sible to say for sure what proportion belonged to each species, as the two species appear identical in the field. I speculate that all the adult males were *P. modesta*, because *P. subis* adult males would be expected to be in Central America or northern-most South America during this time. The adult male that I collected is definitely *P. modesta*. The single specimen of *P. subis* I collected is a juvenile male. First-year *P. subis* males normally do not breed (Allen and Nice 1952). It may be that all the *P. subis* in the Iquitos flock are such birds, which remain in South America rather than migrate north for a non-reproductive summer.

Despite the severe disruption in 1978, the birds returned in 1979 (McDowell 1979). The eugenias apparently regrew many of their branches and the artificial perches were removed.

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VARIATION IN *PEENT* CALLS OF AMERICAN WOODCOCK

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Birds are capable of identifying conspecific individuals by their vocalizations in various contexts (e.g., neighbor/non-neighbor discrimination—Weeden and Falls 1959, Goldman 1973, Brooks and Falls 1975, Falls and Brooks 1975, Harris and Lemon 1976; mate recognition—Beer 1970; parent-offspring mutual recognition—Beer 1970, Evans 1970, Stevenson et al. 1970). The basis for individual recognition presumably lies in some combination of the frequency-time-amplitude patterns of the calls and/or in the individuality of the syllable sequences in complex vocalizations. Many species use simple calls of one or few syllables and in these the former is probably the most important. Studies of variation within and among individuals (e.g., Marler and Isaac 1960, Borror and Gunn 1965, Hutchinson et al. 1968, White and White 1970, White et al. 1970) have all shown that variation within individuals is lower than that among individuals, suggesting that researchers may be able to identify individuals through laboratory analysis of their calls. However, only two studies have successfully done this. White et al. (1970) used computer matching of the amplitude patterns of calls of Sandwich Terns (*Sterna sandvicensis*). Beightol and Samuel (1973) relied on two techniques involving visual matching of sound spectrograms of *peent* calls of American Woodcock (*Philohela minor*) and statistical analysis of five measured parameters. One of us (TGD) attempted to apply the latter approach of Beightol and Samuel to a field study of American Woodcock in Maine and New Brunswick and found the technique not always capable of separating individuals in this geographic region.

Our purposes in the current study were to examine intra- and inter-individual variation in *peent* calls of territorial male American Woodcock and to attempt to identify individuals on the basis of inherent components of the calls.

METHODS

We conducted this study from 22 April to 21 May 1974 near Hanwell (45°51′N, 66°42′W), 9 km southwest of Fredericton, New Brunswick. Each evening we recorded at least nine *peent* calls from each of one or more males using a 90-cm sound parabola and microphone (Grampian Reproducers, Feltham, Middlesex, England). We standardized the distance between the bird and the microphone (9 m) and maintained an obstacle-free sound path.

Eleven recordings of nine captured and marked males were used in the analyses. The recordings were processed using a model 7029 Kay sonagraph coupled with a model 6070A contour display unit (Kay Elemetric Co., Pine Brook, N.J.; wide band filter, FL-1 circuit, 80–8,000 Hz range). The contour display unit modifies the conventional sound spectrogram to portray amplitude in seven contour intervals (6 dB apart) descending from a standardized 42 dB. Such displays provide objective frequency-time-amplitude position markers for measurements. From each spectrogram we measured five parameters. Four of these were based on the 30 dB or second contour line: (1) maximum frequency; (2) minimum frequency; (3) frequency span; and (4) duration. The fifth parameter was a measure of the area enclosed by the 24 dB (third) contour. Measurements of the first four parameters were made from a plastic overlay grid and were accurate to 0.1 cm, representing 80 Hz on the frequency scale and 7 ms on the time scale. The area measurements were made with a planimeter accurate to 0.05 cm².

