Prairie Chicken National Wildlife Refuge, Colorado County, Texas (APCNWR, described in Farquhar 1986, 1988) on five days during 7–16 June 1991. Four of the adults were members of mated pairs (assigned matching numbers); the other two were mated to individuals not recorded in this study. All recordings were made with a Sony TCM-5000 cassette recorder, and a Sennheiser ME-80 shotgun microphone (fitted with a wind screen and a 20 dB pre-amplifier).

I elicited alarm calls from adults during the breeding season by entering their nesting territories and walking in circular directions within one to twenty meters of the nest. The hawks, which called either while flying or perched, typically had young that had recently fledged and were in the immediate vicinity of the nest. But in one case (male 3 and female 3) a fully feathered juvenal,

whose ability to fly had not yet been determined, was still in the nest. While recording calls I maintained approximately equal distances from the young. I observed adult White-tailed Hawks with 10× binoculars, or a 15–45× spotting scope, and determined sex by noting size differences of individuals in close proximity to one another (body and wing length greater in females; Voous 1968, Snyder and Wiley 1976). Individuals were recognized by differential molt patterns in the remiges and rectrices.

I generated and measured sonograms of recorded calls using "C-Canary" software (Cornell Bioacoustics Research Program, Laboratory of Ornithology, Ithaca, NY). Only sonograms of complete calls were analyzed from birds whose sex and individual identities were positively known. As in previous work (Farquhar 1986) I identified two major subunits in each White-tailed Hawk alarm call (Fig. 1): (1) an initial note (segment AB), followed by (2) a series of bisyllabic notes (syllable 1 = segment CD; syllable 2 = segment EF). In an attempt to quantify elements of spectrographic structure in each sonogram I measured eight continuous variables (duration, in seconds; frequency, in kHz): *number of notes* in call, including initial note plus all subsequent bisyllabic notes; *initial note duration* (segment AB), *inter-note duration* ([total call duration minus initial note duration, minus sum of intersyllable duration for all notes] divided by total number of notes); *intersyllable duration* (summed measurements of duration between syllable frequency maxima of bisyllabic notes divided by total number of syllables); *total duration* of call (segment AG); *frequency change of initial note* (ending frequency minus beginning frequency, to discriminate among ascending and descending notes); *difference between syllable frequency maxima* (syllable 1 minus syllable 2; = Syldif max); *total call frequency* (sum of beginning and ending frequencies of initial notes and frequency maxima of bisyllabic notes, divided by number of notes). Measurements of all variables were obtained from the dominant frequency band (*d*; Fig. 1), generally appearing as the second harmonic. The term spectrographic structure refers to the audiospectrographic pattern of frequency modulation, as displayed in a sonogram (Becker 1982, Nowicki and Marler 1988). Frequency (Hz) is also referred to as "pitch" (Nowicki and Marler 1988) and will be so used here. Rate refers to the number of notes in a call per unit time. Means ($\pm$SE) for individuals within each variable were compared with analysis of variance (ANOVA) using individual ($n = 6$) as the grouping factor. Statistically significant ($P < 0.05$) ANOVAs were then sub-
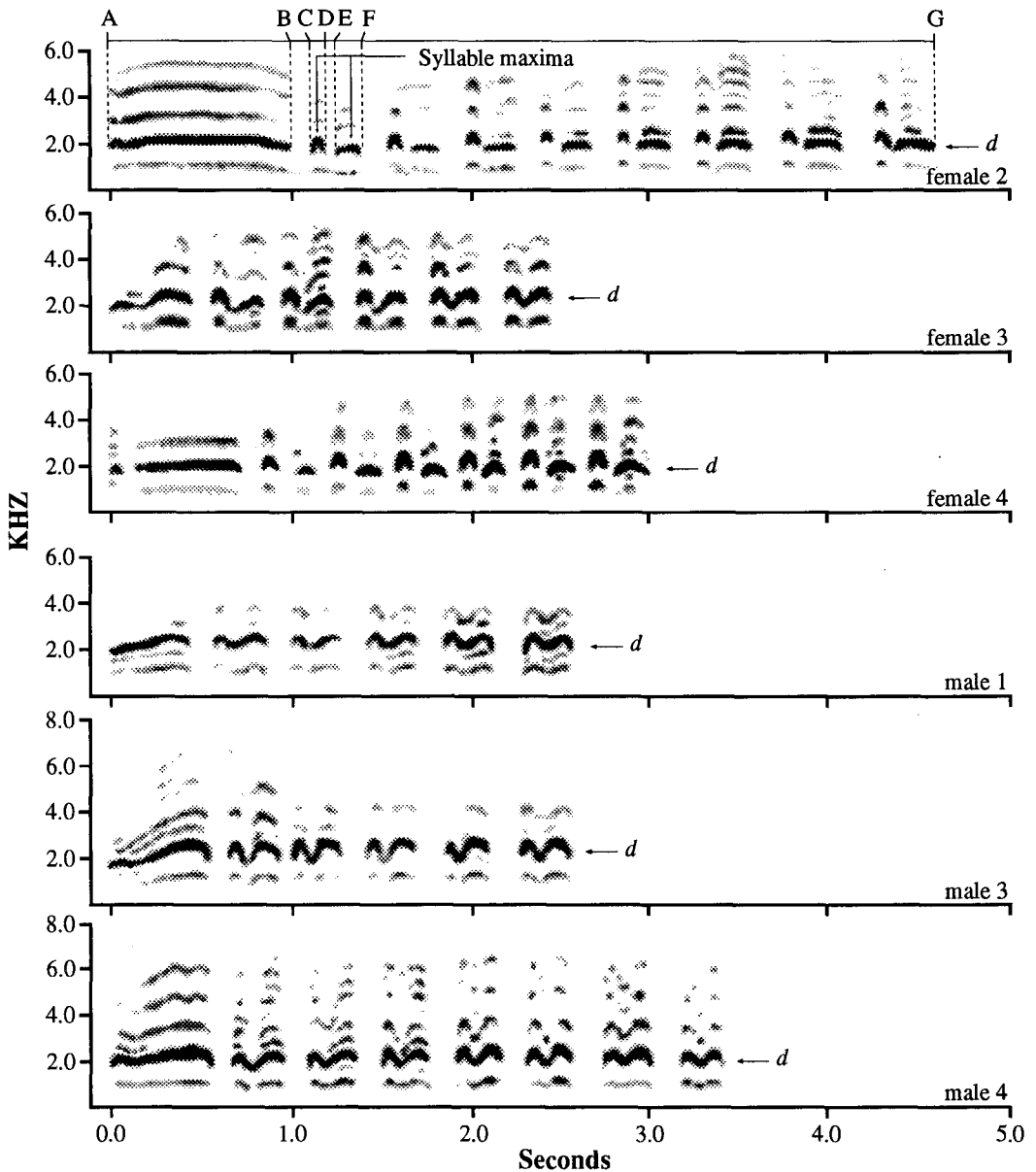
FIGURE 1. Representative sonograms from each of six White-tailed Hawks recorded at Attwater Prairie Chicken National Wildlife Refuge, Texas. All measurements were of the dominant frequency band (indicated by *d*). Uppercase letters refer to note segments described in text.

