VOCALIZATIONS AND NESTING BEHAVIOUR OF THE PACIFIC-SLOPE FLYCATCHER, *EMPIDONAX DIFFICILIS*

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ABSTRACT

Variation in vocal characteristics within a population of Pacific-slope Flycatchers (*Empidonax difficilis*) has not been described in detail. Species status of the Pacific-slope Flycatcher and the Cordilleran Flycatcher (*E. occidentalis*) has only recently been established. The Western Flycatcher (*E. difficilis*) was reclassified into these two species, partially on the basis of geographic variation in voice. This study provides a basis for comparison of this variation among populations to variation within a population of *E. d. difficilis* on the Queen Charlotte Islands, British Columbia.

Seven breeding pairs were studied in detail. Tape and written recordings of vocalizations were made on a regular basis. Inventories of the amounts and types of vocalizations produced by each bird were compiled. The context in which each vocalization was used was noted. Vocal behaviour and behaviour around the nest were observed. The date of each stage of breeding was noted.

The song of *E. difficilis* consists of three syllables presented in a semi-regular sequence. A 'Pee-ist' call is commonly inserted into this sequence. A 'Tsip' call is the most commonly heard female vocalization. Other calls include 'Chrrip', 'Ti-ti-ti', 'Weet-weet-weet', 'Seet', and 'Zeet'. Spectrograms are presented for all but the Zeet call.

Extensive variation among individuals was found in proportions of syllables (including the Pee-ist call) within song, sequence of syllables, syllable durations, intervals between syllables, and frequencies. Some variation among individuals in spectrographic form of song syllables was also noted. Significant temporal variation was found in syllable proportions, in sequence of syllables, in intervals between syllables, and in low frequencies. On the basis of these patterns of variation, I recommend protocols for gathering and analyzing vocal data used for the purpose of geographic comparison.

Singing begins shortly after dawn and declines to nil around noon. Males sing extensively before females arrive, and while females build the nest and incubate. On the basis of these patterns of variation, I recommend that population surveys on this species be conducted within three hours of sunrise and prior to the arrival of females.

Phenomena underlying variation in vocal features are investigated. The probability of two-syllable sequences appears to depend on the abundance of the second syllable of the sequence, on predilection for sequences, on the kind of syllable preceding the sequence, and on the length of the interval between syllables. Correlations among frequencies, syllable durations, and intervals between syllables are moderate.

Song appears to be used primarily in mate attraction, while Pee-ist calls are used in interactions between neighbouring males and in communication between mates. This study provides the first documentation of polygyny in this species. There is no apparent association between song complexity and mating system in *Empidonax*.

Frequencies, frequency spreads, and one interval measurement are greater than any reported previously in *E. difficilis* or in *E. occidentalis*. The physical structure of song syllables is similar to those of other *difficilis* populations described previously. Pee-ist calls, however, are less frequency-modulated than previously reported.

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Dedicated to Chantaal and Seth
the joys of my life

INTRODUCTION

A description of variation in songbird vocalizations can facilitate an understanding of the evolutionary processes shaping them. The Pacific-slope Flycatcher (*Empidonax difficilis*)[1] has a close congener, the Cordilleran Flycatcher (*E. occidentalis*), only recently classified as a separate species, partly on the basis of differences in vocalizations. Therefore, this understanding is relevant to the species' taxonomic status. Both the current taxonomic status of *E. difficilis* and the insights that may be gained from a study of variation will be reviewed here.

1. The Species

The Pacific-slope Flycatcher, *Empidonax difficilis* (family Tyrannidae), is found in thick, shaded woods, often near flowing water (Baird et al., 1874; Henshaw, 1886; Davis et al., 1963; Johnson, 1980). Such habitat is common on the Queen Charlotte Islands, where the species is ubiquitous. Because of this ubiquity, and because an island at the edge

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[1] Common and scientific names for the Pacific-slope and Cordilleran Flycatchers are from A.O.U. (1989). All other North American bird species names are from A.O.U. (1983). European bird species names are from Cramp (1977).

of a range potentially contains a differentiated population (Futuyma, 1986), Graham Island of the Queen Charlotte Islands complex was chosen as the study site.

Empidonax difficilis's breeding distribution extends from southeastern Alaska to southern Baja California along the Pacific Coast of North America, generally west of the Cascades and the Sierra Nevada (A.O.U., 1989) (Fig. 1). In British Columbia, greatest densities are found on the coast and coastal islands. Okanagan Valley population densities are lower (Johnson, 1980; Cannings et al., 1987). Interior distributions extend at least as far north as Prince George (Richard J. Cannings, pers. comm.). The Pacific-slope Flycatcher winters in southern Baja and from northwestern Mexico to the Isthmus of Tehuantepec (A.O.U., 1989).

Davis et al. (1963) and Sakai (1988) have described vocal and other behaviour associated with mate attraction, maintenance of territories, courtship, and involvement of the sexes in nest building, incubation, brooding, and feeding of the young. In the Discussion, I compare my observations with theirs. Physical aspects of breeding biology, such as nest location, number of young, and nest materials, have been described by Brewer (1879), Taylor (1890), Bent (1942), Davis et al. (1963), Sakai (1988), and Sakai and Noon (1991).

Following a 1989 American Ornithologist's Union (A.O.U.) reclassification, the Western Flycatcher (*E.*

Figure 1. Breeding distribution of species within the *Empidonax difficilis* complex. From Johnson (1980). Work in progress indicates that the complex extends also to northeastern Washington and to the central interior of British Columbia (Richard J. Cannings, pers. comm). Not shown are *E. d. insulicola* and *E. d. cineritius*.

difficilis) was divided into two species, the Pacific-slope Flycatcher (E. difficilis) and the Cordilleran Flycatcher (E. occidentalis). Incorporated into the former are the subspecies E. d. difficilis, E. d. insulicola (confined to the Channel Islands, California), and E. d. cineritius (confined to southern Baja California). Empidonax occidentalis now contains former subspecies E. d. hellmayri and E. d. occidentalis.[2] This reclassification was based on differences in voice, on morphological and genetic studies, and on observations of sympatry (A.O.U., 1989). The principal studies involved will be examined below.

1.1. Vocalizations

1.1.1. Definitions

I define 'song' and 'call' so as to have a convenient means of referring to the vocalizations of difficilis. Song is artificially distinguished from calls on the basis of elaborate or ordered structure (e.g. Thorpe, 1961; Armstrong, 1973; Hartshorne, 1973; Jellis, 1977;). Thorpe (1961:15) defined song in the following fashion:

> What is usually understood by the term song is a series of notes, generally of more than one type, uttered in succession and so related as to form a recognisable sequence or pattern in time. Thus the song as a whole displays the features of

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[2] E. d. difficilis, E. d. insulicola, E. occidentalis will hereafter be referred to as difficilis, insulicola, and occidentalis respectively.

> accent, increased duration, increased rhythmical complexity, etc. ... which are not discernible to anything like the same extent in call notes.

Song is also defined on the basis of advertising function or on pattern of use. Jellis (1977:53-54) wrote:

> Full, primary, territorial or advertising song ... is a complex, ritualized signal, of great biological importance both to the individual and the species. It is distinctive in its proclamatory function and, in most species, in its limitation to a particular part of the year.

Calls are by implication those vocalizations that are not song (Hartshorne, 1973).

A wide array of conflicting terminologies for naming parts of songs exists in the literature (reviewed by Shiovitz, 1975). These conflicts reflect the difficulty in applying terminology formed for one species to another. The following terms, used in this study, are a compromise between Shiovitz's recommendations and common usage for this species. An _element_ is a continuous trace on a sound spectrograph. A _syllable_ is an arrangement of elements that produce an impression of continuity and are separated by silences of less than 0.2 seconds.

Elements and syllables are arranged to form a _song_ (Armstrong, 1973; Thielke, 1976). The start and end points of a particular song are identified on the basis of relative intervals of time. Armstrong (1973:36), for instance, wrote that "The song is a succession of notes or groups of notes with detectable pauses between them."

1.1.2. Song[3]

Peterson (1961) described the song as consisting of three syllables ('Pseet-Trip-Seet') with variable arrangement, while Davis et al. (1963) described the song as 'Ps-seet Ptsick Seet'. Johnson (1980) maintained that the song begins with the high-frequency Seet syllable. Although I find no convincing evidence for either order, I will refer to and number the syllables according to the arrangement described by Davis et al. (1963). Some variability in syllable sequence has been described. Davis et al. (1963) noted repetitions of S3[4], omissions of S2, and insertions of Pee-ist calls between two of the S1's or between S3 and S1. Johnson (1980) stated that the songs never started with S2 (Ptsick) and that S1 never followed S2. He also noted repetitions of S1 and replacements of S3 by 'Pee-ist' calls in a population from the Channel Islands, California.

Johnson (1980) measured a variety of song-syllable frequencies, intervals, and durations. Both frequency spreads and frequencies are higher in coastal populations than in interior populations, while Channel Island populations are intermediate. S1 is longer in the interior and on the Channel Islands than on the coast.

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[3] Refer to Fig. 3 (p. 41) for this and the following section.

[4] Hereafter, syllable 1 will be referred to as S1, syllable 2 as S2, and syllable 3 as S3. Element A of syllable 1 will be referred to as E1A, and so on.

Qualitative variation in syllable form was described by Johnson (1980). The coastal version of S1 differs from the interior in that E1B has a rounded peak and rises in frequency slowly then rapidly instead of rapidly then slowly as in interior birds (on spectrograms E1B thus has a 'convex' shape in coastal birds and a 'concave' shape in interior birds). Unlike in coastal birds, E1B and E1C of interior birds are joined through emphasis of the terminal portion of E1B. As well, E1C is reduced in interior and in Channel Island birds. Finally, E1C rises in frequency more rapidly in interior than in coastal birds. The frequency sequence of S2 elements is high-low in interior birds and low-high in coastal birds. One of the two elements of S2 is often missing from Channel Island samples. Another unique feature of these island samples is that S3 tends to be inflected downward. A few interior S3's presented in Johnson (1980) rise in frequency by approximately 1 kHz, a much greater increase than found in any coastal samples.

1.1.3. Calls

Both Davis et al. (1963) and Johnson (1980) referred to the most common calls of males and females ('Pee-ist' and 'Tsit') as position notes. Davis et al. (1963) stated that 'Pee-ist' is used primarily, but not exclusively, by the male, and that 'Tsit' is exclusively female. The interior 'Pee-ist' call consists of two parts and rises steeply, whereas the coastal version forms a continually curving figure on a spectrogram (Johnson, 1980). 'Pee-ist' calls from the Channel Islands emphasize the steeply rising 'ist' portion (Johnson, 1980).

Davis et al. (1963) described three other adult calls: alarm notes, 'Chrrips', and 'Pik-pik-pik'. As with the major female vocalization, alarm notes are described as 'Tsit'. 'Chrrip' is used in aggressive contexts. The male also uses this call when exchanging positions at the nest with the female. A use of this call by the female near the nest is also described. 'Pik-pik-pik' is given by either parent when approaching the young with food.

Davis et al. (1963) mentioned a 'Peep' vocalization given by the young when approached with food.

1.2. Morphological and Genetic Features

Johnson (1980) found that coastal *difficilis*, interior *occidentalis*, and Channel Island *insulicola* populations were differentiated in size, bill shape, and three measures of breast colour. On most size measurements, coastal *difficilis* is smaller than interior *occidentalis*, while *insulicola* is intermediate.

Johnson and Marten (1988) examined genetic variation in *difficilis*, *insulicola*, and *occidentalis* populations. Their analysis showed a close relationship among *difficilis* populations. Populations of occidentalis were more loosely joined, but were generally set off from populations of difficilis or insulicola. Populations of insulicola were more closely linked to difficilis than to occidentalis.

1.3. Choice of Study Species

Empidonax difficilis was chosen as a study species for a number of reasons. First, studies of vocalizations of this particular species may have a bearing on a current taxonomic problem. Second, the vocalizations of the species are simple relative to oscine Passeriformes ('higher' songbirds). This simplicity allows repeatable measurements of features that are comparable across time, individual birds, and geographic range. The third advantage is that vocalizations in Empidonax are innate (Kroodsma, 1984). Thus, I expect that geographic and individual variation in vocalizations reflect genetic differences and not cultural ones.

1.4. Summary

In this section, I have reviewed studies of geographic variation within the E. difficilis complex. Based on differentiation in vocal, morphological, and genetic features, and on the fact that "Interbreeding has not been demonstrated conclusively...," Johnson and Marten (1988:177) concluded that *E. d. difficilis* and *E. d. occidentalis* are separate species. I have, however, two criticisms of Johnson (1980) and Johnson and Marten (1988). The first is that only one song per bird was measured (Johnson, 1980: 8). This precludes consideration of the effect of date, time, or situation on variation within individuals. These effects are considered in this thesis. My second criticism concerns the methodology used to discern assortative mating in sympatry (Johnson and Marten, 1988). Discriminant function analysis for seventeen males and eight females was said to show clear separation into interior and coastal types, with little hybridization evident. My impression of the data shown is one of continuous gradation between interior and coastal types. The conclusion of assortative mating was also based on similar discriminant function scores (based on size and colour) between members of four breeding pairs. I see two problems with this. First, the sample size is very small. Second, comparisons of scores between mates are only meaningful when compared with those of pairs drawn at random from within a small area. Further work is needed to determine the extent of assortative mating between interior and coastal populations.

2. The Genus Empidonax

The genus Empidonax contains sixteen species, including E. occidentalis (Lanyon, 1986). Species in this genus are quite uniform in appearance, with drab colours, pale eye-rings, and two wing bars (Zink and Johnson, 1984; National Geographic Society, 1987). Relationships among these species will be examined in this section.

Various and conflicting relationships among Empidonax species have been proposed. Alnorum (Alder Flycatcher) and traillii (Willow Flycatcher) were considered to be conspecific until Stein (1958, 1963) showed them to be distinct on the basis of vocal evidence. Other proposed relationships include hammondi (Hammond's) and minimus (Least) (Johnson, 1963); minimus, hammondi, oberholseri (Dusky), wrightii (Grey), and affinis (Pine) (Mengel, 1970); and hammondi, alnorum, and traillii (Shields, 1987). Difficilis and flavescens (Yellowish Flycatcher) are recognized as component species of a superspecies on the basis of similarities in morphology and vocalizations (Johnson, 1980). The only relationship consistently revealed in a study of protein variation by Zink and Johnson (1984) was between alnorum and traillii. Difficilis and flavescens were less clearly grouped. Other relationships were equally or more unclear. No pattern corresponding to the geographic ranges of the species was apparent. At the time of Zink and Johnson's study, *occidentalis* was not designated as a separate species.

Close relationships may be inferred from the maintenance of interspecific territories among species (Johnson, 1980). Interspecific territoriality has been reported in the following pairs of species: *alnorum*-*traillii* (Prescott, 1987), *occidentalis*-*oberholseri* (Johnson, 1980), *wrightii*-*oberholseri* (Johnson, 1963), and *difficilis*-*hammondi* (Johnson, 1980). A probable case of interspecific territoriality between *traillii* and *occidentalis* was reported by Frakes and Johnson (1982).

Only the western North American *Empidonax* species, *difficilis*, *occidentalis*, *oberholseri*, *wrightii*, *hammondi*, and *fulvifrons* (Buff-breasted Flycatcher), have multi-syllabic song (Johnson, 1963, 1980; Stein, 1963; Farrand, 1983). If multi-syllabic song may be assumed to be a derived character, this suggests that these species form a monophyletic group. As I have noted, however, relationships among these and most of the remaining *Empidonax* species are equivocal. Zink and Johnson (1984:213) suggested therefore that species of *Empidonax* evolved over a short period of geological time, resulting in a pattern resembling "more a 'bush' than a dichotomous sequence of cladogenetic events." If so, it would be difficult to determine the vocal affinities of the species.

3. Variation

In this thesis I describe the sources and extent of variation in vocalizations of the Pacific-slope Flycatcher. Recently, there has been an increased awareness of the importance of variation as a phenomenon and as an integral part of a complete description (e.g. Mayr, 1963; Slater, 1981; Johnson, 1982; Miller, 1986; Clark and Ehlinger, 1987; Stamps, 1991). A study of variation is based on two premises. The first is that there is insight to be gained from the pattern of variation to be uncovered, and the second is that it is reasonable to expect variation in the measured traits. Although there is some overlap in these premises, I will attempt to establish their validity separately in the following two sections. I conclude in Section 4 by describing insights that I expect specifically from this study.

3.1. Insight From Variation

Insight into function may be gained from an analysis of variation. This is based on the well-supported view that at least some variation is functional (e.g. Slater, 1981; Kroodsma and Byers, 1991). To begin to understand those functions, it is necessary to know at least the extent of the variability. As Miller (1991:144) noted, analyses of variability "reveal broad trends that may be of physiological, ecological, and evolutionary interest." Patterns of variation within and among individuals provide insight into how animals recognize both individuals and the limits of their species. Features that vary strongly among and weakly within individuals offer the potential for individual recognition. Conversely, features that vary little either within or among individuals may function in species recognition [Marler and Isaac, 1960a; Emlen, 1972; Becker, 1982; but see Miller (1982) and Nelson (1988, 1989) for an alternative viewpoint]. Insight into the function of vocalizations may also be gained from analysis of patterns of temporal variation. The well-known tendency of birds to sing primarily early in the day is one such pattern. If it was established, for instance, that territorial challenges in a given species were more common early in the day (Kacelnik and Krebs, 1983), territorial defence could be postulated as one of the functions of song in that species. Patterns of variation across contexts may also help to elucidate the function of song. Influential in this area is the message-meaning model of W. J. Smith (1963, 1965, 1977; see p.25). Numerous studies have focused on variation in vocalizations across contexts; some explicitly use Smith's model and some do not. Major examples of each type will be reviewed in the next section.

Secondly, analysis of variation may provide insight leading to appropriate taxonomic decisions. Taxonomy in the past has been strongly influenced by typological thinking (Futuyma, 1986). The primary source of typological thinking has been the Platonic philosophy of type, or "eidos", which holds that God created each of the creatures of the earth to conform to a particular type and that variability stems from the vicissitudes of the material world (Mayr, 1963; Futuyma, 1986). A more recent source of typological thinking is the notion that natural selection molds organisms perfectly to their environment (Clark and Ehlinger, 1987). An example of past typological thinking is the abundance of subspecies in ornithology (Barrowclough, 1982; Gill, 1982; Mayr, 1982; Storer, 1982; Futuyma, 1986). The naming of a subspecies implies uniformity over its range (Barrowclough, 1982). Systematic analyses of geographic variation have often rendered previously named subspecies irrelevant (Johnson, 1980; Barrowclough, 1982; Gill, 1982; Mayr, 1982; Storer, 1982). Barrowclough (1982) and Storer (1982) concluded therefore that detailed description of variation must precede categorization of taxa into subspecies. Although their argument referred to the subspecies concept, it is an equally valid point applied to higher taxa.

Since vocalizations often form the basis of estimating bird populations, appropriate survey techniques may be chosen when the pattern of variation in vocalizations is known. Emlen (1977) described a procedure for estimating population densities from transect counts. In this procedure, counts are adjusted for cue frequency (the proportion of time that a detectable cue, such as song, is produced). To make this adjustment accurately, the extent and sources of variation in cue frequency need to be known. This thesis will provide a means for estimating cue frequency and determining its variation for this species.

Insight into constraints affecting vocal behaviour may be gained from studies of variation. The above-mentioned tendency of birds to sing early in the day has been attributed to low food availability in the morning (Kacelnik and Krebs, 1983), to superior acoustic transmission (Morton, 1975; Wiley and Richards, 1982), and to early morning light levels that restrict foraging efficiency (Kacelnik, 1979). Variation in song rates has been linked to the mass of male birds at different times of the season, suggesting that a bird's current energy reserves limit its singing (Gottlander, 1987). Patterns of variation among species in song pitch and body size reveal an inverse correlation (Ryan and Brenowitz, 1985), suggesting that the latter forms a constraint on the range of frequencies available to a bird. Finally, Lambrechts and Dhondt (1988), after a study of individual variation in Great Tit (Parus major) songs, suggested that birds switch song types to avoid neuromuscular exhaustion. Analyses of variation have thus suggested diverse constraints on bird vocal behaviour.

Related to the above, studies of variation may also provide insight into selective forces shaping the vocalizations. These include predation risk (e.g. Alatalo and Helle, 1990; Ficken, 1990), species or subspecies recognition (e.g. Marler, 1957; Salomon, 1989; reviewed by Miller, 1982), avoidance of habituation (Hartshorne, 1956, 1973), environmental selection on acoustic structure (Morton, 1975; Richards and Wiley, 1980), and various forms of social selection (reviewed by West-Eberhard, 1983). Prominent in recent research, and central to understanding the evolution of bird song (West-Eberhard, 1983), is sexual selection, one form of social selection.

Sexual selection is thought to produce exaggerated and rapidly evolving characteristics (West-Eberhard, 1983). Effects of sexual selection are commonly inferred by studies that relate variation of vocalizations among species to different mating systems. For example, an examination of variation in song among species of North American wrens revealed that regularly polygynous species have songs more complex than those of monogamous species (Kroodsma, 1977). Kroodsma concluded that polygyny confers greater sexual selection on male song for variety and intensity. A contradictory pattern was found in Acrocephalus warblers (Catchpole, 1980) and in European Emberiza buntings (Catchpole and McGregor, 1985). Catchpole (1980, 1982) reasoned that since males of polygynous species do not feed the young, females of these species would choose males on the basis of territory quality. It followed therefore that males of polygynous species would have little need to advertise their personal quality, and their songs would therefore be simpler.

The effect of sexual selection on vocalizations has also been measured by comparisons of individual variation in male song with breeding success. Krebs and Kroodsma (1980) and Kroodsma and Byers (1991) reviewed this method with special emphasis on individual variation in repertoire size. Examples of this approach include Howard (1974), Catchpole (1980), McGregor et al. (1981), Greig-Smith (1982), Gottlander (1987), Reid and Weatherhead (1990) and Eens et al. (1991). Eens et al. (1991) found that among late-arriving male European Starlings (Sturnus vulgaris), those with more complex songs paired earlier and produced more fledglings. This correlation, and an experimental study of female choice, led Eens et al. (1991) to conclude that male European Starling song evolved as a result of sexual selection.

3.2. Expectation of Variation

While insight into function is something to be gained from a study of variation, function is also a reason to expect variation. For example, the importance of individual recognition (Wilson, 1975) leads to an expectation of individual variation in most species of birds. This does not imply that variation necessarily evolved for the function that it now serves or is expected to serve. Variation may arise from a variety of "nonadaptive evolutionary processes" (Clark and Ehlinger, 1987:1). Examples of these include the absence of strong selection for a particular form of a trait, an unpredictable environment (Slater, 1981), and genetic drift (Clark and Ehlinger, 1987). A second reason to expect variation in vocalizations is that past studies have shown variation to be a common phenomenon, both in other species of birds and, to a limited extent, in <u>difficilis</u>. The following review attempts to demonstrate both that variation in bird vocalizations is common and that it has been shown to serve a biological function.

Studies of variation in bird song usually consider one or more of the following types: individual, temporal, situational, geographical, and species. The first three of these, dealt with directly in this study, are more closely related to function and will therefore be described more fully.

3.2.1. Individual variation

Studies of individual variation focus either on function or on a comparison with geographic or subspecies variation. A primary function of individual variation is individual recognition, either as an end in itself or as a means of kin recognition (Falls, 1982). Researchers have sought evidence of individual recognition in contexts in which it might be presumed to be most necessary. These are recognition between mates, recognition between parent and young, and recognition of neighbours (Falls, 1982).

Individual recognition between mates has been demonstrated in colonially nesting species (reviewed by Falls, 1982). Jouventin et al. (1979) found that brooding male Emperor Penguins (*Aptenodytes forsteri*) raise their heads, call, or leave the nest in response to playback of their mates' calls, but not to those of other females. Bretagnolle and Lequette (1990) recently demonstrated that both male and female brooding Cory's Shearwaters (*Calonectris diomedea*) call when recordings of their mates' calls are played from near the entrance to their burrow.