To calculate the intra- and inter-individual variation for each parameter, a matrix was constructed. Each row contained values for nine calls from one bird and, hence, each column contained one call from each of nine birds. We calculated the coefficients of variation for rows to estimate the intra-individual variation (V_{intra}) and for columns to estimate the inter-individual variation (V_{inter}). We subsequently calculated the coefficient of individuality ($I = \bar{V}_{intra}/\bar{V}_{inter}$; cf. Williams 1971) to provide a relative comparison of the two measures. Values of I approaching unity indicate a random

TABLE 1. Coefficients of intra- and inter-individual variation ($\bar{V}_{intra}$ and $\bar{V}_{inter}$) and coefficients of individuality (I) for five parameters measured from calls of nine male American Woodcock.

Parameter	$\bar{V}_{intra}$	$\bar{V}_{inter}$	I
Maximum frequency	0.03	0.06	0.50
Minimum frequency	0.04	0.07	0.57
Frequency span	0.07	0.14	0.50
Duration	0.04	0.11	0.36
Area	0.10	0.25	0.40

distribution of elements in the matrix, while values approaching 0 indicate lower intra- than inter-individual variation. Parameters suitable for statistically separating individuals should have low values of I.

Parameters were evaluated with an F test (Sokal and Rohlf 1969) for normal distributions. Each parameter was then tested for significant differences between individuals ($P < 0.05$) using a one-way analysis of variance (ANOVA); individuals that did not differ significantly were grouped into subsets using Duncan's multiple range test. Three-dimensional scattergrams for all possible combinations of three parameters were also constructed to examine the separation and overlap of individuals on a multivariate level.

RESULTS

Coefficients of individuality show that for all parameters variation within individuals was lower than that among individuals (Table 1). This is notable in visual comparisons of sound spectrograms of calls from one individual with calls from several individuals.

For each parameter, F tests showed no significant deviation from a normal distribution, permitting the use of parametric statistics. While the ANOVA showed significant differences among the nine birds for all parameters, the multiple range test indicated that the differences were not sufficient to permit the separation of all individuals (Table 2). For every parameter examined certain birds did not differ significantly and in only one case were two recordings of the same individual grouped together. The same pattern of overlap among different birds and separation of successive recordings of the same bird was apparent in all of the scattergrams constructed using three parameters simultaneously.

DISCUSSION

For individual recognition to be possible three conditions must be met: (1) intra-individual variation must be lower than inter-individual variation among short call sequences; (2) birds must not vary through time; and (3) one or some combination of parameters must be equally useful in discriminating between individuals and in identifying separate recordings of the same individual.

In our study no single parameter or combination of three parameters satisfied these conditions. In all but one case, individuals varied their call components over periods of 10 and 15 days. This contrasts with the findings of Beightol and Samuel (1973), who noted no significant change in one individual over two years. The difference could be due either to the techniques (vellum tracings of the major energy bands versus contour delineation) or to real differences between the populations.

Studies of bird calls have consistently shown greater variation among birds than within birds (Marler and Isaac 1960, Borror and Gunn 1965, Hutchinson et al. 1968) and on this basis some authors have concluded that individual recognition would be possible through statistical analyses. Our results suggest caution in pursuing such simplified conclusions.

Coefficients of inter-individual variation for four parameters were less than the 0.1 level suggested by Narins and Capranica (1977) to represent an extremely stereotyped signal. American Woodcock mating behavior exhibits many of the characteristics of a lek, a situation where the extremes in sexual selection are found (Emlen and Oring 1977). Intense selection pressure on this advertisement call may result in extreme stereotypy and give rise to a situation where overlap in call components would be expected.

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TABLE 2. Summaries of Duncan's multiple range tests performed on means of (A) maximum frequency, (B) minimum frequency, and (C) duration measurements of calls from nine male American Woodcock. Means underscored by the same line are not significantly different ($P > 0.05$) while means not underscored by the same line differ significantly. Subscript letters signify separate recordings of the same individual.