jected to Scheffe's *F*-test; statistically significant (*P* < 0.05) pairwise differences among individuals within each parameter were regarded as evidence of individual or intersexual variation (e.g., Miller 1978, Falls 1982).

RESULTS

Individual and intersexual call variation is strongly suggested by differences in spectrographic structure among sonograms for each individual (Fig. 1), defying the depiction of a single "typical" sonogram for this species. Results of ANOVA on means for each parameter, specifically the Scheffe's pairwise comparison tests (Table 1) as a measure of variation, are summarized below, first for individual variation, then for intersexual variation.

Individual variation. Values for *difference between*

syllable frequency maxima (Syldif max, Table 1) were the most variable, with only female 2 vs. female 4 and male 1 vs. male 4 not exhibiting significant differences. *Initial note duration* also exhibited a notable number of significant pairwise differences, mainly among females which all differed from one another, whereas males differed only between male 3 and male 4. *Frequency change of initial note* exhibited the same degree of variation among females as did Syldif max, but less variation was present among males (only males 1 and 4 differed significantly). Among the remaining variables either one sex or the other lacked any significant variation. Variation in *number of notes* and *total call duration* existed only among females and was dominated by values for female 2. Likewise, only females exhibited variation in *internote duration,* and was limited to female 2 vs. female 4. *Intersyllable duration* did not differ significantly among females, and only the combination of male 3 vs. male 4 exhibited a significant difference. Females exhibited no variation in *total call frequency,* and low variation was computed for males (only male 1 and male 4 differed from each other).