Williams (1969) found that California Quails (*Callipepla californica*) respond differently to recorded calls of their mates than to those of same sex strangers. This demonstrated individual recognition in this species, at least to the level of distinguishing familiar from unfamiliar.

Mate recognition has been demonstrated in passerines. American Goldfinches (*Carduelis tristis*), presented with tape recordings of their mates' and other males' flight calls, solicit only in response to their mates' calls (Mundinger, 1970). Mated female Zebra Finches (Taeniopygia guttata) spend more time near the source of their mates' songs when subjected to recordings of their mates' and other familiar males' songs (Miller, 1979).

Parent-offspring recognition has also been demonstrated in colonially nesting species (Falls, 1982). Beer (1970) and Beecher et al. (1981a,b) found that parent-offspring recognition is closely attuned to a species' nesting habits and to the mobility of the young. Beer (1970) showed that Laughing Gull (Larus atricilla) chicks respond negatively to calls of non-parents only when they begin to stray beyond the bounds of the nest. Similarly, Bank Swallow (Riparia riparia) parents show a preference for recorded calls of their young only when their young are old enough to fly (Beecher et al, 1981b). Interspecies comparisons show that species with closely spaced or mobile young have the strongest parent-offspring recognition (Beer, 1970; Beecher, 1982; Falls, 1982).

Interest in the ability of birds to distinguish strangers from neighbours stems from the presumption that strangers pose a greater threat than neighbouring territory holders (e.g. Falls, 1982). Stronger responses to playback of strangers than to playback of neighbours have been demonstrated in Ovenbirds (Seiurus aurocapillus; Weeden and Falls, 1959), White-throated Sparrows (Zonotrichia albicollis; Lemon and Harris, 1974; Brooks and Falls, 1975a), Indigo Buntings (Passerina cyanea; Emlen, 1971), Field Sparrows (Spizella pusilla; Goldman, 1973), and Blue Grouse (Dendragapus obscurus; Falls and McNicholl, 1979). These results only suggest individual recognition, since discrimination in these cases may be based on familiarity. To establish individual recognition, playbacks must be repeated at different locations. A stronger increase in response to playback of the neighbour's vocalizations from the 'wrong' location (at the centre of the subject's territory or at the territory edge opposite to that shared with the neighbour in question) confirms the existence of individual recognition. This method has been used to establish individual recognition in White-throated Sparrows (Falls and Brooks, 1975) and in Common Yellowthroats (Geothlypis trichas; Wunderle, 1978).

Thus far, I have established that individual variation in voice is expected, since it is the basis for individual recognition. A survey of the literature on individual variation reveals a variety of potential bases for recognition. These include use of song types, frequency, duration of syllables or notes, duration of intervals, figure morphology (the shape of a syllable or element on a sound spectrograph), sequence of songs or syllables, and the number of elements or syllables in a given song (Table 1).

3.2.2. Temporal and situational variation

Many functions of bird vocalizations can be inferred through analysis of temporal and situational variation. These include mate attraction and stimulation, territorial defence, maintenance of contact between mates or among flock members, and avoidance of predators (Thielke, 1976; Smith, 1977). Temporal variation is across different dates and times of day, while situational variation is across different stages of breeding, associated activities, and social situations. In this section, I will describe how interpretations of function are made from analysis of such variation. As well, examples will be given of the vocal parameters considered and the categories of situations that have been formed.

Three approaches to determining the function of situational or temporal variations may be discerned in the literature. The first approach is that of message analysis as espoused by W. J. Smith (1963, 1965, 1977). The second is to interpret function from the situations in which displays are used. A third approach is to observe responses to playback of vocalizations (e.g. Ficken and Ficken, 1973; Jarvi et al., 1980; Martin, 1980; Kramer et al.,1985; Simpson, 1985; Piersma and Veen, 1988; Rothstein et al., 1988; Bretagnolle, 1989; Dabelsteen and Pedersen, 1990; Stone and Trost, 1991). Elements of the first two approaches are used in this thesis and therefore will be

Table 1. References of studies of acoustic features potentially used in individual recognition in birds.

Dimension of Variation		Reference[a]
Use of song types		4,14,17,19
Frequency		5,6,8,10,12,13,15,16,18,24,25,26,27
Duration:	syllable/note	1,5,12,13,15,16,18,20,21,27
	interval	1,2,3,5,6,11,12,13,19,20,21
Figure morphology		1,2,3,5,6,9,10,12,22
Sequence		2,3,4,6,7,17,23
No. elements/syllables		1,4,10,13,17,18,19

[a] 1 Beer, 1970; 2 Emlen, 1971; 3 Emlen, 1972; 4 Ficken and Ficken, 1973; 5 Goldman, 1973; 6 Lemon and Harris, 1974; 7 Verner, 1974; 8 Brooks and Falls, 1975a,b; 9 Shiovitz, 1975; 10 Lein, 1978; 11 Jouventin et al., 1979; 12 Beecher et al., 1981a,b; 13 Schroeder and Wiley, 1983a,b; 14 Ritchison, 1985; 15 Sieber, 1985; 16 Baker and Bailey, 1987; 17 Derrickson, 1988; 18 Nelson, 1988; 19 Ritchison, 1988; 20 Bretagnolle, 1989; 21 Bretagnolle and Lequette, 1990; 22 Kreutzer, 1990; 23 Martin, 1990; 24 Taoka and Okumura, 1990; 25 Weary, 1990; 26 Weisman et al., 1990; 27 Weary, 1991

discussed here.

Smith's message-meaning model holds that displays provide information about the identity and characteristics, including probable behaviour, of the communicator. Such information is the message of the display. Meaning, defined as the "response selected by the recipient from all of the responses open to it," is derived from both the message and the context in which the signal is given (Smith, 1965:406). Context is "anything which can be thought of as accompanying a signal" (Smith, 1965:405). A display's functions are the consequences of the response(s) to the display on the fitness of the signaller and the display recipient(s) (Smith, 1977). Thus, the meaning of a display, judged by the recipient's responses, must be identified before its function may be determined, and only limited inferences may be made about function from knowledge of the message of the display (Smith, 1977). In studies that adopt Smith's approach, emphasis is placed on determining the information made available by the display (Smith 1969, 1970a, 1970b, 1988; Smith et al., 1978; Payne, 1979; Schroeder and Wiley, 1983b; Hill and Lein, 1985; Riska, 1986; Trainer, 1987; Howes-Jones and Barlow, 1988). Because the response of the recipient may not be apparent, it is difficult to determine the meaning of a display (Smith 1963; 1977), and consequently, Smith's approach does not emphasize inferences about function. For example, in a study on Yellow-throated

Vireos (Vireo flavifrons), song forms that predominated during nest-centred behaviour became less predominant as the birds moved away from the nest, and were thought to signal a "readiness to interact and a greater likelihood of trying to confront an opponent" (Smith et al., 1978:873). Because the authors did not know whether listening vireos use the information made available to them, they did not speculate about the function of this variation in use of song types.

Payne (1979) followed Smith's approach to determining the information content of a species' song types, but contrary to Smith (1977), maintained that the function of a signal is most readily determined from the behavioural changes of the signaller that accompany the signal. His concept of function, therefore, is akin to Smith's concept of message. In this concept, song types that are temporally associated with certain behaviours function in signalling the likelihood of those behaviours.

Studies by Schroeder and Wiley (1983b), Hill and Lein (1985), Riska (1986), Trainer (1987), and Howes-Jones and Barlow (1988) follow Smith's emphasis on message decoding, but venture further than Smith (e.g. 1969; 1970a,b; 1988) in inferring function. Hill and Lein (1985), for instance, used Smith's methodology to establish that the message of the trill call of male White-crowned Sparrows (Zonotrichia leucophrys) pertains to a probability of attack, but went further than would Smith by suggesting that the male trill functions in territorial defence. Conclusions about functions of this and two other calls were also based on physical structure of the calls in accordance with theories about the relationship between motivation and the physical structure of vocalizations formed by Morton (1977).

The second approach to determining the function of variation is to infer function directly from the situations in which a display is given (e.g. Thompson, 1972; Baptista, 1978; D'Agincourt and Falls, 1983; Gaddis, 1983; Logan, 1983; Howes-Jones, 1985; Johnson, 1987; Derrickson, 1988; Ritchison, 1988; Highsmith, 1989; Montgomerie and Thornhill, 1989; Staicer, 1989; Nelson and Croner, 1991). A variation on this approach is to infer function from the times at which a display is given (e.g. Catchpole, 1973; Holmes and Dirks, 1978; Kroodsma and Verner, 1978; Gottlander, 1987; Ritchison et al., 1988; Rotella and Ratti, 1988; Kroodsma et al., 1989; Morse, 1989; Ganey, 1990). Inferences based on the times at which a display is given are inconclusive since the biological needs of a species may be only loosely related to time of day or date.

A variety of modes and sources of variation has been found to occur in bird vocalizations. Modes of variation include song type, versatility, temporal dimensions, vocalizing rate, recurrence interval, amount of song, percent of birds or groups vocalizing, and repertoire (Table 2). A number of terms in Table 2 warrant explanation.

Table 2. Studies of situational variation. Vocalization variant refers to the aspect of vocalizations found to vary, and situational dimension refers to the situations which are correlated with those variations. See text for further definitions.

Vocalization variant	Reference[a]
Song types/categories	1,3,7,11,13,14,16,17,19,20,22
Number of syllables/song	13
Versatility	5,6,12,20
Temporal	1,5,6,9,12,13,21
Vocalizing rate	1,4,5,9,10,14,17,20
Recurrence interval	12
Amount of song	1,2,8,13,15,21
% of birds/groups vocalizing	2,15

Situational dimension	Reference[a]
Stage of breeding	2,6,8,9,12,13,16,17,20,21
Date	2,4,10,13,14,15,21
Time of day (or night)	2,4,5,6,10,12,15,16,17,19,21,22,22
Song: Spontaneous--exchange	1,5,7,11,13,20,21,22
Proximity to male	3,6,17
Proximity to female	3,9,14,16,17
Proximity to nest	7,9,11,13
Location on territory	13,20
No. of females on territory	6
Lunar activity	21
Weather	10,21

[a] 1 Thompson, 1972; 2 Catchpole, 1973; 3 Baptista, 1978; 4 Holmes and Dirks, 1978; 5 Kroodsma and Verner,1978; 6 D'Agincourt and Falls, 1983; 7 Gaddis, 1983; 8 Logan, 1983; 9 Howes-Jones, 1985; 10 Gottlander, 1987; 11 Johnson, 1987; 12 Derrickson, 1988; 13 Ritchison, 1988; 14 Ritchison et al., 1988; 15 Rotella and Ratti, 1988; 16 Highsmith, 1989; 17 Kroodsma et al., 1989; 18 Montgomerie and Thornhill, 1989; 19 Morse, 1989; 20 Staicer, 1989; 21 Ganey, 1990; 22 Nelson and Croner, 1991

Versatility incorporates both variety of sequence and number of different song types (Kroodsma and Verner, 1978). Temporal dimensions describe lengths of songs, song bouts, and syllables, and the lengths of intervals between these. Vocalizing rate is the rate of presentation in a song bout, lasting on the order of minutes, while the amount of song is the prevalence of singing behaviour over a longer period of time. Recurrence interval is the "number of other song types occurring between two bouts of the same song type" (Derrickson, 1988:593). Studies listed beside 'Song: spontaneous--exchange' examine how song changes when given spontaneously and when given in exchanges with other males.

A few of the studies cited in Table 2 will be briefly discussed to illustrate how inferences about function are made. Ritchison (1988) examined song variation in Northern Cardinals (Cardinalis cardinalis). The amount and complexity of song were found to remain high after the arrival of the female and until after the nest was built, ruling out setting up territories or attracting mates as the sole function of complex song. Ritchison (1988) suggested therefore that complex song also helps to maintain territories or to stimulate mates. As well, complex song during close interactions with other males was said to communicate a high level of excitement or likelihood of interacting.

Correlation of changes in song with the arrival or presence of a female is often cited as evidence for an intersexual function of song. Catchpole (1973) found that, after the arrival of a female, Sedge Warblers (Acrocephalus schoenobaenus) cease singing entirely, while Reed Warblers (Acrocephalus scirpaceus) continue to sing around sunrise and sunset. This was given as evidence that Sedge Warbler song functions primarily in sexual attraction, while Reed Warbler song has a greater role in territorial defence (Catchpole, 1973, 1982). Kroodsma et al. (1989) found that, early in the season, unpaired Chestnut-sided Warbler (Dendroica pensylvanica) males primarily sing accented-ending (AE) songs, but use unaccented-ending (UE) songs when near other males. After pairing, use of UE song increases, but when near the female, the male uses AE songs only. This suggested an intersexual role for AE songs and an intrasexual role for UE songs.

3.3. Summary

This section reviewed the value of examining variation in bird song. The potential insights to be gained and the reasons why variation should be expected as a general phenomenon were discussed. Finally, the particular features of song that are expected to vary and thereby serve various functions were cited.

4. Objectives

The primary purpose of this thesis is describe the vocalizations of a population of _E_. _difficilis_ on the Queen Charlotte Islands. As a basis for this description, observations of the breeding biology of this species are presented. This description of vocalizations includes physical structure, use, song syllable sequence, intervals between syllables, duration of syllables, and frequencies. Extent and sources of variation, and phenomena underlying it, are described. Sources of variation considered are date, time of day, stage of breeding, and individual differences. This description is expected to:

1. Provide a basis for comparison across the geographic ranges of _E_. _difficilis_ and _E_. _occidentalis_. The major study of geographic variation in this complex to date does not consider the effect of date, time, or stage of breeding on the vocal measurements taken (Johnson, 1980).
2. Provide a framework for a standardized population survey procedure for this species. Specific consideration must be given to the expected extent of vocalizations at different times of day or at different dates.
3. Provide insight into the definition of a song in

this species.

4. Provide insight into the function of, constraints on, and evolution of *E. difficilis* vocalizations. Since this is not specifically a study of any of these, inferences will, by necessity, be speculative.

METHODS AND MATERIALS

1. Study Site

The study was conducted on Graham Island, Queen Charlotte Islands, British Columbia (131° 56' W, 53° 35' N). The study site was located near the junction of Provincial Highway 16 and Geikie Creek, approximately 10 km SE of Port Clements.

2. Field Procedures

Seven breeding pairs were studied in detail (Fig. 2). The male of each territory was observed in the portion of the territory in which he sang (Fig. 2) for one hour three times per day, on every second or third day. During sampling periods, the male's (and female's or neighbour's, if present) vocal behaviour was noted continuously. As well, each bird's location was noted relative to marked and numbered trees. During each hour-long observation, two 3-5 minute tape recordings and two 5-minute written recordings of vocalizations were made.

The nest at site A3 was observed daily for one hour or more from initial stages of construction to fledging. Other nests were observed for one hour every second or third day (Section 2.3).

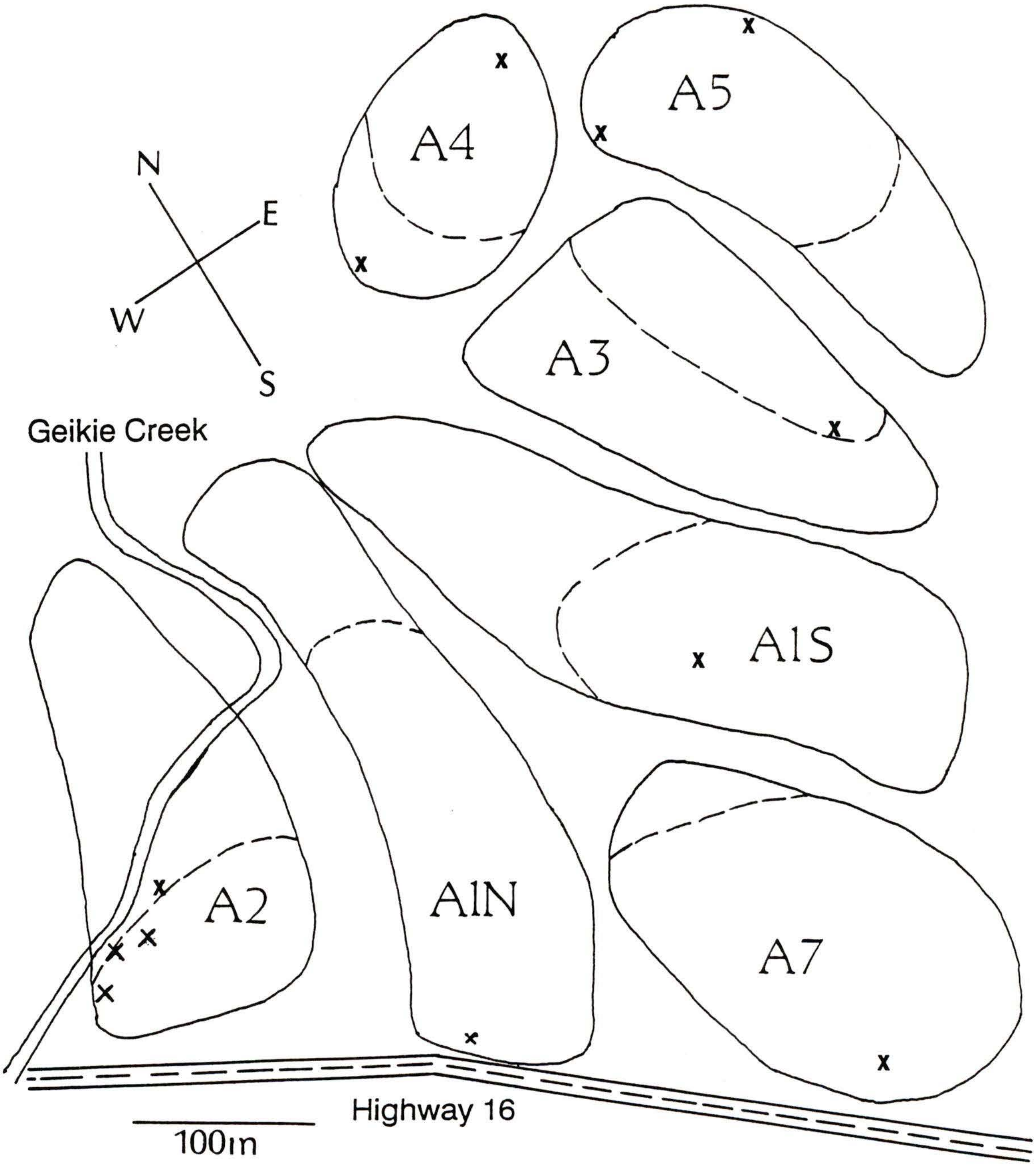

Figure 2. Map of study site showing seven bird territories. X marks nest locations. Dashed lines delineate territory limits prior to the arrival of females. After the female's arrival, males sang on the portion of the territory beyond this dashed line.

2.1 Vocal Inventories

Inventories were made of vocalizations given by each bird during each stage of breeding and through the course of each day. To obtain these inventories, vocalizations were monitored in the song area of each territory according to the following guidelines.

a. The 'predominant vocalization' is defined as the vocalization (song or one of the calls) that was judged to comprise 75% or more of 'utterances'. Each song syllable and each call is an utterance. Song syllables were recorded under the single category of song. Utterances that were not of the predominant vocalization type for a given time period are 'exceptions'.

b. At the start of observation, the predominant vocalization and the time, to the nearest minute, were noted.

c. When the predominant vocalization changed, the time of the change was recorded to the nearest minute.

d. The predominant vocalization was recorded as 'silence' if there were fewer than four utterances per minute.

e. Exceptions to the predominant vocalization type were counted. The number of these was recorded at the end of each minute. For example, if between 11:00 and 11:01, two 'Tsips' (see Results: 1.3) were heard while 'Pee-ist' (see Results: 1.2) was the predominant vocalization, the field record would read '11:00 Pee-ist; Tsip (2)'.

f. 'Ti-ti-ti' calls (see Results: 1.3) were occasionally produced in extended continuous bouts of greater than 10 seconds. The length in seconds of such a bout was noted.

g. 'Pee-ist' calls were not noted as exceptions to song if they comprised less than 25% of the utterances within song. In that case, they were considered to be part of the song. If they comprised 25-75% of utterances within song, neither song or Pee-ist was judged to be predominant (see step h).

h. When no vocalization was judged to be predominant, a mixture was noted (e.g. Song + Pee-ist). If a vocalization was estimated to comprise approximately 25% of vocalizations, it was noted as 'occasional' (e.g. Song + occasional Pee-ist).

The method described here yields an approximate vocal inventory. A more accurate inventory would have been obtained by counting the vocalizations. This was impractical, however, because of the long observation periods used (i.e. 1 hour). This length of sample was necessary because vocalizations were produced intermittently (e.g. 20 minutes of vocalization and 10 minutes of silence), so shorter observation periods would not have yielded a representative vocal inventory at a given time. The method described here allowed observers to monitor vocal performance while noting the bird's location and while making tape and written recordings of vocalizations.

2.2. Recording Technique

Tape recordings for spectrographic analysis were made using a cassette tape recorder (Sony Stereo Cassette-corder WM-D6C) and a directional microphone (Sony ECM-Z200). Written recordings were made by assigning a unique code to each song syllable and call type and recording these on paper. Written recordings were used in analysis of syllable proportions and sequences.

2.3. Nest and Fledgling Observations

Vocalizations and behaviour of males, females, and young around the nest were recorded in detail. Approximately 120 hours of such observations were made. Locations of males and females relative to the nest were continuously noted. Other recorded behaviour included nest construction, arrival at and departure from the nest, and feeding of nestlings or females. Observations of fledglings were done in a similar fashion. In these observations, the location of fledglings was also noted.

The height of each nest was determined. A compass was used to estimate the angle formed between the line of sight to the nest and the ground, and the distance from the observation point to the base of the tree was measured with a measuring tape. Nest height was then calculated using trigonometric relationships.

3. **Data Analysis**

3.1 Vocal Inventories

The proportion of each vocalization in each of 477 hour-long samples was calculated by dividing the number of minutes that a vocalization was given by the total number of minutes in the observation period. The number of minutes that each vocalization was given was tallied as follows.

a. Where no exceptions were noted, each minute that a vocalization was predominant was counted as 1 minute towards that vocalization's tally.

b. One to four exceptions of a given vocalization type, produced in the span of 1 minute, were counted as 15 seconds for that type. Five or more exceptions given in the span of 1 minute were counted as 30 seconds. These amounts were deducted from the tally of the predominant vocalization. Consider, for example, a one minute period in which song is the predominant vocalization and six 'Chrrips' (see Results: 1.3) are recorded as 'exceptions'. Since five or more exceptions count as 30 seconds, Chrrips would be assigned 30 seconds. This amount is deducted from the 1 minute in which song was the predominant vocalization, leaving 30 seconds to be assigned to song.

c. When silence predominated, each utterance was counted as 15 seconds for that vocalization type.

d. Where a mixture of two vocalizations was noted (e.g. song + Pee-ist), each was assigned 50% of the time. If a mixture of three vocalizations was noted, each was assigned 33% of the time. Where one of the mixture was noted as 'occasional', it was assigned 25% of the time. For example, if a given minute had song + occasional Pee-ist, 45 seconds would be assigned to song and 15 seconds to Pee-ist.

e. Where bouts of Ti-ti-ti vocalizations were noted, the length of time for that bout was added directly to its tally.

A mean proportion of each vocalization was calculated for each bird, at each time of day (to the nearest hour), and at each of four stages of breeding (pre-female, courtship, nesting and incubation, and post-hatching).

3.2. Spectrographic Measurements

Spectrographic measurements were made on song syllables and the Pee-ist call. Sound spectrograms were prepared, and frequencies and syllable durations were measured on a personal computer, using the CSL^{tm} Computerized Speech Laboratory (Model 4300, Version 3.00; Kay Elemetrics Corp., Pinebrook, New Jersey). Frequencies were measured using a 72 Hz analyzing filter bandwidth, while syllable durations were measured using a 549 Hz bandwidth. Blackman window weighting was used for all measurements and displays. Sound spectrograms were produced using a 143 Hz analyzing filter bandwidth.