A. Bird	7_b	2	9	7_a	4	8	3	5	1_b	6	1_a
X (Hz)	4,680	4,720	4,720	4,840	5,040	5,080	5,200	5,360	5,380	5,480	5,520

B. Bird	7_b	2	5	8	4	7_a	9	6	1_b	1_a	3
X (Hz)	2,480	2,720	2,750	2,800	2,880	2,920	2,920	2,960	3,120	3,160	3,200

C. Bird	1_b	5	7_b	2	9	1_a	6	4	3	7_a	8
X (ms)	115	117	117	125	129	129	137	139	139	142	154

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COWBIRD PARASITISM OF MARSH-NESTING RED-WINGED BLACKBIRDS

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While upland-nesting Red-winged Blackbirds (*Agelaius phoeniceus*) often suffer a high degree of nest parasitism by the Brown-headed Cowbird (*Molothrus ater*; Hergenrader 1962, Hill 1976, Robertson and Norman 1977), those nesting in marshes have been shown to be infrequent hosts (Nickell 1955, Friedmann 1963, Robertson and Norman 1976). Only Berger (1951) has reported more than 3% of marsh nests parasitized. Friedmann (1963) believed that the incidence of parasitism in marshes was low because most nests in marshes were built over water. I report here the highest recorded incidence of cowbird parasitism of marsh-nesting Red-winged Blackbirds.

During the summer of 1978, I studied two small populations of Red-winged Blackbirds nesting in cat-tail (*Typha latifolia* and *T. angustifolia*) marshes in the Flint Hills region of central Kansas. One of the study areas, Britt Marsh, is approximately 5 km southwest of Manhattan, Riley County, Kansas. The other, a beaver pond near Tuttle Creek Reservoir, lies 8.8 km north of Manhattan. In both areas nests were constructed over water ranging in depth from a minimum of 6.4 cm in the shallower areas at Tuttle Creek to over 50.0 cm in the deepest parts of Britt Marsh. Of 12 nests studied at Britt Marsh, all supported by *T. latifolia*, none was parasitized even though I often saw cowbirds in the area. At Tuttle Creek, where no cowbirds were seen, I found 17 Red-winged Blackbird nests; 8 in *T. latifolia*, and the remainder in woody vegetation (*Salix* spp., 5; *Cephalanthus occidentalis*, 2; *Cornus drum-*

mondii, 1; *Acer* sp., 1) at the water's edge. Of these, 52.3% (five nests in cat-tails, four in trees or shrubs) contained one cowbird egg each in addition to zero to four ($\bar{x}$ = 1.4) host eggs. All nests in cat-tails were lost to predators and only two of the remaining cowbird eggs hatched. Both nestlings survived to the age of 8 to 10 days but I do not know if either managed to leave the nest successfully. The parasitized nests contained a total of 13 Red-winged Blackbird eggs; but only six birds were fledged (0.67 birds/nest), two of which were from one of the two nests that contained a cowbird nestling. Non-parasitized nests produced 1.7 fledglings per nest.

As Shipley (1977) found no parasitism at Tuttle Creek during the 1974 and 1975 nesting seasons, why was the incidence of parasitism so high during the summer of 1978? The nine eggs were laid on different days during the period 12 June to 12 July. Since the Brown-headed Cowbird is quite prolific (Payne 1976), it is possible that all the cowbird eggs were laid by a single female. Robertson and Norman (1977) found relatively fewer nests parasitized in areas of high nest density (≥24 nests/ha) than in areas of lower density. Using this criterion, Tuttle Creek (covering an area of about 3.2 ha) would be an area of low density; one would, however, think that the blackbird population at Tuttle Creek was large enough to defend nests from a single cowbird. Friedmann (1963) and Friedmann et al. (1977), however, believed that the low incidence of parasitism noted in many Red-winged Blackbird nesting areas was due to cowbird preference for alternate hosts rather than to host aggression. Further investigation may show that marsh-nesting Red-winged Blackbirds are suitable hosts that have not been exploited heretofore.