Intersexual variation. All variables were characterized by some level of intersexual variation. Values for Syldif max showed the greatest levels of variation, all females were different from all males; an audible pattern, discernible in the field, and noted by syllable 1 being slightly higher pitched than syllable 2 in females, whereas among males syllables are similar in pitch. *Total call frequency* revealed slightly fewer intersexual differences, due to a lack of significant variation between female 3 and males 3 and 4. Regarding *initial note duration,* female 3 was the only individual of either sex lacking any intersexual differences, and male 4 had only one (vs. female 2), otherwise all pairwise differences were significant. *Frequency change of initial note* tended to descend (negative values, Table 1) from beginning to end in females 2 and 4, whereas they tended to rise (positive values, Table 1) in female 3 and all males; again, these patterns were distinctly audible in the field. Variation in *number of notes* and *total call duration* was relatively minor, consisting only of female 2 being significantly different from all males. *Internote duration* and *intersyllable duration* both exhibited the fewest instances of intersexual variation.

DISCUSSION

Variation in measures of spectrographic structure was great among alarm calls of White-tailed Hawks in terms of the total number of significant pairwise differences on both an individual and intersexual basis. *Frequency difference between syllable maxima* of the bisyllabic notes ranked highest in variability, followed closely by values for *duration of initial note* and *frequency change of initial note.* Thus, the data suggest that these three variables may potentially be an important source of acoustic information in White-tailed Hawks. The average coefficient of variation (standard deviation divided by mean times 100) of all frequency parameters combined (CV = 62.7%) is five times greater than the average of all duration parameters (CV = 12.5%). This suggests that less stereotypy exists and greater explanatory power resides among frequency parameters,

whereas duration parameters may be more important in species-specificity (Hutchinson et al. 1968, Robisson 1992).

Other than the expected *total call frequency* differences, and those listed above, none of the other variables offered clear patterns of individual or intersexual variation. Levels of individual variation were often influenced by values for Female 2, an aberrant individual in that her initial notes were quite long compared to other birds (contributing also to relatively longer total calls). Her mate failed to respond vocally during any of the recording sessions, a unique occurrence among all birds in this study, but it is unknown whether or how such a failure might relate to characteristics of her calls.

Initial notes, such as those analyzed here, are distinct from the subsequent series of bisyllabic notes in the calls and represent a previously unstudied phenomenon in Falconiformes, perhaps deserving more attention from researchers. Such notes have been observed in non-falconiform birds and have either been associated with species-specificity (Shiovitz 1975) or regarded as "alerting" cues in environments where acoustic degradation renders information-packed highly modulated calls, by themselves, less detectable at a distance (Richards 1981). Alarm calls of the White-tailed Hawk can indeed be considered highly modulated, and in all such calls I have observed, a distinctive initial note has been present. Oddly though, out of many published call descriptions for this species only those by Slud (1964) and Snyder and Snyder (1991) suggest any hint of such an initial note. Although further study may reveal them to be more common across falconiform taxa, only the typical calls of some *Circus* harriers (Cramp and Simmons 1980), Swainson's Hawks (*B. swainsoni,* Brown and Amadon 1968), Puna Hawks (*B. poecilochrous,* Farquhar, unpubl. data), and African Mountain Hawks (*B. oreophilus,* Brown and Amadon 1968), regularly contain recognizable initial notes. Subspecies (*B. a. colonus*) of the White-tailed Hawk recorded in Venezuela (P. Schwartz, unpubl. data) have very similar calls to those of the taxon studied here (*B. a. hypospodius*), but no sex data exists for those recordings.

Individual variation is rarely or insufficiently addressed in typical calls (e.g., territorial or alarm) of Falconiformes, and sex-specificity is only slightly better known (e.g., Rosenfield and Bielefeldt 1991). Unlike the complex levels of variation examined here for White-tailed Hawks, sex differences in most species are restricted to pitch (29/45 species; Brown and Amadon 1968, Cramp and Simmons 1980, Brown et al. 1982, Palmer 1988). Consistent with body size expectations (Gaunt et al. 1987), the larger bird (female, in most Falconiformes) generally gives the lower pitched calls. A notable exception is in the female Verreaux's Eagle, *Aquila verreauxi,* which is the larger sex, but gives the higher-pitched calls (Rowe 1947).