Intervals between syllables were measured with a Uniscan II Model 4600 FFT Real Time Spectrum Analyzer, located at the University of British Columbia.

Spectrographic measurements are illustrated in Fig. 3. Throughout this paper, S1 refers to syllable 1, S2 refers to syllable 2, and S3 refers to syllable 3. Similarly, E1A means element A of syllable 1, and so on (see Introduction for definitions of syllable and element). See Appendix A

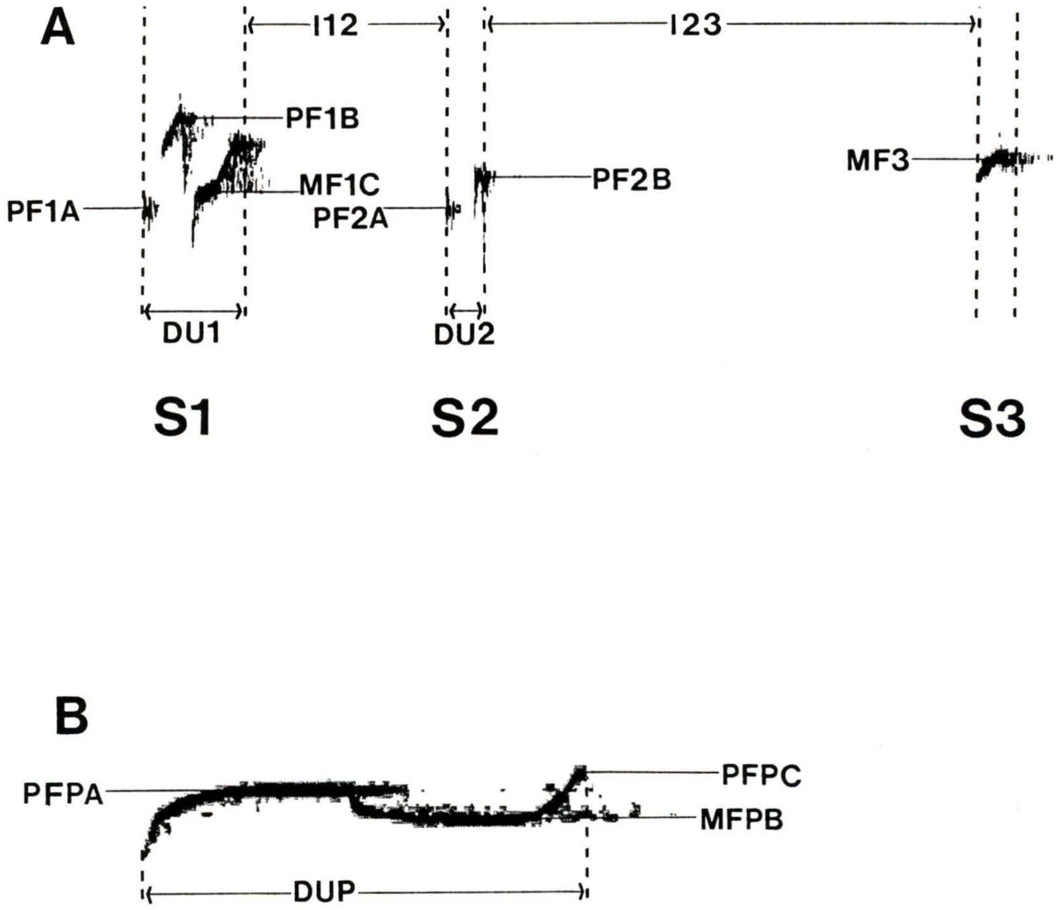

Figure 3. Frequency, interval, and duration measurements of three song syllables (A) and the Pee-ist call (B). Vertical dashed lines mark the beginning and end of each song syllable and the Pee-ist call. I consider portions of song syllables and Pee-ist extending beyond these lines to be echo.

for definitions of the measurements.

Because tape recordings were made in a dense forest, echo is apparent at the end of spectrographic figures (Fig. 3). I distinguished vocalization elements and echo by the greater diffuseness of the latter's spectrographic trace. This required the use of some judgement, and therefore echo was a source of measurement error on temporal measurements. Based on my confidence in that judgement, I estimate the uncertainty of duration measurements to be 3 msec and that of interval measurements to be 30 msec. I estimate the uncertainty of frequency measurements to be 50 Hz.

Nine samples of tape recordings per bird were analyzed, where available (Appendix B). These were chosen from all combinations of early, mid, and late morning (Times 1, 2, and 3 respectively) and early, mid, and late breeding season (Dates 1, 2, and 3 respectively). As much as possible, Time 1 samples were from 0 to 3.1 hours past sunrise, Time 2 samples were from 3.2 to 5.6 hours past sunrise, and Time 3 samples were from 5.7 or more hours past sunrise. Date 1 samples were from April 28 to May 22, Date 2 samples were from May 23 to June 17, and Date 3 samples were from June 18 or later. Where more than one recording was available, the one closest to the mid-point of the Date and Time definition was analyzed.

Within each of the nine samples of each bird, four of each song syllable and four Pee-ist calls were measured.

The value on a measure for a sample was thus the mean of four measurements. Intervals between the first 30 vocalizations of each sample were measured. The value on interval measures I12, I23, I31, and I13 for a sample was the mean of repeated measurements.

Values for each bird on spectrographic measurements are the mean of each bird's nine samples (Table 10).

3.3 Qualitative Descriptions of Physical Structure

Qualitative descriptions of physical structure are based on the spectrograms presented in this thesis and on spectrograms produced on the Uniscan Real Time Spectrum Analyzer.

3.4. Syllable Proportions and Transition Probabilities

Nine samples per bird of written recordings, each consisting of 5 or more minutes of song performance, were analyzed where available (Appendix C). These were chosen in the manner described in Section 3.2. Only the three song syllables and Pee-ist were considered in this analysis. The proportion of time that each vocalization was followed by each of the four vocalizations was calculated for each sample. These proportions are referred to as transition probabilities. Syllable proportions were calculated by counting the numbers of each vocalization type in each sample.

Values for each bird are the mean of five samples from each bird (Tables 6,8). Abbreviating Date and Time as D and T respectively, these samples are D1,T3; D2,T1; D2,T2; D2,T3; and D3,T1. These samples were chosen because they were the only ones available for all birds. By restricting the samples analyzed, I obtained comparable values for each bird. For the same reason, values for each Date and Time (Table 7, Fig. 16) are based on birds A1N, A1S, A2, A3, and A7 only.

The proportion of time that each combination of two syllables was followed by each of the four vocalizations was also calculated for each sample. For example, the proportion of time that each occurrence of S1-S2 was followed by S1, S2, S3, or a Pee-ist call was calculated. These proportions are referred to as second-order transition probabilities. Each data point in Fig. 34 is the mean of the 59 available samples.

3.5. <u>The Relationship of Transition Probability to Syllable Proportion</u>

The probability of occurrence of any transition is partially a function of the abundance of the second syllable of the transition. The following was used to provide a measure of the tendency to produce a transition independent of the proportion of the second syllable:

$$(T-S)/S^{1/2}$$

In this expression, T = transition probability and S = proportion of second syllable in sample. The square root of S was calculated to make the expression less sensitive to small values of S. This in turn produced numbers which could be more clearly graphed. The values provided by this expression are referred to as 'chi-values' in this thesis because of their similarity to the formula for chi-square analysis of contingency tables (Zar, 1984). Mean chi-values for each bird, Date, and Time were calculated in the fashion described for transition probabilities and syllable proportions (Section 3.3).

3.6. The Relationship of Transition Probability to Interval

The relationship of transition probability to interval is illustrated graphically (Figs. 18-33). For each Date, Time, or bird, all intervals up to 3100 msec were classified into 100 msec groups and the transition probabilities within each group were calculated. For example, if there were 70 S1-S2, 20 S1-S3, and 10 S1-S1 transitions that had intervals between syllables of 300 to 400 msec, the probabilities for these transitions at the 350 msec interval would be 70%, 20%, and 10%, respectively.

3.7. Statistical Methods

The SYSTAT_R (version 5.01) statistical package was used to perform all calculations, except where indicated.

3.7.1. Individual variation

For each measure on which individual values are given (syllable proportions, transition probabilities, chi-values, spectrographic measurements), the ratio of the coefficient of variation (C.V.) among individuals to the mean C.V. within individuals was calculated. This ratio provides a measure of individuality in each measure. Jouventin et al. (1979) have previously used this technique.

3.7.2. Syllable and Pee-ist proportions, transition probabilities, and chi-values

Randomization tests (NPSTAT, version 3.01. Copyright, University of Victoria, 1990) were conducted to determine if there were significant differences among Times or Dates in syllable proportions, first- and second-order transition probabilities, and chi-values.

3.7.3. Spectrographic measurements

Repeated-measures ANOVAs were done to determine the significance of the association between date or time of day and each of the spectrographic measurements. This was done according the procedure described by Lorch and Myers (1990). Regression coefficients given in Table 11 are the mean regression coefficients from regressions done separately on each bird for each measure. Date and time were treated as continuous variables in this analysis. Date was coded as the number of days since the start of the study (i.e. April 28 was coded as '1', April 29 as '2', and so on.), while time is the number of hours since sunrise.

Cluster and Principal Components analyses were conducted to determine the correlational structure of the spectrographic measurements. Varimax rotation was used in the Principal Components Analyses; factors retained had eigenvalues greater than 1.0. Cluster analyses used the average linkage method (Sokal and Sneath, 1963) and Pearson's product-moment correlation coefficients as the similarity measure.

Cluster and Principal Components analyses were each done twice, once on a matrix of correlations among variables based on mean individual values and once on a matrix of correlations among variables based on mean values from each combination of Date and Time.[5] The former was done to determine how variables are correlated among individuals, and the latter was done to determine how variables are correlated among times.

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5. These matrices are presented in Appendix D.

3.7.4. Determination of sample size for comparison of populations

Coefficients of variation among individuals found in this study were used to determine appropriate sample sizes for comparison of the means of two populations on a given measure. The method of calculation is described in Zar (1984:134-138). The pooled variance of two populations is used in the calculation, and therefore it is necessary to assume that the variances of the two populations are equal. Recommended sample sizes are based on the assumption that the sample sizes collected from two populations will be equal.

3.7.5. Graphs

Graphs were prepared using the SYGRAPH graphing program, available in the SYSTAT statistical package (version 5.01).

RESULTS

I noted ten kinds of vocalizations, eight by adults and two by chicks. The most common vocalizations of adult males are 'song' and 'Pee-ist'. The most common vocalization of females is 'Tsip'. Both sexes give 'Chrrip' and 'Ti-ti-ti' calls less frequently. 'Weet-weet-weet', 'Zeet', and 'Seet' calls are given rarely. Chick vocalizations include 'Sip' and 'Rasp' vocalizations. In Section 1, I describe the physical structure of all but the Zeet vocalization, while in Section 2, I describe the breeding biology of this species and the use of vocalizations in breeding. In Section 3, I describe the arrangement of song syllables and Pee-ist within a song performance. Finally, in Section 4 I describe frequency, duration, and interval measurements of song syllables and the Pee-ist call.

1. Physical Structure of Vocalizations

In this section, I provide qualitative descriptions of the physical structure of vocalizations. Some frequency measurements, not dealt with in Section 4, are given here in approximate form.

1.1. Song Syllables

Song consists of three syllables, each of which in turn comprises from one to three elements. S1 consists of three elements, occurring in fixed sequence (Fig. 4). E1A is of low amplitude and so often shows up weakly on spectrograms. It begins with a rapid rise in frequency then slowly declines (A1S, A4, A5, A7). It is brief (<25 msec) and relatively low in frequency (ca. 4-5 kHz). E1B is longer (ca. 75 msec). It begins at approximately 6-7 kHz and rises to approximately 8 KHz, then drops abruptly by 2-3 kHz. In birds A5 and A7, the ascending portion rises slowly at first and then more rapidly, while in bird A1N, the rise is initially more rapid and ends more slowly. The peak of E1B in birds A5 and A7 is sharp, and in birds A1N and A3 it is relatively blunt. This latter feature may be an artifact of the recording conditions. E1C begins at approximately 4 kHz, rises abruptly, holds steady at approximately 5 kHz for a short time, then rises again to around 6.5 kHz. It is approximately 160 msec in duration. E1C of A1N is exceptional in that there is no portion in which the frequency does not increase. The middle portion of this element in birds A2 and A3 declines slightly in frequency before rising again. E1B and E1C are clearly separated in all birds.

The frequency spread of S1 for the seven males shown in

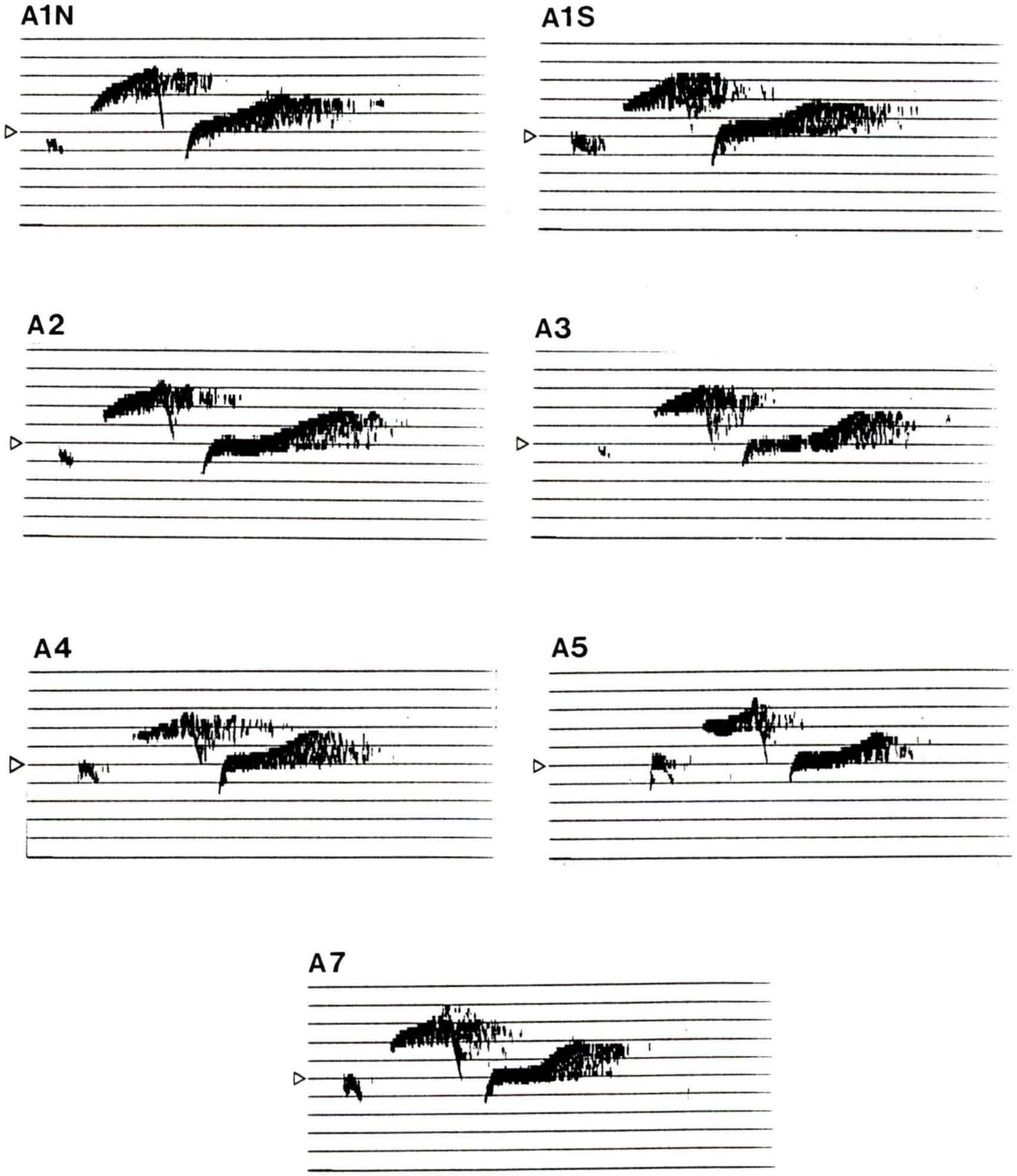


Figure 4. Spectrograms of S1 in seven male Pacific-slope Flycatchers. Frequency is from 0 to 10 kHz; each spectrogram is 500 msec long. Horizontal lines mark 1 kHz. Triangles mark 5 kHz.

Fig. 4 averages 4.9 kHz (range 4.4-5.4 kHz). The mean frequency spread of E1C is 3.5 kHz (range 2.8-4.0 kHz).

S2 consists of two elements in fixed sequence. E2A is very similar to E1A (Fig. 5). E2B is qualitatively similar to E2A, but is higher in both frequency (ca. 5.5 kHz) and amplitude. It is also longer in duration (ca. 30 msec). In all birds, the descending portion is longer than the ascending portion.

S3 consists of a single high-frequency element, approximately 100 msec long (Fig. 6). S3 begins at about 7 kHz then rises slightly in frequency (ca. 0.5 kHz), emphatically in birds A1N and A4. S3 occasionally declines slightly in frequency. This is evident in the spectrograms of birds A2 and A3, but was common only in bird A2 (Fig. 6).

1.2. Pee-ist Call

Pee-ist is of high amplitude and consists of one element (Fig. 7). It is similar to E1C in initially rising in frequency and then changing only gradually for a period of time. After the first peak, the frequency declines by 0.5 to 1 kHz before rising, sharply in birds A1S and A3. Individuals vary in the particulars of this call. In male A1S, the call declines abruptly in frequency at the mid-point of the element. The first ascending portion is longer in male A1N than in the other birds. There is little change

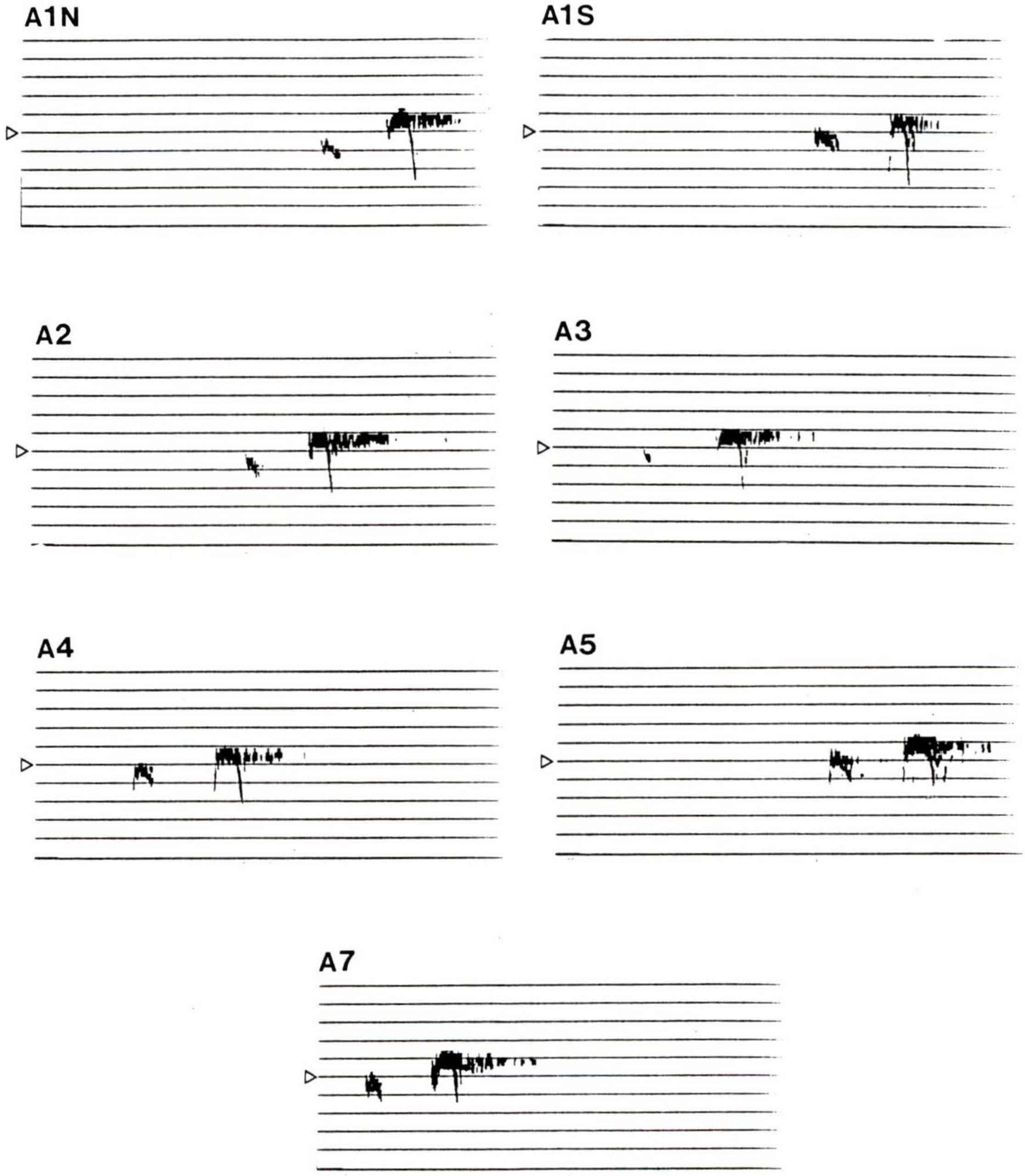


Figure 5. Spectrograms of S2 in seven male Pacific-slope Flycatchers. Frequency and time scales are as in Fig. 4.

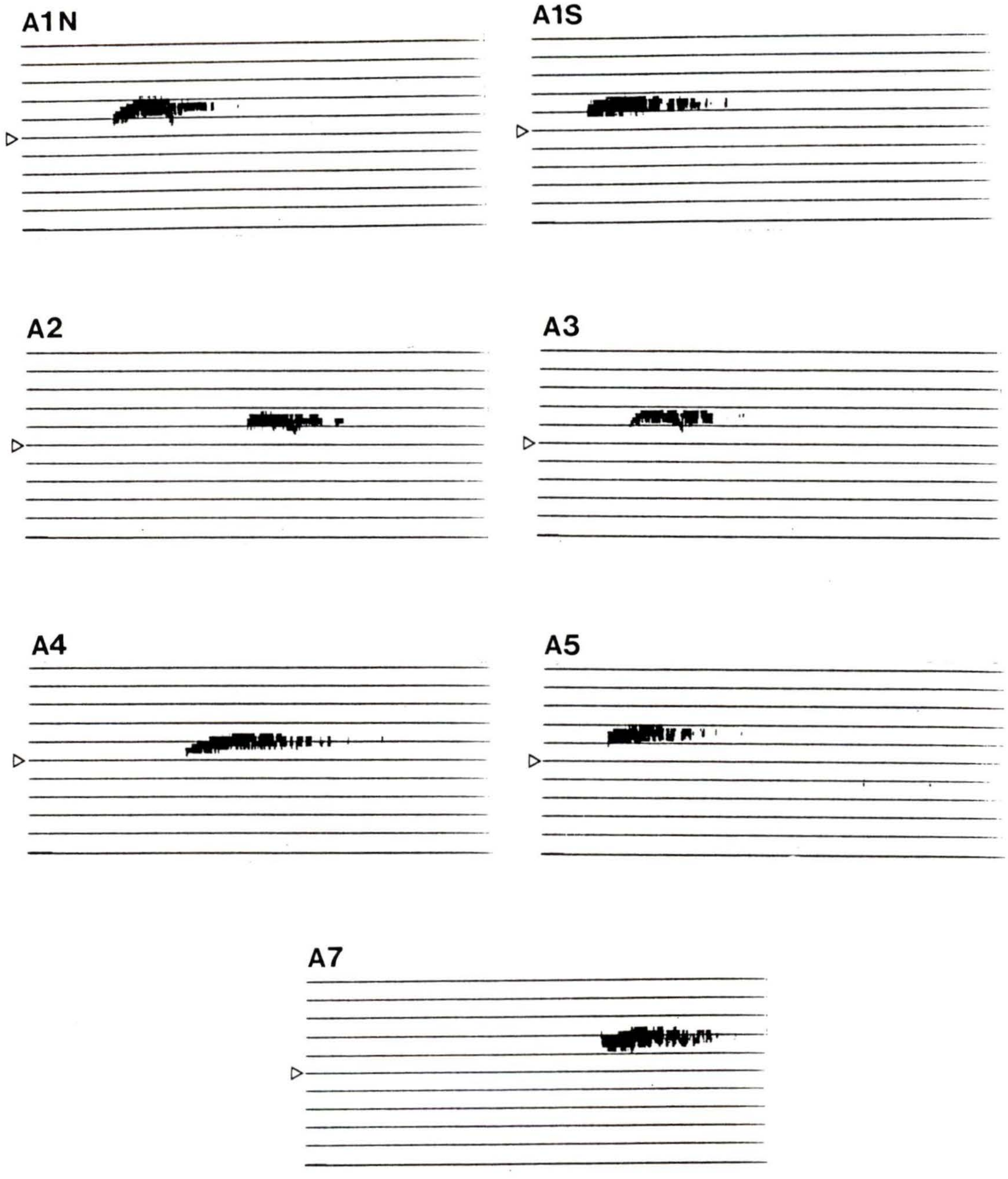


Figure 6. Spectrograms of S3 in seven male Pacific-slope Flycatchers. Frequency and time scales are as in Fig. 4.