There are several additional ways in which calls may potentially differ intersexually among Falconiformes; further work is needed, however, to substantiate the differences noted. For example, two species, European Honey Buzzards (*Pernis aviporis*: female, "piuhu"; male, "piha"; Brown and Amadon 1968) and Red-footed Falcons (*Falco vesperitinus*: female, "chi-chi-chi"; male,

TABLE 1. Summary statistics for measured parameters of alarm calls of adult White-tailed Hawks recorded at APCNWR. Number in parentheses represents number of separate calls recorded. Within-parameter significance values (P) for ANOVAs on means appear in last row of each column. Means in each column with matching superscript letters are significantly different (Scheffe's F-test, $P < 0.05$) from each other.

Indi-vidual	No. notes	Duration (sec)				Frequency (kHz)		
		Initial note	Internote	Intersyllable	Total call	Initial note	Syldif max	Total call
Female 2 (8)								
Mean	9.33^{abcde}	0.90^{abcde}	0.35^{a}	0.17	4.61^{abcde}	-0.25^{abcd}	0.38^{abcd}	2.13^{abc}
SE	0.33	0.03	0.03	<0.01	0.15	0.04	0.02	0.02
Range	8–10	0.81–0.91	0.23–0.26	0.13–0.21	3.90–4.90	−0.31−−0.11	−0.23–0.56	1.52–2.56
Female 3 (2)								
Mean	6.00^{a}	0.44^{af}	0.33^{b}	0.17	2.43^{a}	0.28^{ae}	0.15^{aefgh}	2.31^{d}
SE	0.00	<0.01	<0.01	<0.01	0.01	0.08	0.02	0.05
Range	6–6	0.43–0.45	0.18–0.19	0.14–0.21	2.40–2.46	0.19–0.37	0.03–0.37	1.69–2.73
Female 4 (9)								
Mean	6.33^{b}	0.63^{bfgh}	0.31^{acde}	0.16^{a}	2.57^{b}	-0.08^{ef}	0.39^{eijk}	2.21^{eig}
SE	0.24	0.03	0.01	<0.01	0.09	0.07	0.02	0.03
Range	5–7	0.49–0.77	0.14–0.21	0.12–0.21	2.21–3.01	−0.34–0.34	0.00–0.62	1.52–2.82
Male 1 (13)								
Mean	5.92^{c}	0.46^{cg}	0.37	0.17	2.65^{c}	0.51^{big}	-0.04^{bifi}	2.51^{adeh}
SE	0.38	0.02	<0.01	<0.01	0.14	0.06	0.01	0.03
Range	3–7	0.31–0.57	0.18–0.24	0.13–0.32	1.57–3.13	0.11–0.79	−0.25–0.17	1.48–3.07
Male 3 (6)								
Mean	5.83^{d}	0.38^{thi}	0.34^{d}	0.18^{ab}	2.38^{d}	0.27^{c}	0.05^{eqjim}	2.48^{bf}
SE	0.54	0.03	0.01	<0.01	0.26	0.08	0.01	0.03
Range	4–8	0.26–0.46	0.15–0.31	0.15–0.23	1.45–3.38	0.11–0.57	−0.06–0.23	1.59–2.90
Male 4 (12)								
Mean	6.92^{e}	0.53^{ci}	0.35^{e}	0.16^{b}	2.98^{e}	0.28^{dg}	-0.10^{dhkm}	2.43^{sgh}
SE	0.24	0.02	<0.01	<0.01	0.11	0.05	0.01	0.02
Range	6–8	0.45–0.73	0.19–0.30	0.14–0.20	2.46–3.52	0–0.45	−0.20–0.06	1.59–2.79
P	<0.0001	<0.0001	<0.0017	<0.0007	<0.0001	<0.0001	<0.0001	<0.0001

"i i i i i"; Cramp and Simmons 1980) seem to have intersexual call differences based solely upon spectrographic structure (that is, no differences in pitch or rate). Eurasian Sparrow-hawks (*Accipiter nisus,* Cramp and Simmons 1980) seem to differ intersexually in both pitch and rate. Grey Goshawks (*A. novaehollandiae,* Brown and Amadon 1968) may be the only falconiforms exhibiting sex-specific differences in rate only. In several non-falconiform orders differences in pitch or rate represent significant sex-specific signals (Miller 1982, James and Robertson 1985, Cavanagh and Ritchison 1987, Taoka and Okumura 1990), but elements of spectrographic structure have rarely been studied.