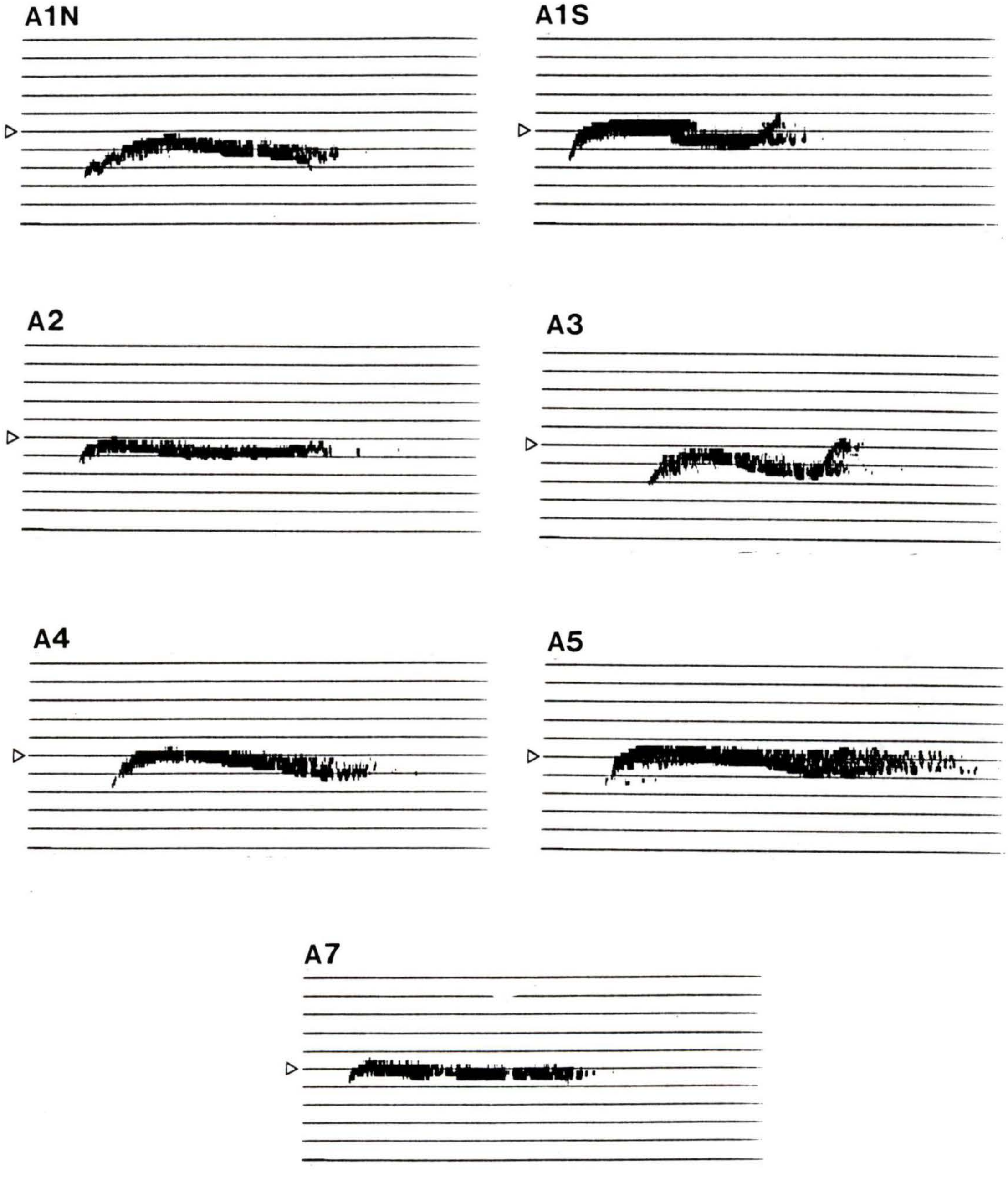


Figure 7. Spectrograms of the Pee-ist call of seven male Pacific-slope Flycatchers. Frequency and time scales are as in Fig. 4.

in frequency over the course of this call in birds A2, A5, and A7.

1.3. Other Calls

The Tsip vocalization sounds similar to S3, and can be distinguished from it by ear only with practice (Fig. 8). Tsips are, however, 0.5-1.0 kHz higher in frequency than S3. Unlike S3, Tsip begins by descending in frequency by 0.5 to 1.0 kHz. The frequency then remains relatively constant at approximately 7 kHz or, more commonly, rises to near the starting frequency. The duration of Tsip calls is difficult to determine because of the echo present in the spectrograms of Fig. 8. It appears to be somewhat less than 100 msec in length.

The Chrrip call consists of a number of elements given rapidly over a few seconds (Fig. 9). There are at least two types of elements. Type 1 rises sharply in frequency by 2 to 3 kHz and then declines less sharply by 1.5 to 2 kHz. It is approximately 15 msec long. Type 2 rises sharply in frequency by as much as 5 kHz then declines sharply by up to 3 kHz; it is less than 10 msec long. The frequency of these elements ranges from 1.5 to 7.0 kHz. Type 1 elements are preceded and followed by intervals of approximately 75 msec, while the intervals preceding and following type 2 elements are less than 10 msec.

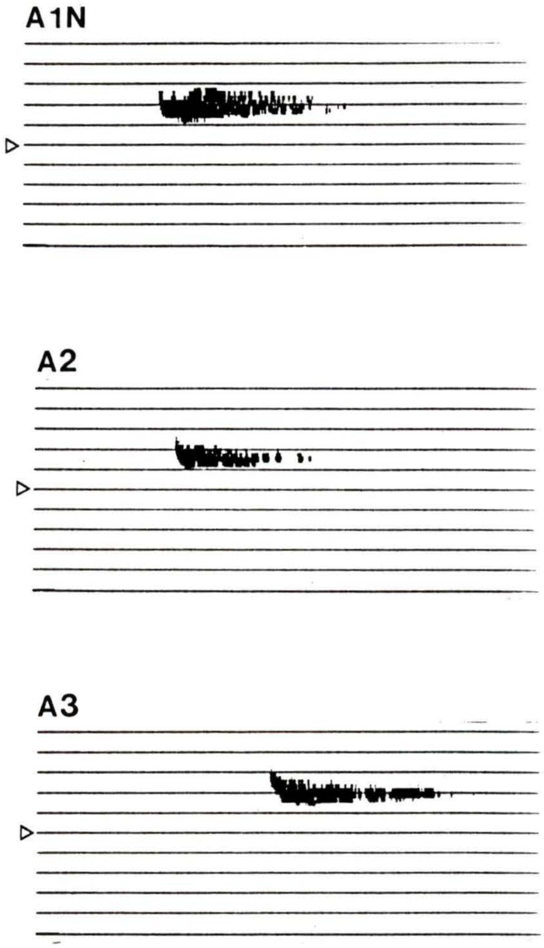


Figure 8. Spectrograms of the Tsip call in three female Pacific-slope Flycatchers. Frequency and time scales are as in Fig. 4.

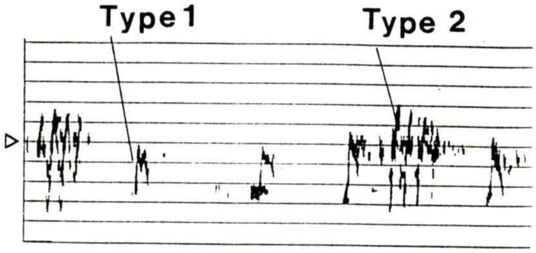


Figure 9. Spectrogram of a portion of the Chrrip call of A1N. Frequency and time scales are as in Fig. 4. Marked are two types of elements found in this call.

The Ti-ti-ti call also consists of elements given rapidly (Fig. 10). These are usually produced continuously for a few seconds, but may last for up to a minute. These elements are of two types. Type 1, centred at approximately 6.6 kHz, strongly resembles S3. Type 2, occurring between 2 and 5 kHz, is similar to the type 1 Chrrip element described above (Fig. 9). The type 1 Ti-ti-ti element occurs singly, while type 2 occurs in groups of 2 or more. Each element is separated by intervals of 40 to 120 msec. Note also in Fig. 10 the inclusion of two S2's in the 5 second sample of Chrrip. The relationship between Ti-ti-ti and Chrrip is illustrated in Fig. 10 by an unusual Ti-ti-ti call that includes elongated elements, similar to type 2 Chrrip elements.

The Weet-weet-weet call consists of a string of similar elements, typically three, with intervals of about 200 msec (Fig. 11). These resemble S3 in duration (ca. 100 msec), and in the fact that they rise slightly in frequency (ca. 0.5 kHz) and then hold steady. Unlike S3, they are centred around 3.0 kHz in frequency. Intervals between elements are approximately 120 msec long.

The rarely heard Seet call is similar to E1C in frequency, duration and form (Fig. 12). After the initial rise in frequency, however, frequency declines by approximately 0.5 kHz before the final increase in frequency. In this respect, it resembles the Pee-ist call.

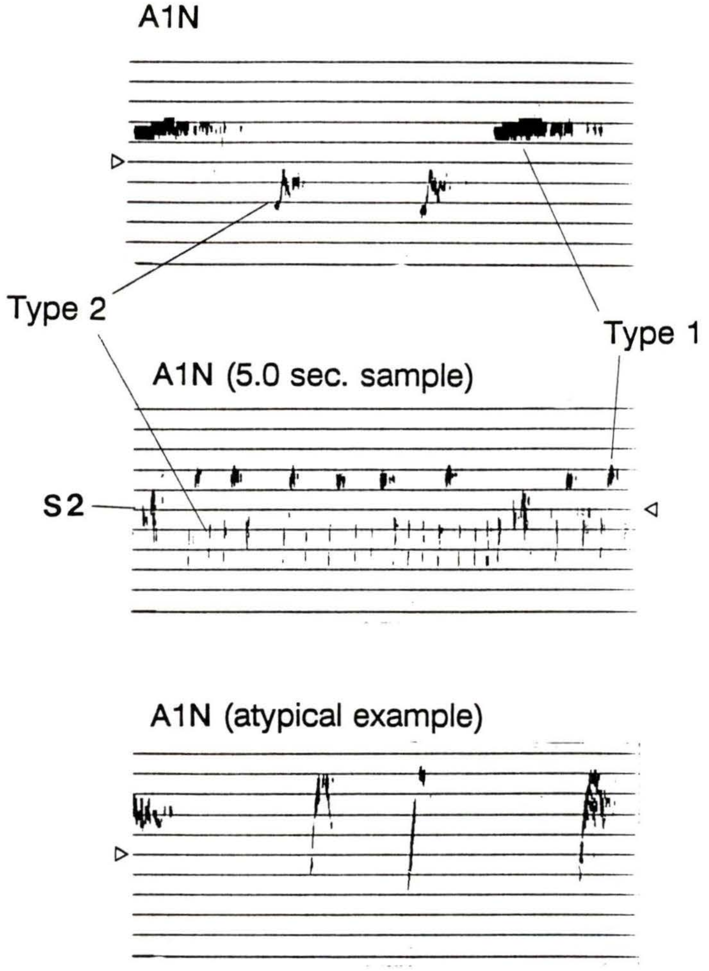


Figure 10. Spectrograms of portions of the Ti-ti-ti call. Frequency and time scales are as in Fig. 4 except where indicated. Marked are two types of elements found in this call.

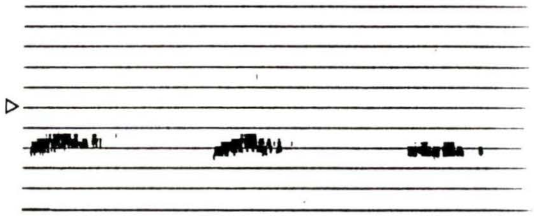


Figure 11. Spectrogram of the Weet-weet-weet call of A1S. Frequency and time scales are as in Fig. 4.

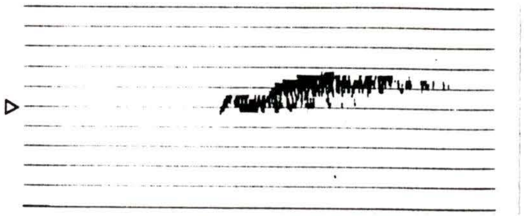
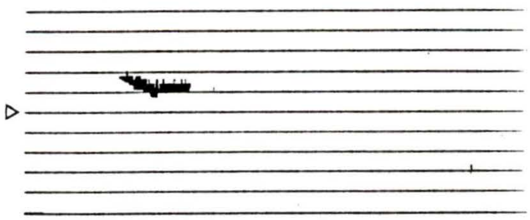


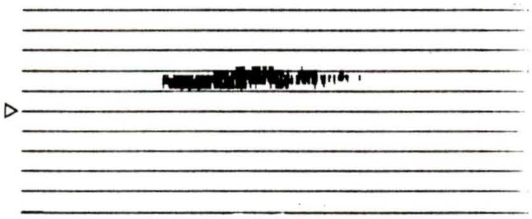
Figure 12. Spectrogram of the Seet call of A4. Frequency and time scales are as in Fig. 4.

Two types of vocalizations were heard from chicks (Fig. 13). Sip resembles either the adult Tsip or S3 in frequency, duration, and shape, but is of lesser amplitude. The Rasp vocalization is similar in form to Ti-ti-ti. That is, it consists of single high-frequency elements, separated by groups of elements that have wide ranges of frequency. It is an extremely soft vocalization.

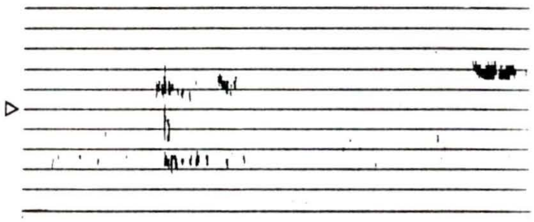
Sip (A1S)



Sip (A1S)



Portion of Rasp (A1S)



Portion of Rasp (A1S, 5.0 sec. sample)

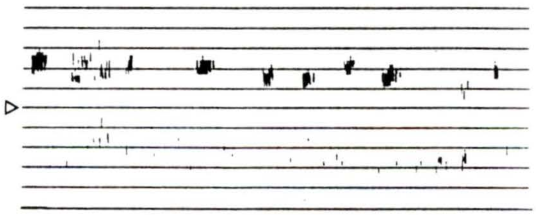


Figure 13. Spectrograms of chick vocalizations. Frequency and time scales are as in Fig. 4, except where indicated.

2. Breeding Biology

The breeding cycle of the Pacific-slope Flycatcher may be divided into six stages: pre-female, courtship, nest construction, incubation, brooding, and post-fledging. Male and female behaviour during each of these is described below. The emphasis will be on vocal behaviour and other behaviour that has a direct influence on vocal performance. As well, I will describe the duration and dates of occurrence of each stage, and note exceptions to the general pattern.

2.1. Stages of Breeding

2.1.1. Pre-female

During this stage, males sing almost continuously for the first two or three hours after sunrise (Fig. 14).[6] Thereafter, the amount of song gradually declines until ceasing about ten hours past sunrise (1:00 p.m.). Variation from this pattern is common. Bird A1N, for example, sang for only 63% of the time from 6:40 to 7:00 a.m. on May 5, and bird A5 sang continuously from 11:40 a.m. to 12:07 p.m. on May 14. On one occasion, a brief song performance was

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[6] Two observations were made of the first vocalization of the day. First vocalizations were 19 and 24 minutes past sunrise. In the first instance, Pee-ist calls were given for 3 minutes before song began. Vocalizations began with song in the second case.

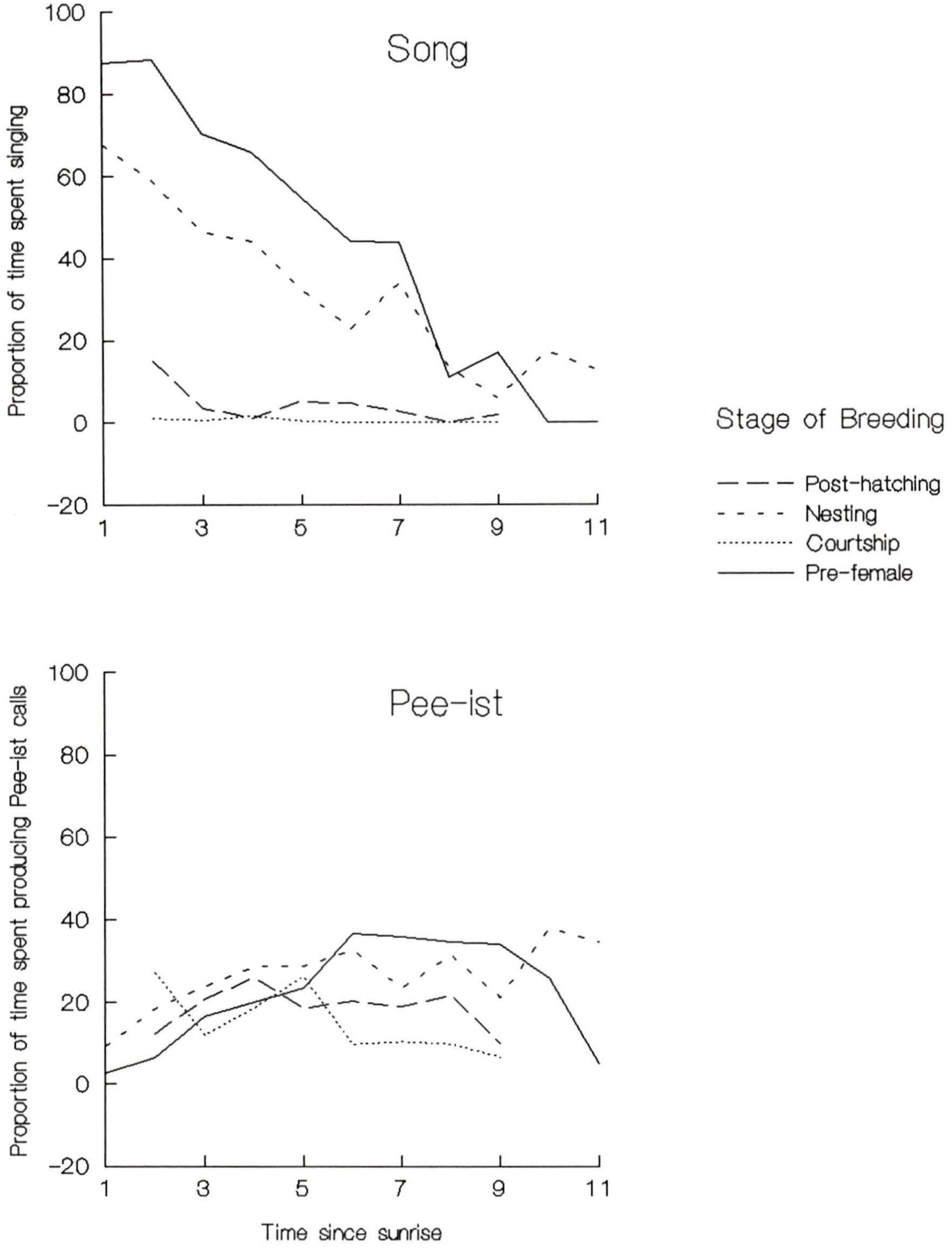

Figure 14. Song and Pee-ist production at different times of day and stages of breeding. Plotted are the mean of seven birds. 'Nesting' includes nest construction and incubation.

heard past 3:00 p.m.. With the partial exception of bird A2, which often sang into the early afternoon, variation could not consistently be attributed to particular birds. For example, on May 11, bird A5 displayed the opposite extreme to that reported above. From 6:59 to 8:00 a.m. on that date, he did not sing at all over the course of an hour. Variation among individuals in proportion of time singing and producing Pee-ist calls is summarized in Table 3. Of note are the relatively low levels of variability in song production early in the morning during the pre-female and nesting stages.

Males typically sing for up to half an hour, or occasionally longer, at one end of their territory, then fly directly to the opposite end and repeat the performance there. As examples, bird A7 went to one end of its territory and back four and a half times in 1.5 hours on May 25, while bird A1S did so seven times in 5.5 hours on May 3. Movements of up to 10 metres while the bird is singing at one end of its territory are frequent. Five to ten movements per minute are typical, although stationary spells of up to a minute are also common.

Pee-ists are commonly incorporated into song performances (see Section 3). Use of Pee-ists outside of song gradually increases until six hours after sunrise, holds steady for three hours, then declines until ceasing at eleven hours past sunrise (Fig. 14). Pee-ist calls are

Table 3. Variability among individuals in time spent singing and producing Pee-ist calls. Figures given are mean coefficients of variation among individuals for the group of times indicated.

	Time Since Sunrise (hrs) 1-3	4-6	6-10
Song			
Male alone	0.21	0.37	0.95
Courtship	1.15	1.34	2.23
Nesting	0.31	0.66	1.04
Chicks	1.45	1.92	2.66
Pee-ist			
Male alone	0.86	0.55	0.69
Courtship	0.53	0.76	1.14
Nesting	0.60	0.54	0.54
Chicks	0.59	0.95	1.33

associated with two general activities. The first is vocal exchange with a neighbouring male. In response to the vocalizations of a neighbour, a singing bird typically switches to Pee-ists, accompanied by one or more of the other calls discussed below. Frequently, males exchange Pee-ists for several minutes before one becomes silent or moves away. Pee-ist calls also occur shortly after physical contact between birds. The second general activity associated with Pee-ists is flight. In one sample of song, consisting of 882 song syllables and 73 Pee-ist calls, 31 of 39 flights of various lengths (generally < 10 m) were immediately preceded or followed by Pee-ists.

Ti-ti-ti and Chrrip vocalizations are occasionally given during this stage. Chrrips are strongly associated with situations that may be construed as 'aggressive'. These include vocal exchange at territorial borders, physical contact with conspecific birds, and chasing of other species of birds [e.g. Townsend's Warbler (Dendroica townsendi), Varied Thrush (Ixoreus naevius)]. While Ti-ti-tis occurred during vocal exchanges between neighbouring males, most were given by lone birds, very often in association with flights of less than 10 m and with Pee-ists. Ti-ti-tis are most common between one and four hours after sunrise.

Tsip vocalizations are rarely heard before females arrive, a consequence of the fact that males rarely give this call. Tsips are given by males both in response to a neighbour's song and in situations of no apparent provocation.

2.1.2. Courtship

During the most intense early stages of courtship, physical contact, displacement from perches, and chases are very common. Virtually every call in the species' repertoire is produced at this stage. While maintaining vocal contact, the female primarily gives Tsips and the male gives Ti-ti-ti, Pee-ist, or Tsip calls. Physical aggression is often accompanied by these calls and always by Chrrips. Both the attacker and the attacked bird are liable to call. Both sexes initiate chases, displacement, and physical contact. All of the above calls are used at least occasionally by both sexes during courtship.

During courtship, a variety of less common calls were heard. A Weet-weet-weet was given by a male in the apparent absence of its mate. A Zeet was given by one or the other bird in the course of a brief mid-air entanglement. A Seet was given while the birds were perched 7 metres apart.

Singing virtually ceases during courtship (Fig. 14). Between six and nine hours after sunrise, Pee-ists are given less frequently in courtship than they are before the female arrives on the territory.

2.1.3. Nest building and incubation

Nests are constructed and incubated by the female. They are placed in a hollowed-out portion of a tree or at the base of a large branch, and are constructed primarily of moss and cedar twigs. The height of nests varies from 6 to 27 metres.

During the first few days of nest construction, interactions between male and female are similar to those of the courtship stage, but involve fewer chases and less physical contact. From about the third day of nest construction and during incubation, males resume singing in a diurnal pattern similar to that of the pre-female stage, but with slightly less song in the morning and slightly more in the early afternoon (Fig. 14). Males at this time extend those parts of their territories that are distant from the nest, and sing only there. Pee-ists are used on this new song portion of the territory about as frequently as prior to the arrival of the female (Fig. 14). Pee-ist, Chrrip, and Ti-ti-ti calls are used on the song territory in contexts similar to those of the pre-female stage.

Periodically, males return to the nest site and give a few Pee-ists. Females respond with Tsip or, rarely, Pee-ist calls just before or after leaving the nest. Rarely, females remain in the nest (during incubation), either silently or calling softly while the male calls. When females leave or arrive at the nest in the absence of the male, they only utter Tsips. Again, this call is sometimes given in the nest before departure or after arrival. Chrrip and Ti-ti-ti calls are occasionally given around the nest during incubation.

The time spent by males near the nest is highly variable. During nest construction, visits are generally less than a minute long and occur approximately every 20-30 minutes.[7] While females are incubating, nest visits last from 2-20 minutes and are about 10-50 minutes apart.

2.1.4. Brooding and feeding of nestlings

Only females brood the young. Both parents feed the nestlings, and, accordingly, the male stops singing very soon after the eggs hatch (Fig. 14). The start of this stage marks the last time in the season that males sing.

Both males and females call extensively around the nest while the female broods. The following general description of parental feeding behaviour starts with the female sitting quietly on the nest. Males fly to within 10 metres of the nest and give Pee-ists; females are silent during this, but sometimes respond with Tsip or Ti-ti-ti calls. After 2-5 minutes, the male flies silently to the nest and feeds the young, occasionally giving Ti-ti-ti calls while doing so.

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[7] Since the male was not consistently vocalizing during the nest construction stage, it is possible that the male was silent and near the nest for longer periods than those reported.

This takes less than ten seconds. The female leaves the nest while the male calls and before he approaches the nest. If she leaves just as the male is arriving, one or the other gives a Chrrip call. Feeding lasts about 5 seconds, then the male moves to about 10 metres away and gives Pee-ists for up to 5 minutes. Females vary in their Tsip calling while off the nest. Some call rarely, while others call almost every time they are off the nest. Females return to the nest within 5 minutes in the first 3 days of brooding, and often feed the young before beginning to brood. Females do not always leave the nest when the male approaches. In those cases, the male transfers the food to the female and she feeds the young. Often, one bird or the other produces a Chrrip call during the exchange. At about 3 days after the eggs hatch, females spend progressively less time on the nest. At 8 or 9 days after hatching, brooding stops entirely. At this time, the pattern of vocal behaviour changes. Vocalizations by both sexes before and after feeding decline to one or two calls, and silent visits become progressively more common. Although aggression (chases and physical contact) between the sexes after brooding ends is generally rare, there are occasional chases with Chrrip calls. Within a day or two before fledging, the nestlings begin to produce soft Sips.

2.1.5. Post-fledging

Both sexes continue to feed the young after fledging. In one case, the female stopped feeding the young before the male did. Later observations suggested that this female stopped feeding in order to re-nest (see Section 2.2.3).

For the first week after fledging, the young spend much of their time huddled together on a branch, rarely moving. After that time, they move more frequently, more distantly, and more independently of one another. Foraging attempts by the young were observed in two different territories eight days after fledging.

Parental vocal behaviour after fledging is similar to that of the post-brooding nestling stage. Both males and females commonly call just before or after feeding the young, but just as often feeding is done silently. The chicks, however, are quite vocal. Between feedings, fledglings produce soft Sips continuously. During feeding, and for about a minute after, fledglings increase their rate of calling. Fledglings produce a quiet Rasp vocalization while being fed.

2.2. Variation in Breeding

To follow some of the material in the present section, it is helpful to recall the correlation of male vocal performance with stage of breeding. Briefly, the male sings before the female arrives, stops during courtship, resumes singing during nest construction and incubation, and stops again at the start of brooding.

2.2.1. Nest destruction

There were five instances of destroyed nests in the seven observed territories. Three were in one territory (A2), and two were in separate territories (A4 and A5). Two of the nests were likely destroyed by stormy weather, and others were probably depredated. One nest may simply have been abandoned after being constructed, since no damage was apparent. Nests were destroyed at stages ranging from during construction to approximately 12 days after hatching.

After a nest was destroyed, females constructed a new nest in four of the five cases. Female A2 began to build within 1 day of the previous nest's destruction in three cases, while female A5 began within 5 days. On three occasions, the nest was destroyed at a stage in which the male was not singing. In these, the males started singing when reconstruction began. On one occasion the nest was destroyed at a stage in which the male was singing. In this case, the male continued uninterrupted. All nests were constructed in different locations than previous ones.

2.2.2. Polygyny

The female that did not rebuild (see Section 2.2.1) was the second mate of male A4. At the time of nest destruction, brooding at male A4's first nest had just begun. Accordingly, this male did not sing at any time after his second nest was destroyed. This was the only observed instance of polygyny.

When the first female of site A4 began nest construction, the male started singing in the typical way in the end of his territory distant from the nest site. At about the time when the first female began incubating, a second female was observed in the song portion of the territory. During this second courtship, the male stopped singing and only resumed singing when the second female had finished construction of her nest and while the first female was still incubating. All this occurred over a period of five days, after which the male expanded his territory in a second direction, away from both nests.

2.2.3. Renesting

I observed one renesting after fledging of a first brood. As noted above (Section 2.1.5), the female at this site (A1S) ceased feeding the first set of fledglings about 12 days after fledging, while the male fed the fledglings for an additional 11 days. The second nest was not discovered until very near the end of incubation, but if the incubation period was of typical length, the female would have begun incubation 2 days after ceasing to feed the first brood. The second brood was raised in the same nest as the first.

2.3. Breeding Dates

The difficulty in finding nests and the five occasions in which located nests were destroyed precluded direct observation of the start and finish of each stage of the breeding cycle in many cases. The durations given in Table 4 are based on those observations that were made directly. The start and finish of each stage of the breeding cycle for the remaining birds was pieced together from indirect evidence. For example, infrequent feeding forays were characteristic of the first few days after hatching, and so if there was little feeding at a newly located nest, I inferred that the nestling stage had recently begun. These estimates are given in Table 5.

Table 4. Duration of stages (in days) of the breeding cycle based on direct observations at four sites.

Breeding Stage	Site A3	A4	A7	A1S	Mean
Nest building	8	6			7
Off-nest[a]	4	6			5
Incubation	16	13	16		15
Nestlings - Brooding	9	12		7	9
Nestlings - Post-brooding	7	3		9	6
Fledglings	17	18		23	19
Total	61	58			61

[a] Off-nest includes the time between completion of nest construction and the start of incubation.

Table 5. Starting and finishing dates (month/day) of key stages in the breeding cycle at the seven territories.

		Breeding Stage			
Site	Female Arrival	Nest Building	Incubation	Nestlings	Fledglings
A1N	5/13	6/05-6/12	6/17-7/05	7/06- ---[a]	---
A1S	---[a]	5/13-5/19	5/20-6/05	6/06-6/21	6/22-7/14
	---	----	7/06-7/20	7/21- ---[a]	---
A2	5/10	5/15-5/17[b]	---	---	---
	---	5/18-5/26[b]	---	---	---
	---	5/27-5/30	5/31-6/16	6/17-6/25[b]	---
	---	6/26-6/29	6/30-7/15	7/16- ---[a]	---
A3	5/11	5/13-5/20	5/25-6/10	6/11-6/26	6/27-7/13
A4	5/16	5/21-5/26	6/02-6/14	6/15-6/29	6/29-7/16
	6/02	6/04-6/09	6/14-6/16[b]	---	---
A5	5/15	5/20-5/27	5/27-6/11	6/12-6/20[b]	---
	---	6/25-7/01	7/02-7/16	7/17- ---[a]	---
A7	6/13	6/16-6/23	6/24-7/10	7/11- ---[a]	---

[a] Date could not be determined.
[b] nest destroyed

3. Arrangement of Syllables Within Song

3.1. Proportions of Syllables Within Song

S1 and S3 were the most common syllables in the song performances analyzed (Table 6). Pee-ists commonly occurred in song performances.

Proportions of S2 and Pee-ist within song are each more variable within and among birds than are proportions of S1 and S3 (Table 6). Only the ratios of C.V. among individuals to C.V. within individuals associated with S2 and S3 are greater than 1.0. The ratio associated with S1 is moderate (0.7-1.0).

Proportions of syllables at different dates and times of day are shown in Table 7. Late in the day, the proportion of S2 declines and the proportion of Pee-ist increases. No other effect of time of day, and no effect of date, was detected.

3.2. Sequence of Syllables Within Song

Proportions of each of the sixteen possible first-order transitions are illustrated in Fig. 15 and summarized in Table 8. As might be expected by the names of the syllables, S1 is most commonly followed by S2, S2 is almost always followed by S3, and S3 is often followed by S1.

Table 6. Proportions of syllables used within the song performance of each bird.

				Bird					(A) C.V.[b]	(B) C.V.[c]	
Syllable	A1N	A1S	A2	A3	A4	A5	A7	Mean[a]	Among	Within	A/B
S1	33.1	34.3	34.4	32.3	37.5	34.5	36.5	34.7	0.052	0.067	0.78
S2	17.8	16.4	26.0	23.0	29.2	21.5	13.2	22.6	0.267	0.201	1.33
S3	36.5	35.5	30.9	39.1	29.5	37.6	41.3	35.8	0.119	0.072	1.65
Pee-ist	12.5	14.3	8.7	5.6	3.8	6.4	9.1	8.6	0.435	0.776	0.56

[a] Mean is of the seven individual means.
[b] 'C.V. among' is among the seven individual means.
[c] 'C.V. within' is the mean of seven within-individual C.V.'s.

Table 7. Temporal variation in proportions of song syllables and Pee-ist calls within song.

	Syllable[b]			
Date/Time[a]	S1	S2	S3	Pee-ist
Date 1	33.6	21.2	38.6	6.51
Date 2	35.1	20.1	36.2	8.60
Date 3	34.0	18.9	35.8	11.3
Time 1	34.7	24.1*	37.5	3.64*
Time 2	34.0	20.2*	36.7	9.08*
Time 3	34.0	16.0*	36.4	13.7*

[a] Dates 1-3 are April 28-May 22, May 23-June 17, and June 18 or later, respectively. Times 1-3 are 0-3.1, 3.2-5.6, and 5.7+ hours past sunrise, respectively.

[b] * Randomization test indicates significant among-group differences ($p<0.05$).

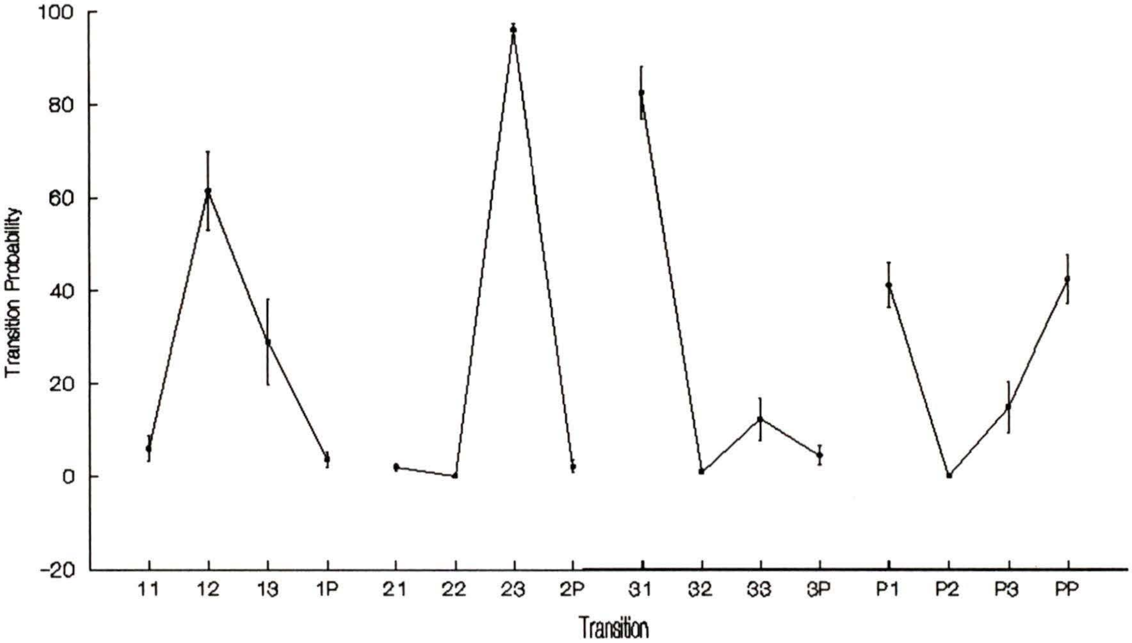

Figure 15. Probabilities of first-order transitions between syllables (1=S1, 2=S2, 3=S3, P=Pee-ist). Plotted are $\bar{y}$±s.d. for the seven individual males.

Table 8. Summary of first-order transition probabilities (in %) between vocal elements for individual males.

Trans-[a] ition	A1N	A1S	A2	Bird A3	A4	A5	A7	Mean	(A)[b] C.V. Among	(B)[b] C.V. Within	A/B
11	4.7	4.7	7.5	4.7	17.1	1.1	5.0	6.4	0.794	0.670	1.19
12	54.2	48.7	75.3	71.4	79.3	60.5	36.2	60.8	0.256	0.193	1.33
13	31.9	42.2	15.1	20.6	3.2	36.8	53.4	29.0	0.592	0.444	1.33
1P	9.2	4.4	2.1	3.3	0.5	1.6	5.4	3.8	0.768	1.017	0.76
21	0.2	0.0	4.7	1.8	0.9	1.1	1.3	1.4	1.053	1.828	0.58
22	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	---	---	---
23	97.4	92.5	92.8	97.8	97.1	99.0	97.2	96.3	0.026	0.040	0.65
2P	2.4	7.5	2.4	0.4	2.0	0.0	1.5	2.3	1.074	1.338	0.80
31	70.8	81.2	93.8	72.5	97.6	87.7	75.6	83.9	0.128	0.081	1.58
32	0.2	0.7	0.7	0.0	0.0	1.3	0.0	0.4	1.198	1.319	0.91
33	18.4	11.2	3.6	24.8	0.7	9.1	16.7	12.0	0.703	0.713	0.99
3P	10.6	6.8	1.9	2.7	1.6	1.9	7.7	4.7	0.754	0.863	0.87
P1	45.0	50.7	30.7	31.0	52.5	46.1	36.4	41.7	0.217	0.568	0.38
P2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	---	---	---
P3	17.4	10.2	14.0	15.3	0.0	16.1	34.4	13.5	0.669	0.908	0.74
PP	37.6	39.1	55.3	53.7	47.5	37.9	29.2	42.9	0.222	0.699	0.32

[a] 1=S1, 2=S2, 3=S3, P=Pee-ist
[b] See Table 6.

Pee-ist is usually followed by S1 or by another Pee-ist. S1 is also frequently followed by S3. Note also that S2 is never preceded by another S2 or by a Pee-ist.

Variation within and among individuals is highest in rare transitions such as 1P, 21, 2P, and 32, and lowest in common transitions such as 12, 13, 23, and 31 (Table 8). Ratios of among- to within-individual C.V.'s are high (>1.0) for transitions 11, 12, 13, and 31, moderate (0.7-1.0) for transitions 1P, 2P, 32, 33, 3P, and L3, and low (<0.7) for transitions 21, 23, P1, and PP. The high score for transition 11 reflects the propensity of one bird (A4) to repeat S1. High ratios for transitions 12 and 13 occurred because some birds (A2, A3, and A4) tended to follow S1 with S2, while others followed S1 with S3 (A7). A high score for transition 31, and moderate scores for transitions 33 and 3P, resulted from variation among birds in transition probabilities following S3: A2 and A4 tended to follow S3 with S1; A3, A7, and A1N tended to repeat S3; and A1N tended to follow S3 with Pee-ist. Moderately high scores for transitions from song syllables to Pee-ist were because a few individuals tended to use Pee-ists after song syllables (A1N, A1S, and A7). A moderately high ratio associated with transition P3 was a consequence of two outlying individuals: bird A4 never followed Pee-ist with S3, while bird A7 did so over one-third of the time. Finally, low ratios are associated with transitions 21, P1, PP, and 23. P1, PP, and

21 are highly variable within individuals, while transition 23 is essentially invariable among individuals.

Comparison of Tables 5 and 7 shows that high values for particular transitions in a given individual are generally matched by a high proportion of the second syllable of the transition. One of the few exceptions is the high frequency of the 31 transition in bird A2 despite its slightly below average usage of S1.

Frequency of transitions at different times of day are shown in Fig. 16. As the day progresses, S1 is followed with S3 more often and with S2 less often. Also as the day advances, Pee-ist, S1, and S3 are followed by Pee-ist more often. Finally, S1 follows Pee-ist less often later in the day. No other change with time of day, and no change with date, was detected.

3.3. Effect of Preferences for Certain Sequences on Transition Probabilities

To determine whether first-order transition probabilities are affected by general predilections to use the second syllable, or conversely by preferences for certain sequences, a 'chi' statistic was calculated (see Methods and Materials). Mean chi-values indicate considerable deviation from transition frequencies expected on the basis of proportions of the second syllable in the

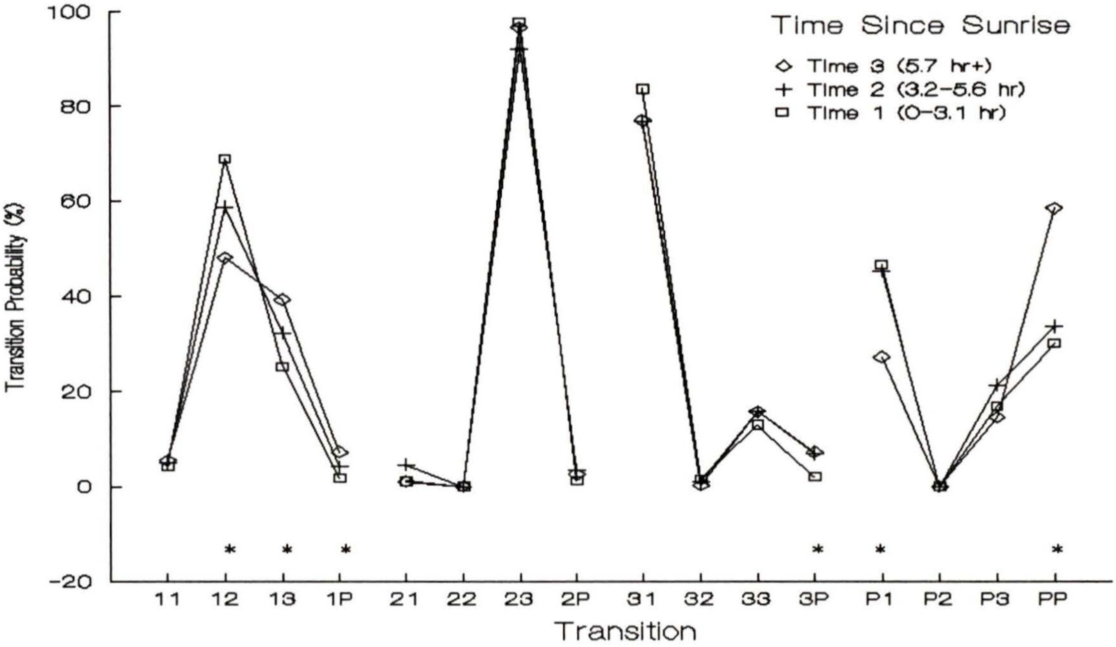

Figure 16. Relationship of first-order transition probabilities between syllables to time of day (1=S1, 2=S2, 3=S3, P=Pee-ist). * $p<0.05$.

samples (Table 9). Transitions 12, 23, 31, P1, and PP are the only ones that exceed expected values.

Ratios of among- to within-individual C.V.'s are high for transitions 11, 12, 23, 31, 32, 33 (>1.0), moderate for transitions 13 and PP (0.7-1.0), and low for transitions 1P, 21, 2P, 3P, P1, and P3 (<0.7). Comparison of Tables 7 and 8 reveals that, for the most part, individual variation in the chi-statistic mirrors individual variation in transition frequencies. That is, transition frequencies for particular individuals are strongly related to preferences for certain transitions above and beyond a simple predilection for producing the second syllable in the transition. An exception is high frequencies for transitions 1P, 2P, and 3P in bird A1S despite average or below-average chi-values. A general propensity to produce Pee-ist accounts for the high frequencies for these transitions in this bird (Table 6).

Change in the chi-statistic with time of day is illustrated in Fig. 17. Chi-values of transitions 13 and 32 increase as the day progresses, while those of transitions 1P and 2P decline. The change in chi-value for transition 13 is matched by the change in the probability of this transition, while changes in chi-values for transitions 32, 1P, and 2P are not (Fig. 16). No other transitions varied significantly in chi-value by time of day, including some transitions that change in probability with time of day (12, P1, PP, and 3P). Changes in transition probability of the

Table 9. Summary of tendencies in different individuals to produce each transition once the proportion of the second syllable in the sample has been accounted for. Chi-values are shown for each bird (see Methods and Materials).

Transition[a]	Bird A1N	A1S	A2	A3	A4	A5	A7	Mean	(A)[b] C.V. Among	(B)[b] C.V. Within	A/B
11	-4.9	-5.1	-4.6	-4.9	-3.4	-5.7	-5.2	-4.8	0.15	0.10	1.46
12	8.6	7.9	9.7	10.1	9.2	8.5	6.3	8.6	0.15	0.13	1.19
13	-0.8	1.2	-2.8	-3.0	-4.9	-0.1	1.9	-1.2	2.04	2.33	0.87
1P	-0.9	-2.2	-1.8	-1.0	-1.6	-1.2	-1.2	-1.4	0.32	0.97	0.33
21	-5.7	-5.9	-5.0	-5.4	-6.0	-5.7	-5.8	-5.6	0.06	0.09	0.68
22	-4.2	-4.0	-5.1	-4.8	-5.4	-4.6	-3.6	-4.5	0.14	0.10	1.36
23	10.1	9.8	11.1	9.4	12.4	10.1	8.7	10.2	0.12	0.09	1.38
2P	-2.7	-1.6	-1.5	-2.1	-1.0	-2.0	-2.4	-1.9	0.31	0.74	0.42
31	6.5	8.0	10.1	7.1	9.8	9.1	6.5	8.2	0.19	0.15	1.27
32	-4.2	-3.8	-4.9	-4.8	-5.4	-4.3	-3.6	-4.4	0.15	0.12	1.30
33	-3.0	-4.0	-4.9	-2.3	-5.3	-4.6	-3.8	-4.0	0.27	0.18	1.53
3P	-0.6	-1.8	-2.1	-1.0	-1.0	-0.8	-0.4	-1.1	0.55	1.57	0.35
P1	1.9	2.7	-0.7	-0.2	2.4	1.8	-0.0	1.1	1.25	15.85	0.08
P2	-4.2	-4.0	-5.1	-4.8	-5.4	-4.6	-3.6	-4.5	0.14	0.10	1.36
P3	-3.2	-4.2	-3.1	-3.8	-5.4	-3.5	-1.1	-3.5	0.38	0.70	0.54
PP	7.2	5.8	15.6	21.5	21.6	12.3	6.5	12.9	0.53	0.76	0.70

[a] 1=S1, 2=S2, 3=S3, P=Pee-ist

[b] See Table 6.