Less than five percent of Falconiformes (13/272 extant species, Amadon et al. 1988) appear to differ in both pitch of the entire call and spectrographic structure of the component notes; features shown here for White-tailed Hawks. Included in this group are White-tailed Sea Eagles (*Haliaeetus albicilla*), Marsh Harriers (*C. aeruginosus*), Northern Harriers (*C. cyaneus*), Pied Harriers (*C. melanoleucus*), Montagu's Harriers (*C. pygargus*), Little Sparrow-hawks (*Accipiter minullus*), Sharp-shinned Hawks (*A. striatus*), Cooper's Hawks (*A. cooperi*), Black Goshawks (*A. melanoleucus*), Verreaux's Eagles (*A. verreauxi*), Crowned Hawk-Eagles (*Spizaetus coronatus*), and Merlins (*Falco columbarius*) (Brown and Amadon 1968, Cramp and Simmons 1980, Brown et al. 1982, Palmer 1988).

The unusual complexity of spectrographic characteristics found in one type of loud, long-distance communication signal, the alarm call used by White-tailed Hawks, may encode information related to sex and individual identity of the caller. Further studies, such as playback experimentation (Becker 1982, Kroodsma 1989), are needed to better understand the dimensions of this phenomenon in White-tailed Hawks and other members of the Falconiformes.

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OLD NESTS AS CUES FOR NEST-SITE SELECTION BY BIRDS: AN EXPERIMENTAL TEST IN SMALL EVEN-AGED FOREST PLOTS[1]

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Nest-site selection in birds is a function of various factors, e.g., philopatry, microclimate, degree of concealment from predators, and density and characteristics of vegetation (Welty and Baptista 1988, Gill 1990). Recently, Erckmann et al. (1990) tested experimentally whether old nests were used by Red-winged Blackbirds (*Agelaius phoeniceus*) as cues to assess the quality of habitat for placement of nest-sites ("old-nest" hypothesis). They concluded that old nests were of little or no importance as cues in nest-site selection, based on their findings that nest densities did not necessarily increase in plots containing old nests compared to plots without old nests. Moreover, Erckmann et al. (1990) recommended that the old-nest hypothesis be examined in other avian species.

Management of small (1 ha), even-aged plots for Ruffed Grouse (*Bonasa umbellus*) habitat via forest clear-cutting creates suitable habitat for an assemblage of breeding-bird species that are adapted to nesting in brushy vegetation or along edges (Yahner 1987, 1991). Several of these species, such as Gray Catbirds (*Dumetella carolinensis*) and Field Sparrows (*Spizella pusilla*), arrive on breeding grounds prior to complete leaf-out of vegetation. Furthermore, above-ground nests

established during the previous breeding season in even-aged plots can remain intact on nesting substrate into the subsequent breeding season (R. H. Yahner, pers. observ.). Thus, old bird nests may serve as indirect cues of habitat suitability to these birds when establishing nest-sites (after Cody 1985). If this were the case, then I would predict that birds arriving in spring would preferentially select even-aged plots with higher densities of old nests than those with lower densities. In this study, I tested whether numbers of nests established by birds of all species combined in even-aged plots were affected by removing or increasing the numbers of old nests from the previous breeding season.

My study was conducted on a 240-ha portion of the Barrens Grouse Habitat Management Area (HMA), State Game Lands 176, Centre County, Pennsylvania (Yahner 1991). The study area was located within the treated sector of the Barrens Grouse HMA, which was managed by the Pennsylvania Game Commission since 1976 using an even-aged system of forest clear-cutting to create habitat for Ruffed Grouse (Yahner 1991). The study area contained 60 contiguous, 4-ha blocks; each block was subdivided into four 1-ha (100- × 100-m) plots arranged in a clockwise pattern (termed plots A–D). Plot A (western plot) was clear-cut in winter 1976–1977, plot B (northern plot) in winter 1980–1981, and plot C (eastern plot) in winters 1985–1986 or 1986–1987; plot D (southern plot) consisted of 60-year-old forest stands. This resulted in a checkerboard pattern of four age classes in each block (Yahner 1991).