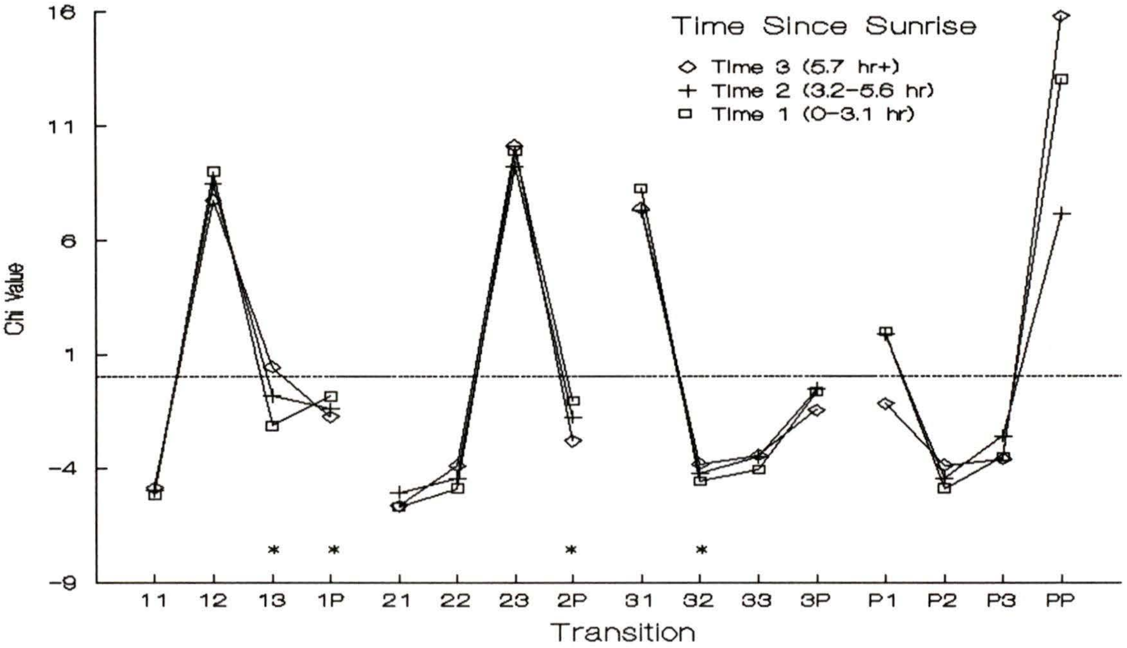

Figure 17. Summary of tendencies to produce transitions at different times of day. Chi values are given for each Time (see Methods and Materials). 1=S1, 2=S2, 3=S3, P=Pee-ist. * $p<0.05$.

first three of these (12, P1, and PP), however, correspond to non-significant changes in chi-values. No significant variation in chi-value by date was detected.

3.4. Relationship of Interval to Transition Probability

To further understand the structure of variation in transition frequencies, the probability of the following syllable as a function of the time elapsed since production of the first syllable was examined.

3.4.1. Following S1

S2 is the most likely syllable to occur from 3-12 dsec after production of S1 (Fig. 18). At intervals greater than 12 dsec after production of S1, S3 is most probable. Repetitions of S1 occur commonly only after 10 dsec. Pee-ists are the most common following syllable after 30 dsec.

Minor variation on this pattern was found among the seven birds (Fig. 19). Birds vary in how early S3 more commonly follows S1 than does S2. A1S, A7, and A5 followed S1 with S3 sooner than did the other birds. Conversely A2 and A4 followed S1 with S2 earlier than did A1S, A7, A5, and the other birds. Bird A4 repeated S1 much more commonly from 14 to 20 dsec than did the other birds, while A5 and A7 rarely repeated S1 at any elapsed time. Bird A1N followed S1 with a Pee-ist from 14 to 20 dsec more commonly than the

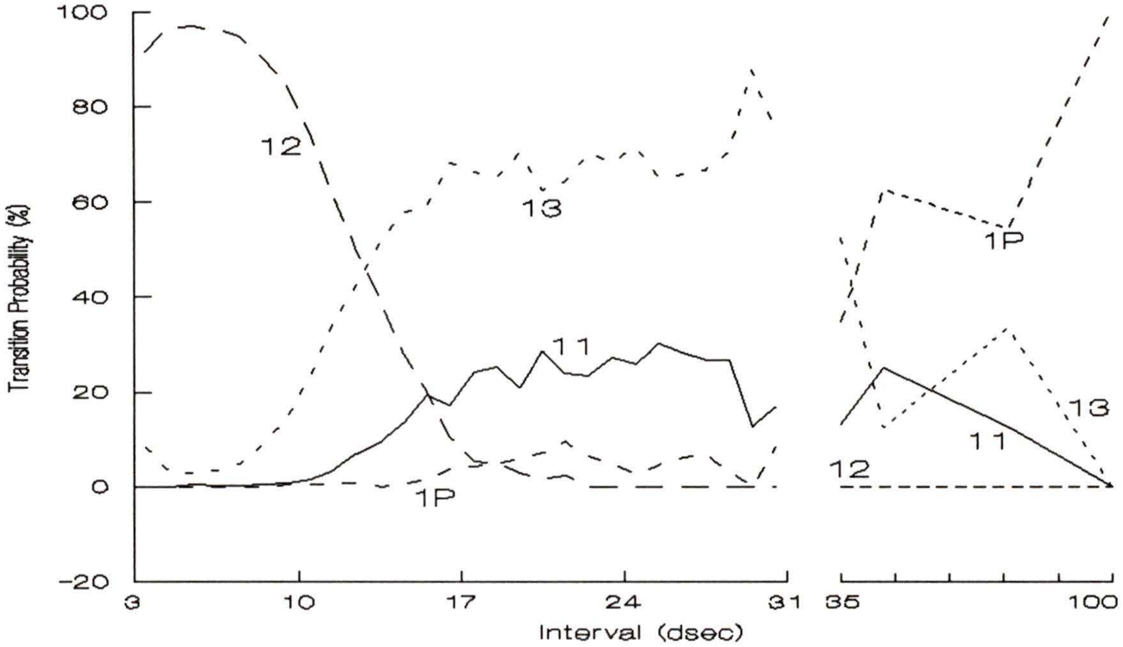

Figure 18. Relationship of first-order transition probabilities to time elapsed since production of S1. 1=S1, 2=S2, 3=S3, P=Pee-ist.

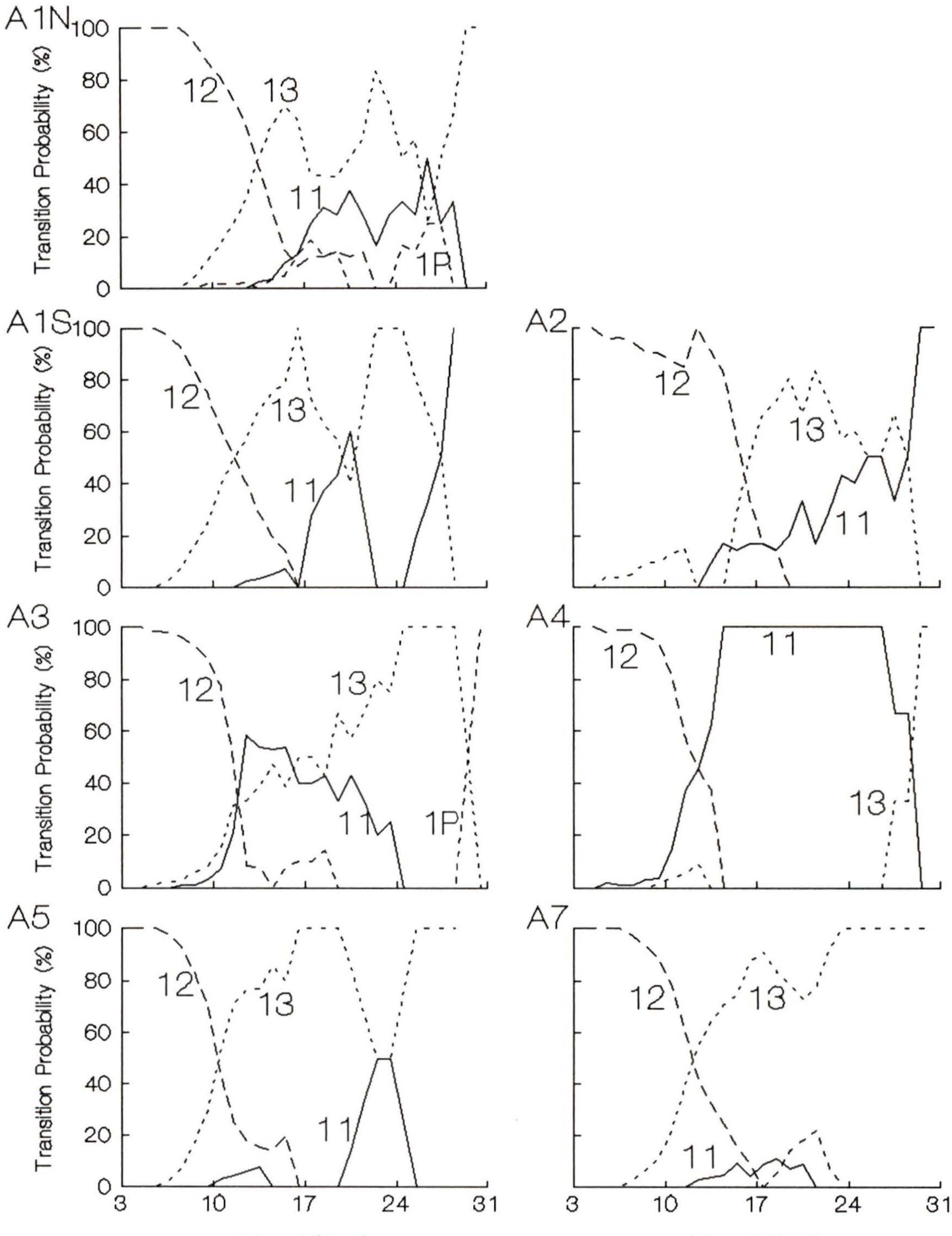

Figure 19. Relationship of first-order transition probabilities to time elapsed since production of syllable 1 in different birds. 1=S1, 2=S2, 3=S3, P=Pee-ist.

other birds did.

The pattern following S1 varies with time of day (Fig. 20). S3 becomes the most common following syllable 2 dsec sooner at Times 1 and 2 than at Time 3. Repetitions of S1 become progressively less common for a given amount of time elapsed at later times of day. Conversely, there is an increased probability of Pee-ist, and a less marked increase in probability of S3, as the morning progresses. At Time 1, no Pee-ists are given until more than 30 dsec have elapsed.

With advancing date, repetition of S1 becomes less probable in the 18 to 28 dsec range (Fig. 21). At Date 3, there are no Pee-ists following S1 until more than 30 dsec have elapsed.

3.4.2. Following S2

After S2, S3 follows almost exclusively (Fig. 22). At 50 dsec, Pee-ist becomes the more common following syllable. S1 follows S2 in small numbers at intervals greater than 27 dsec.

The seven birds analyzed varied little from this standard pattern (Fig. 23). A1N, A3, A5, and A7 followed S2 only with S3. A1S and A4 never followed S2 with S1.

With advancing time of day, there is a slightly greater tendency to follow S2 with a Pee-ist after 30 dsec (Fig. 24). At Time 3, S2 was never followed by S1 in the samples gathered.

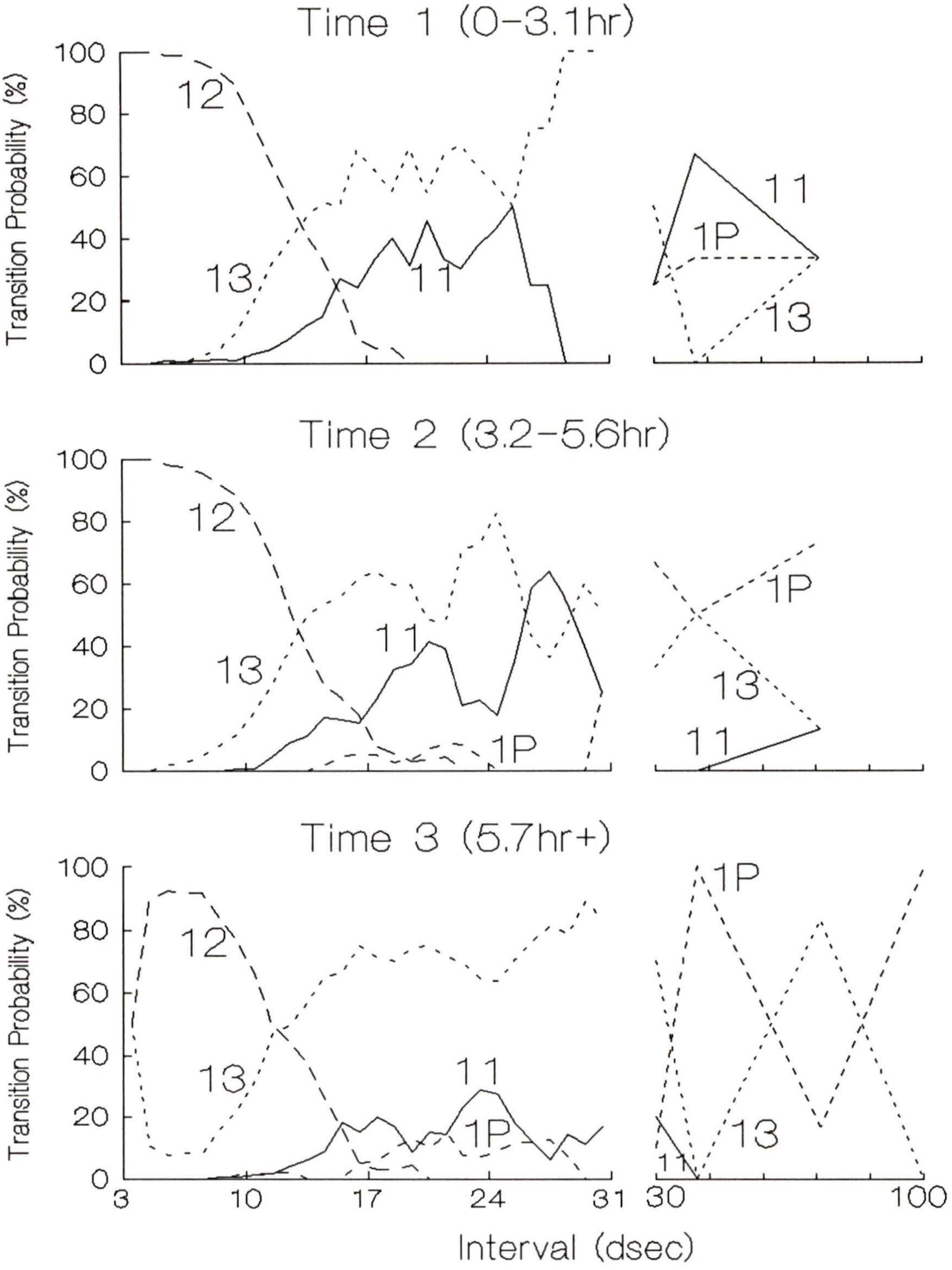

Figure 20. Relationship of first-order transition probabilities to time elapsed since production of S1 at different times since sunrise. 1=S1, 2=S2, 3=S3, P=Pee-ist.

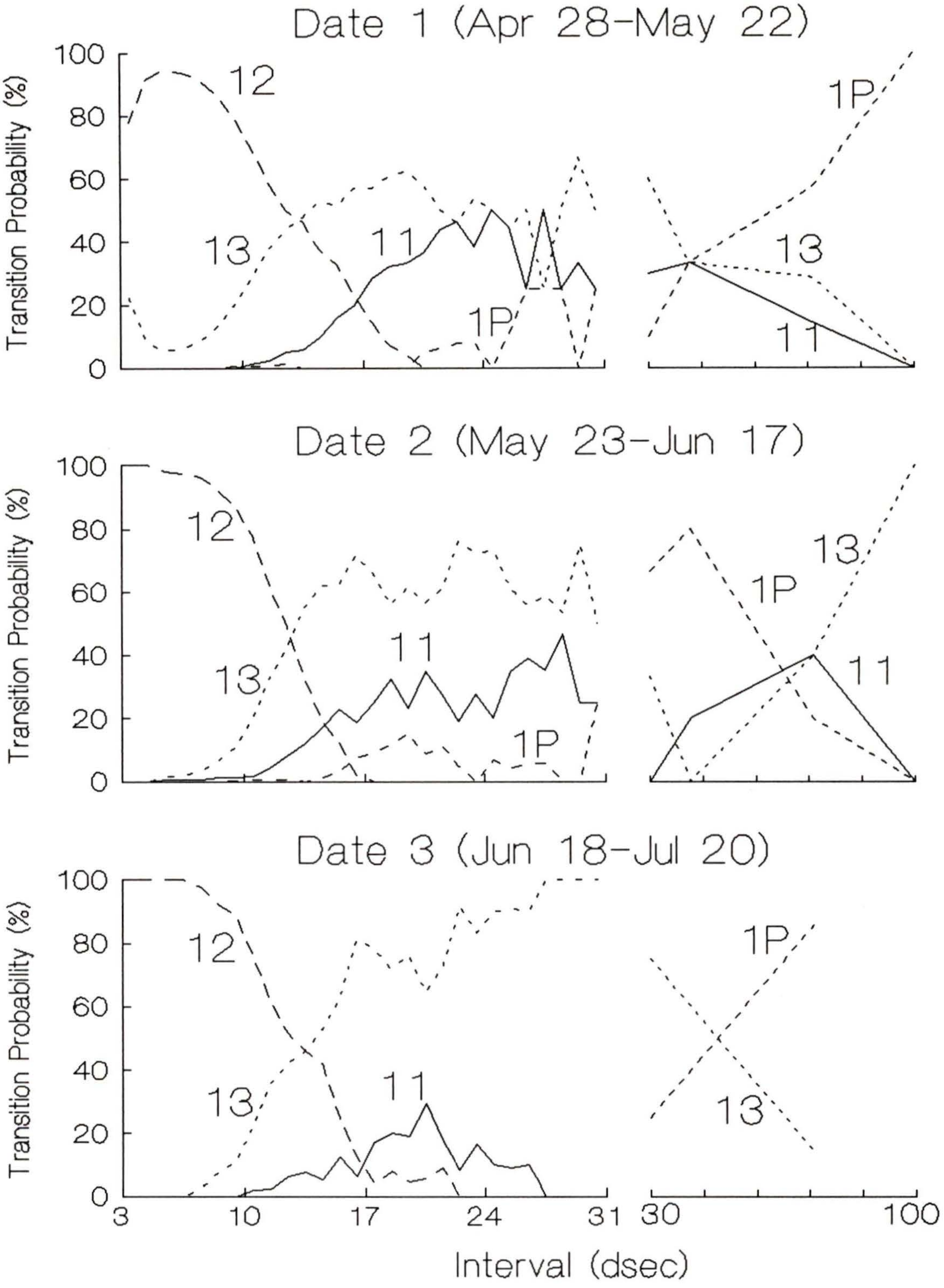

Figure 21. Relationships of first-order transition probabilities to time elapsed since production of S1 at different dates. 1=S1, 2=S2, 3=S3, P=Pee-ist.

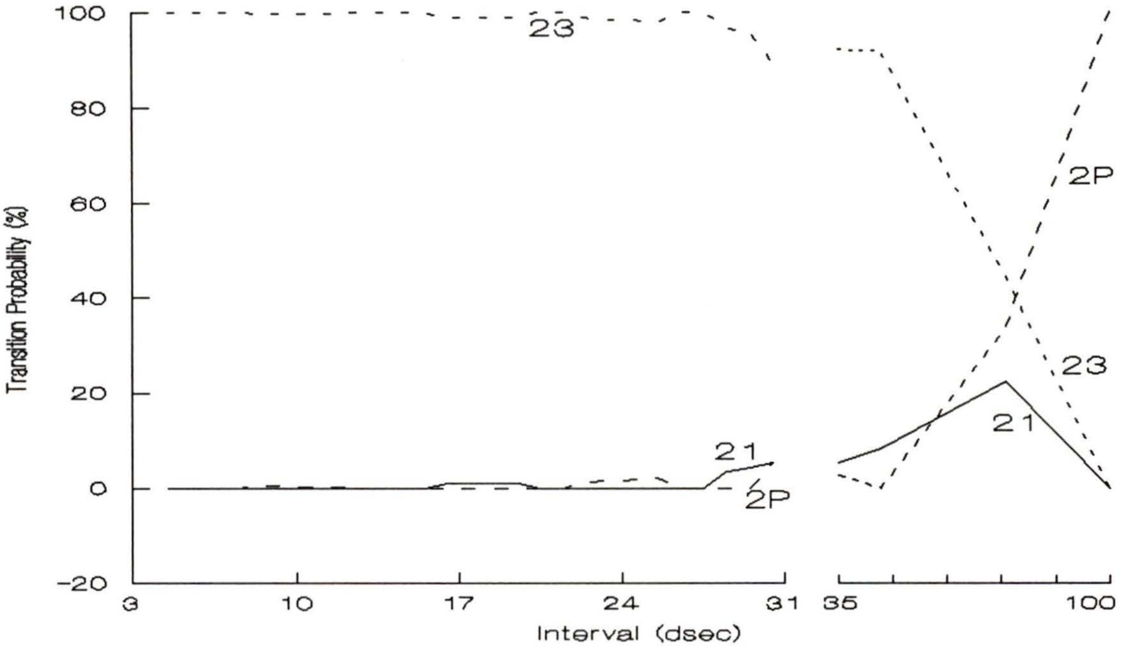

Figure 22. Relationship of first-order transition probabilities to time elapsed since production of S2. 1=S1, 2=S2, 3=S3, P=Pee-ist.

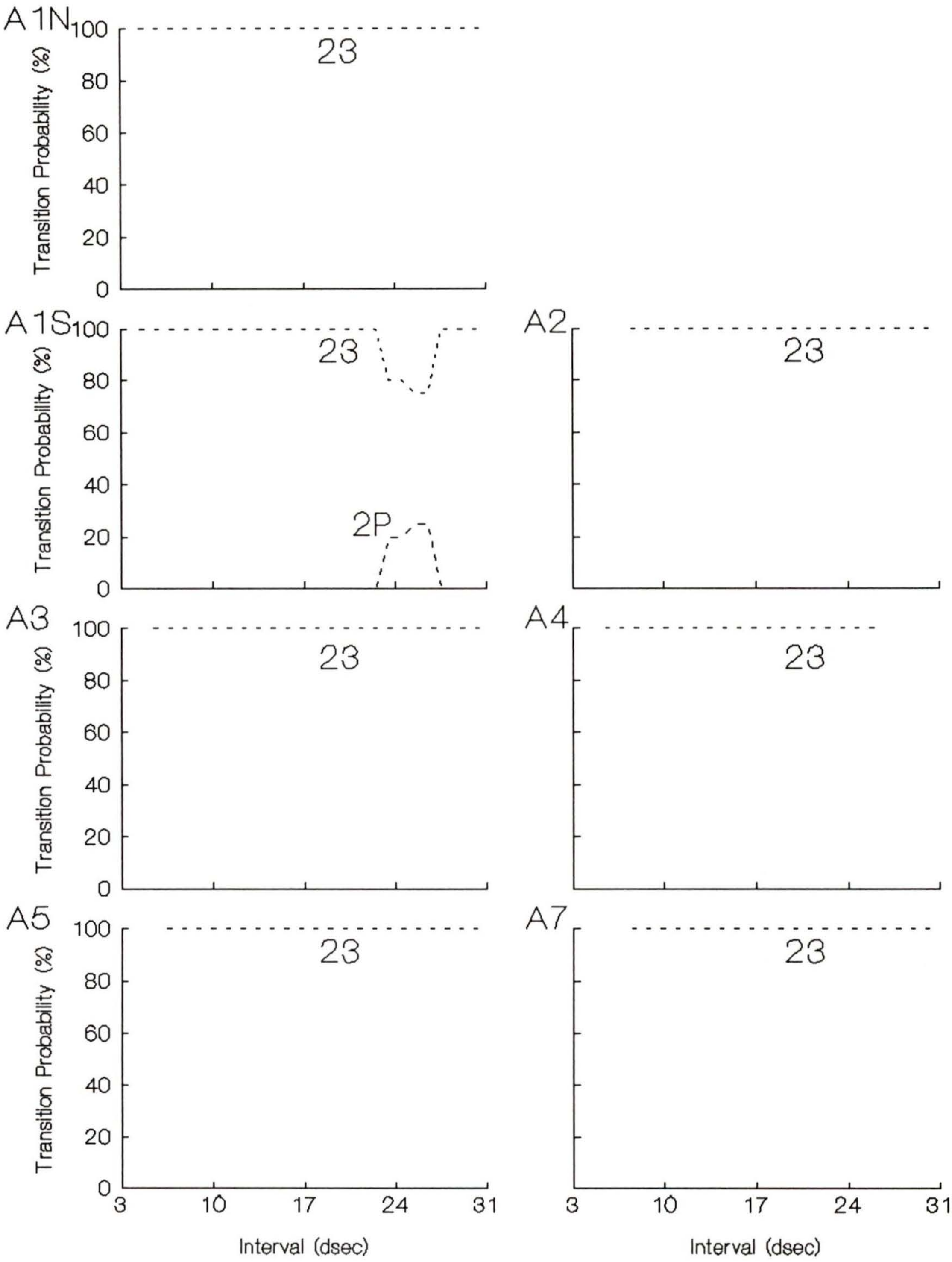

Figure 23. Relationship of first-order transition probabilities to time elapsed since production of S2 in different birds. 1=S1, 2=S2, 3=S3, P=Pee-ist.

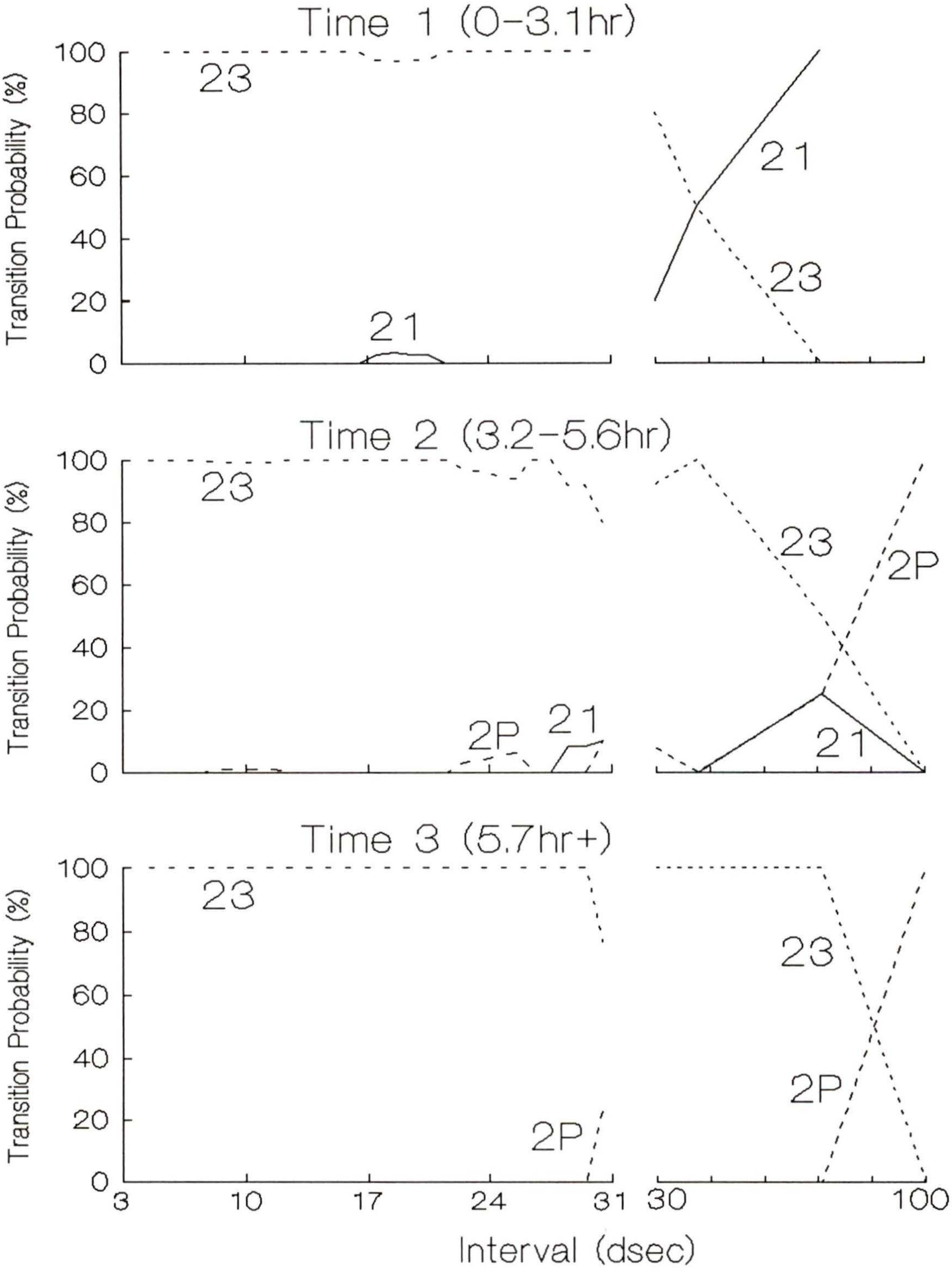

Figure 24. Relationship of first-order transition probabilities to time elapsed since production of S2 at different times since sunrise. 1=S1, 2=S2, 3=S3, P=Pee-ist.

At Date 3, S2 is followed by S3 only (Fig. 25).

3.4.3. Following S3

Following S3, S1 is initially the most common syllable, diminishing gradually in incidence from 12 to 23 dsec, when S3 becomes equally probable (Fig. 26). From 23 to 30 dsec, S3 is only slightly more probable than S1. S2 follows S3 only within the 3-6 dsec range. Pee-ists occur almost only after 20 dsec have passed. Pee-ist becomes the most common follower only after 50-100 dsec have elapsed.

Birds vary substantially from this pattern (Fig. 27). Birds A4 and A2 did not commonly follow S3 with S1 until 24 dsec had elapsed; remaining birds produced S1 much sooner. Bird A3 commonly repeated S3 sooner than did other birds. Birds A1N and A1S were likelier to follow S3 with a Pee-ist in the 20 to 30 dsec range than were other birds.

The pattern following S3 varies with time of day (Fig. 28). In the 14 and 22 dsec range, S3 becomes more likely and S1 less likely as the day progresses. Also, at short time intervals after S3, there was a greater probability of a S2 at Time 3 than at Times 1 or 2.

Repetitions of S3 become more likely in the 15 to 30 dsec range with advancing date (Fig. 29).

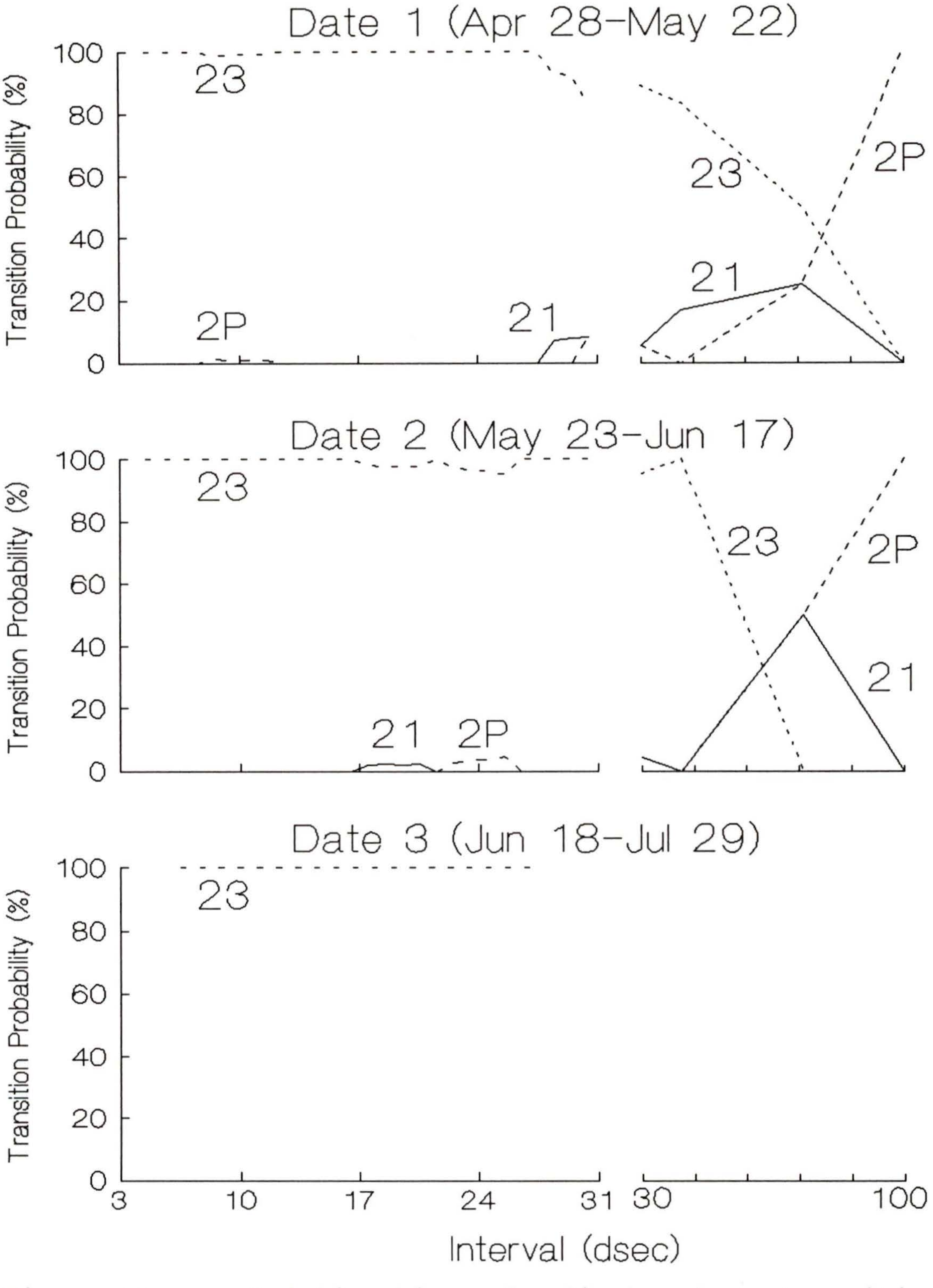

Figure 25. Relationship of first-order transition probabilities to time elapsed since production of S2 at different dates. 1=S1, 2=S2, 3=S3, P=Pee-ist.

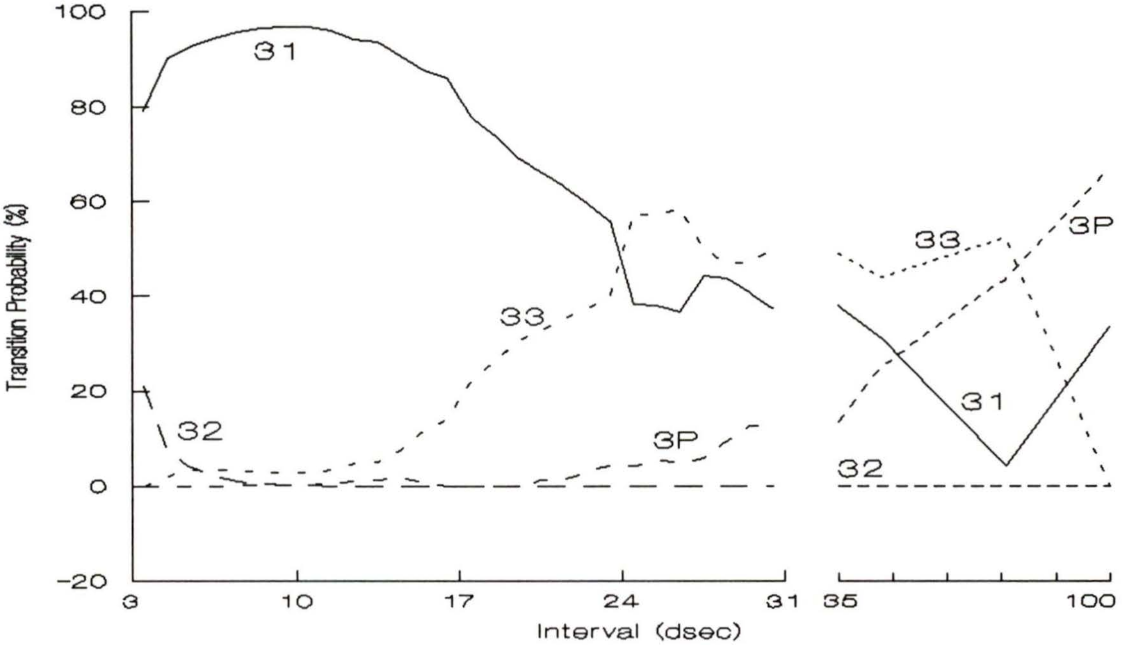

Figure 26. Relationship of first-order transition probabilities to time elapsed since production of S3. 1=S1, 2=S2, 3=S3, P=Pee-ist.

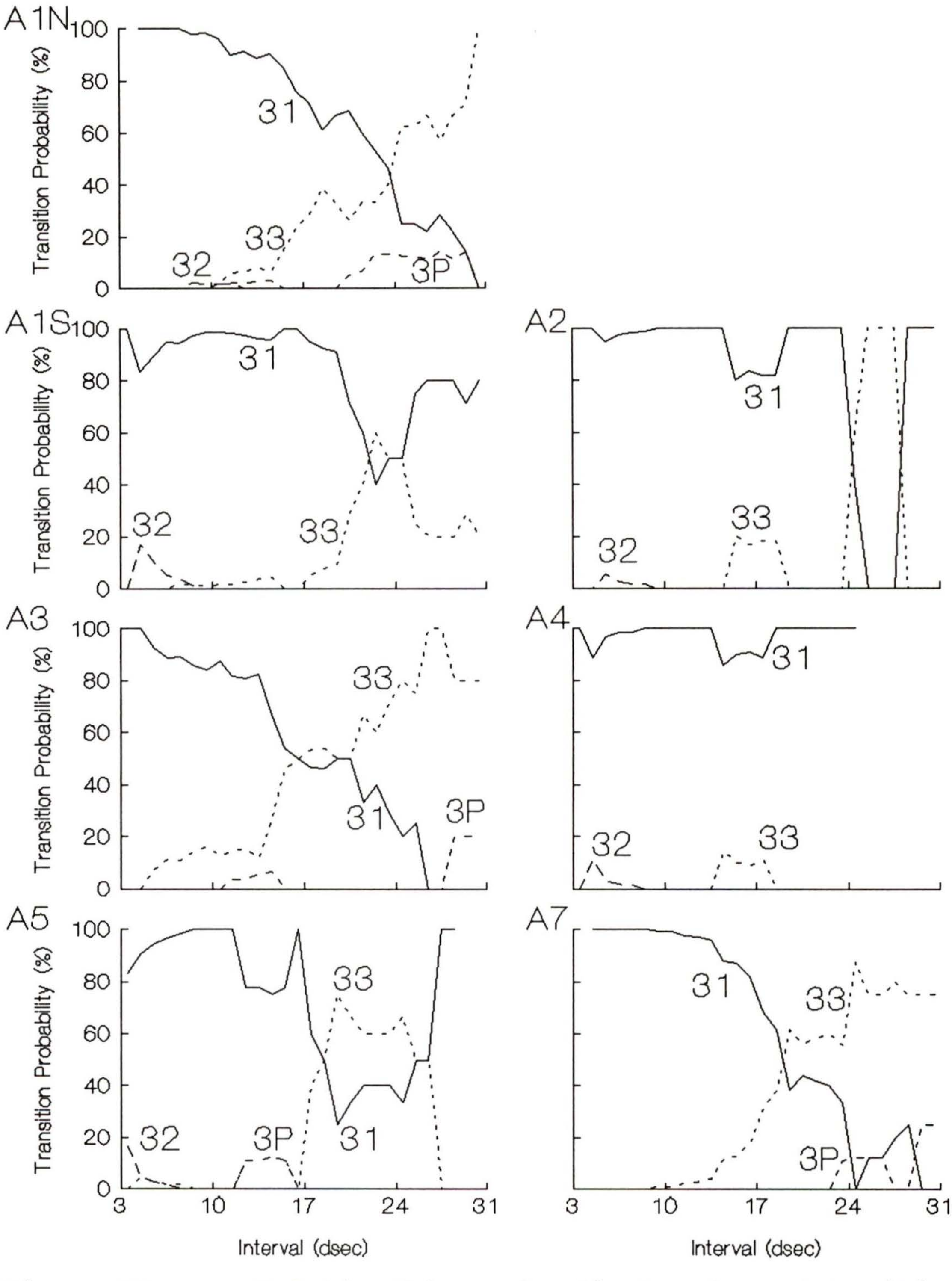

Figure 27. Relationship of first-order transition probabilities to time elapsed since production of S3 in different birds. 1=S1, 2=S2, 3=S3, P=Pee-ist.

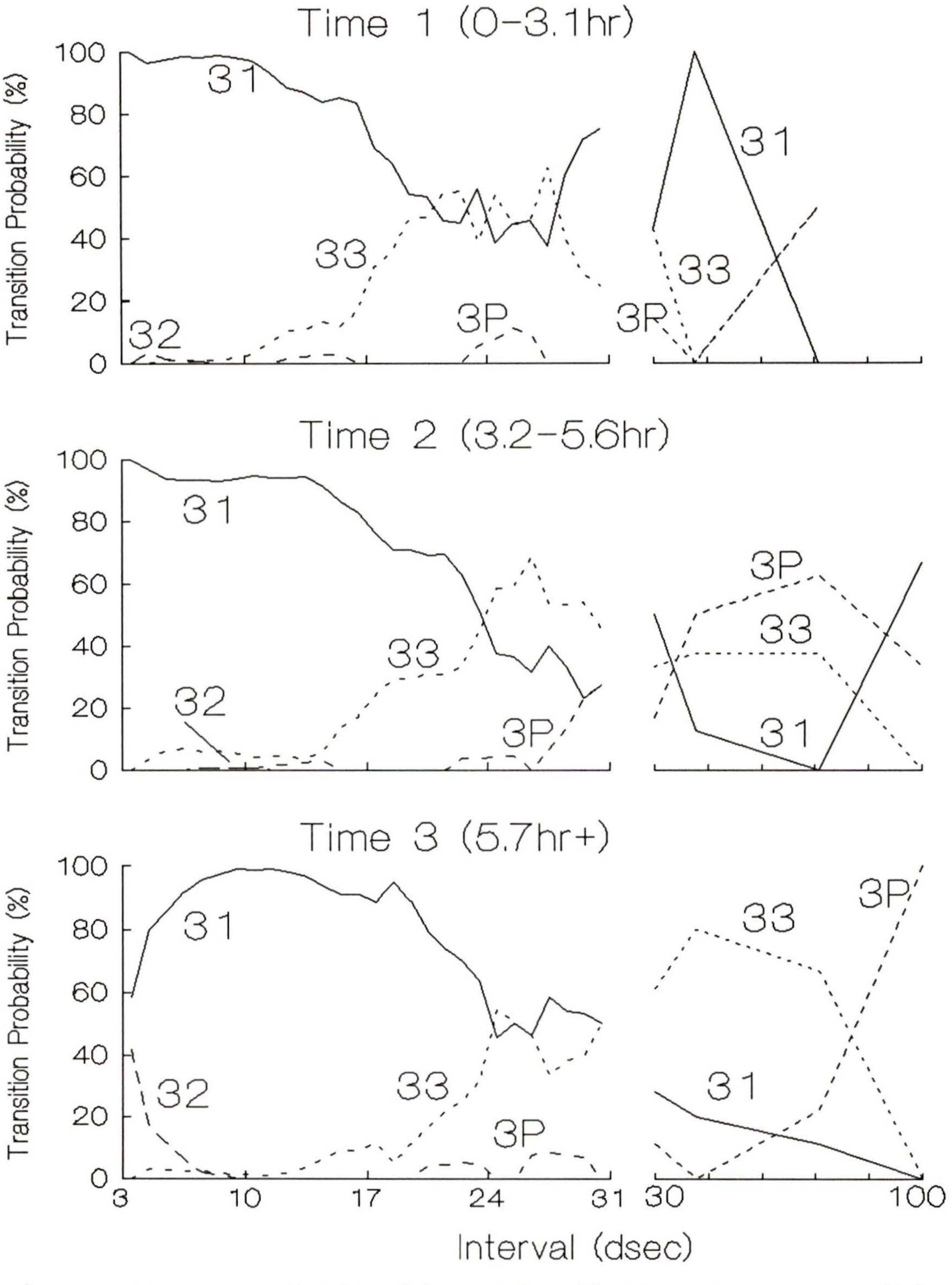

Figure 28. Relationship of first-order transition probabilities to time elapsed since production of S3 at different times since sunrise. 1=S1, 2=S2, 3=S3, P=Pee-ist.

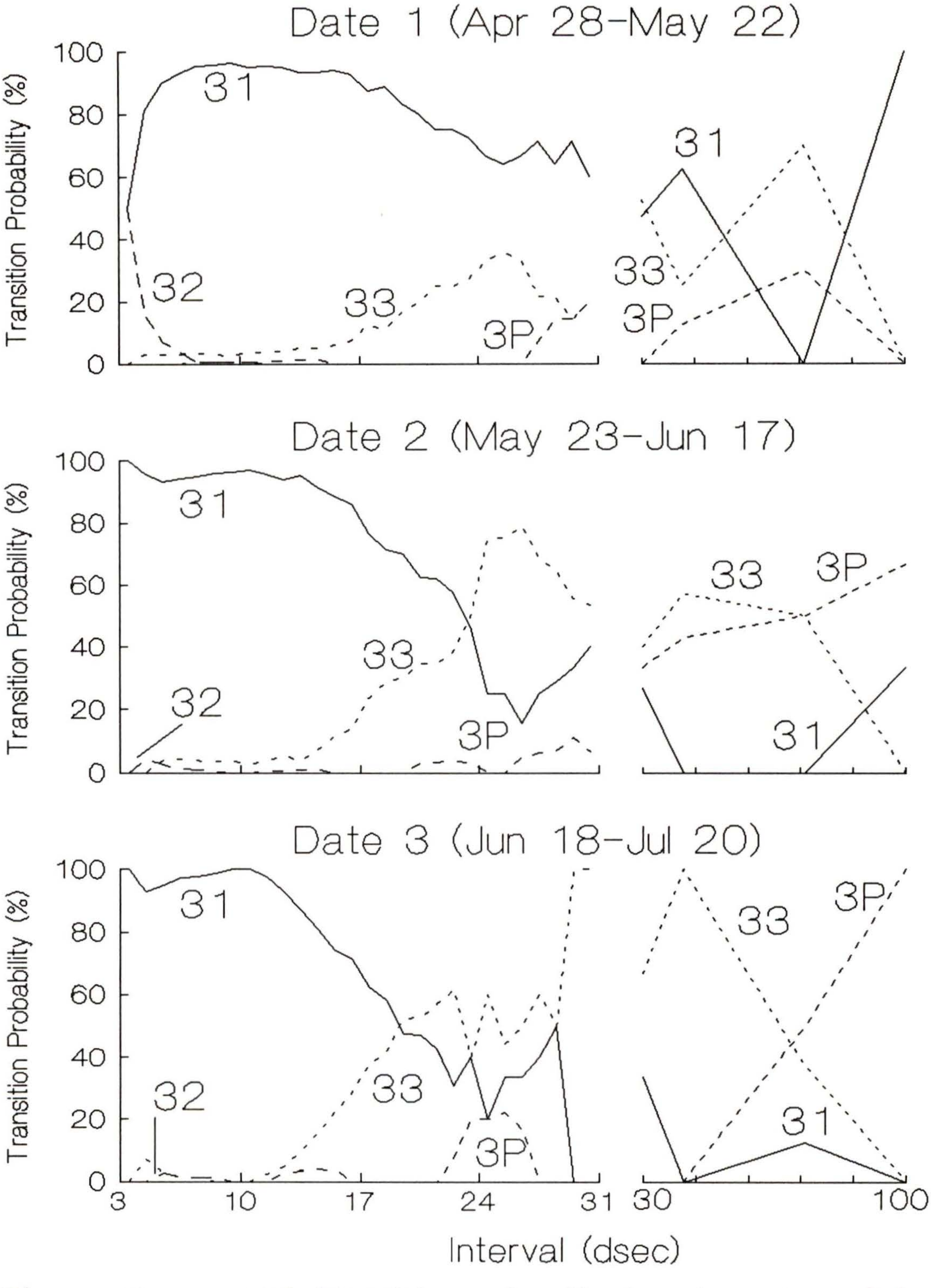

Figure 29. Relationship of first-order transition probabilities to time elapsed since production of S3 at different dates. 1=S1, 2=S2, 3=S3, P=Pee-ist.

3.4.4. Following the Pee-ist call

S1 most commonly follows the Pee-ist call until 27 dsec, when a repetition becomes most probable (Fig. 30). The probability of S3 increases with elapsed time from 7 to 20 dsec. After 20 dsec, the probability of S3 varies irregularly. Repetitions of Pee-ist do not occur until 20 dsec have elapsed.

Variation among birds in the pattern following the Pee-ist call is difficult to discern because relatively few intervals following Pee-ists were analyzed (Fig. 31). Birds A1S, A3, A4, and A5 did not follow Pee-ists with S3 at any time interval.

Repetition of Pee-ist commonly occurs with less elapsed time at Time 1 than at Times 2 or 3 (Fig. 32).

With advancing date, there is an increased probability of S3 within 10 to 22 dsec after a Pee-ist call (Fig. 33). Also there is an increased probability of repetition and a decreased probability of S1 in the 20 to 30 dsec range.

3.5. Second-order Transition Probabilities

Transition probabilities as a function of the preceding two syllables are illustrated in Fig. 34. Transition 12 is most likely when preceded by S2 and is progressively less likely when preceded by S3, Pee-ist, or S1. The effect of the preceding syllable on transitions 13 and 1P is in the

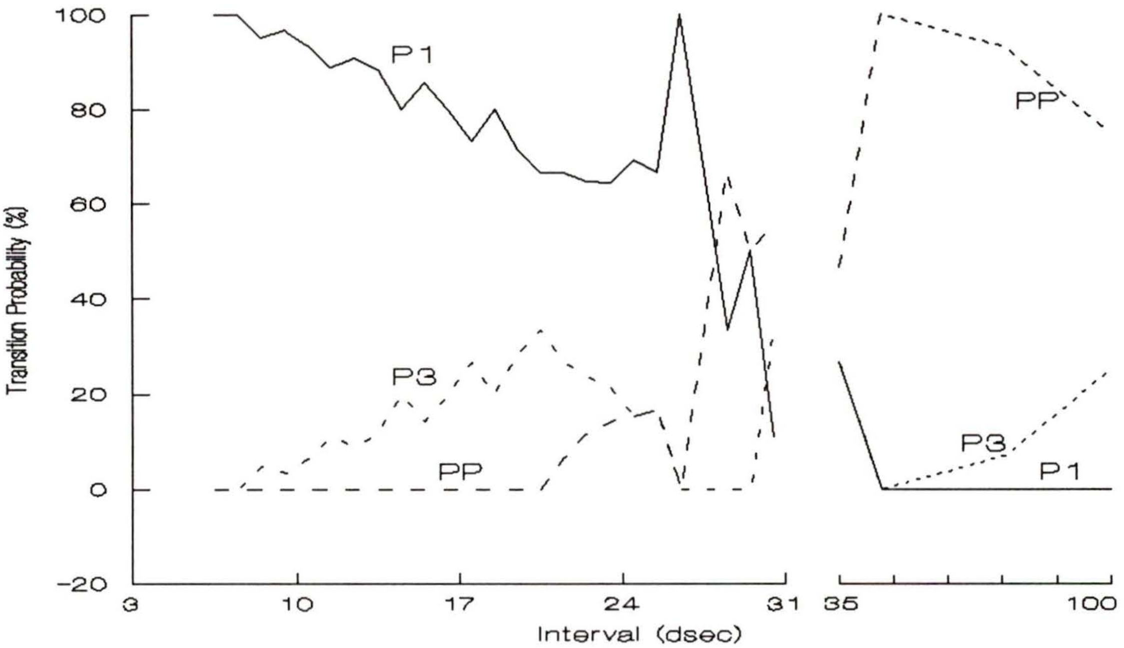

Figure 30. Relationship of first-order transition probabilities to time elapsed since production of the Pee-ist call. 1=S1, 2=S2, 3=S3, P=Pee-ist.

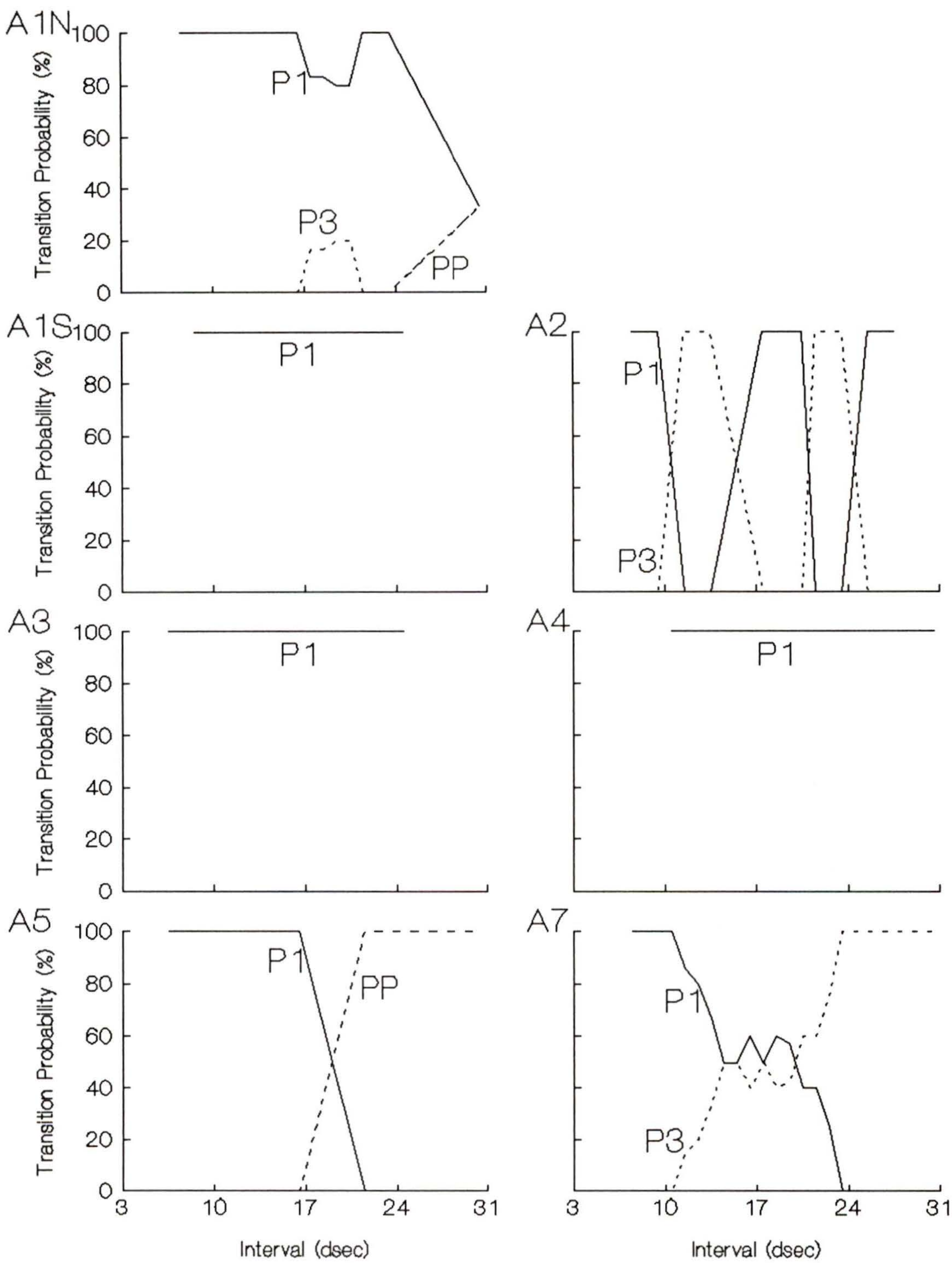

Figure 31. Relationship of first-order transition probabilities to time elapsed since production of a Pee-ist call in different birds. 1=S1, 2=S2, 3=S3, P=Pee-ist.

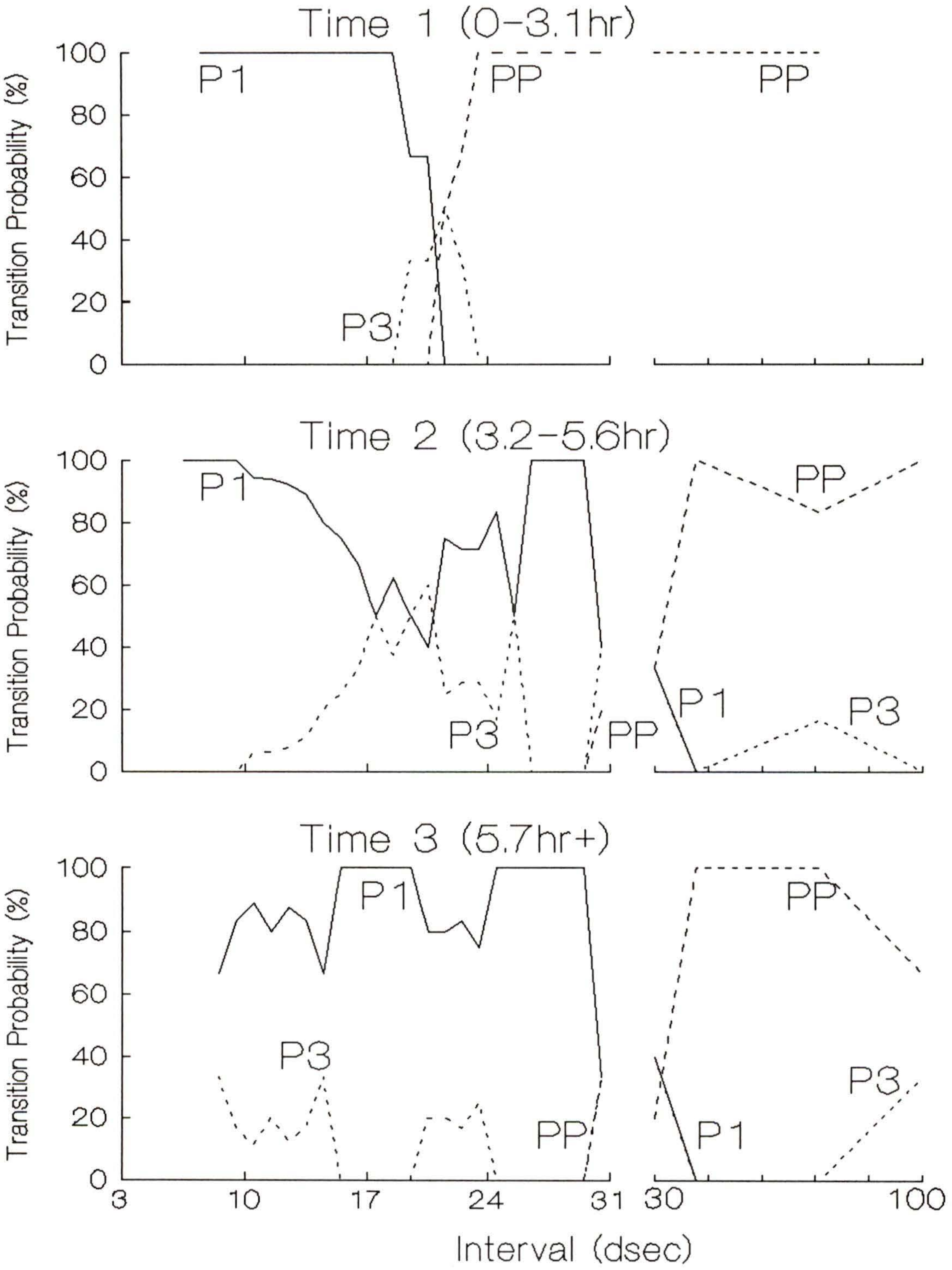

Figure 32. Relationship of first-order transition probabilities to time elapsed since production of a Pee-ist call at different times since sunrise. 1=S1, 2=S2, 3=S3, P=Pee-ist.

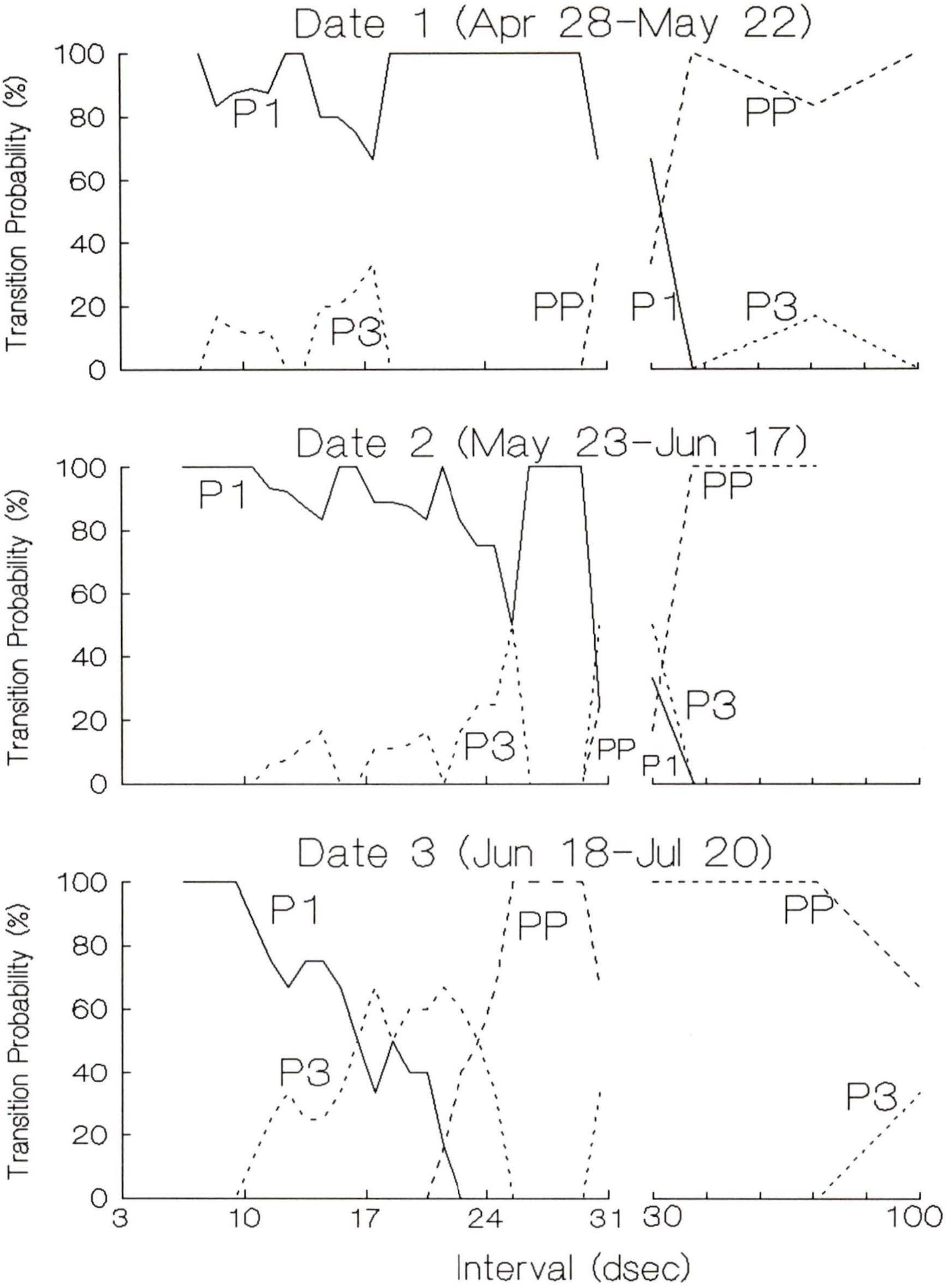

Figure 33. Relationship of first-order transition probabilities to time elapsed since production of the Pee-ist call at different dates. 1=S1, 2=S2, 3=S3, P=Pee-ist.

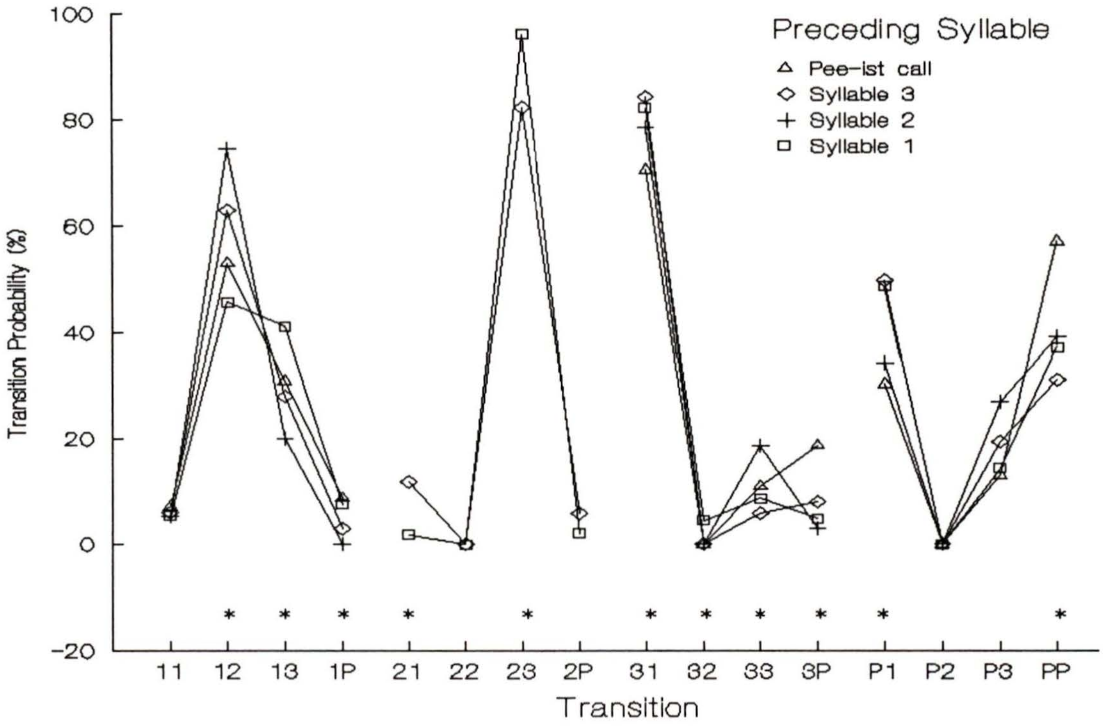

Figure 34. Relationship of first-order transition probabilities to the syllable preceding the transition. Values plotted are second-order transition probabilities. *$p<0.05$.

opposite direction.

Transition 23 is more likely, and transition 21 less likely, when preceded by S1 than when preceded by S3.

Transition 31 is most likely when preceded by S3 or S1 and least likely when preceded by Pee-ist. Transition 32 only occurs when preceded by S1. Repetition of S3 is most likely when preceded by S2 and least likely when preceded by another S3. Transition 3P is most likely when preceded by Pee-ist.

Transition P1 is more likely when preceded by S3 or S1 and less likely when preceded by S2 or Pee-ist. The PP transition is most likely when preceded by another Pee-ist.

4. Frequency, Duration, and Interval Measurements of Song Syllables and Pee-ists

4.1. Interval, Duration, and Frequency

Mean values for each of the sixteen spectrographic measurements are given in Table 10. Some strong trends are apparent. S2 is much briefer than S1 or Pee-ist in all males. Of the intervals presented here, I12 is briefest, followed by I31, then I23, and I13. Trends in frequency are also strong and consistent across males.

Variation among individuals of intervals is greater than that of durations. Conversely, durations exhibit greater individuality than do intervals (see last column in Table 10). Of the interval measurements, only I12 has an among- to within-C.V. ratio greater than 1.0. Of frequency variables, only the C.V. of PFPC within individuals is greater than 10%. In general, Pee-ist and high-frequencies are more individualistic than are low-frequencies.

The relationships of date, time and presence of female to spectrographic variables are summarized in Table 11. Duration variables are not strongly related to date, time, or female presence. DU2 increases significantly with advancing date and with female presence, but the effects are very small in both cases. The relationship between DU2 and female presence was the only significant association with

♀ presence.

Table 10. Summary of means for each bird on each spectrographic variable.[a]

			Bird					(A)[b] C.V.	(B)[b] C.V.	
Variable	A1N	A1S	A2	A3	A4	A5	A7	Mean	Among	Within	A/B
Durations (msec)											
DU1	292	284	318	305	289	269	278	291	0.056	0.032	1.75
DU2	105	99	97	113	119	115	104	107	0.079	0.034	2.32
DUP	264	241	289	221	276	229	261	254	0.098	0.054	1.81
Intervals (msec)											
I12	959	826	834	690	712	730	957	821	0.137	0.101	1.36
I23	1480	1913	1645	1111	1256	1268	1712	1485	0.194	0.236	0.82
I31	1217	1067	1146	823	1083	849	1075	1037	0.142	0.195	0.73
I13	1771	1609	1645	1459	3900[c]	1247	1883	1603	0.141	0.267	0.53
Low Frequencies (Hz)											
PF1A	4467	4600	4204	4553	4768	4913	4493	4571	0.050	0.033	1.52
MF1C	5264	5219	4854	4895	5218	5194	5064	5101	0.033	0.023	1.43
PF2A	4424	4622	4284	4546	4701	4877	4463	4560	0.043	0.037	1.16
PF2B	5675	5537	5585	5643	5540	5773	5710	5638	0.079	0.018	4.39
High Frequencies (Hz)											
PF1B	7812	7899	7621	7926	7360	8184	8194	7857	0.038	0.021	1.81
MF3	6524	6299	6093	6519	6076	6518	6682	6387	0.037	0.019	1.95
Pee-ist Frequencies (Hz)											
PFPA	4812	5195	4604	4402	5157	5302	4718	4884	0.069	0.033	2.09
MFPB	4119	4458	3974	3550	4284	4573	4405	4195	0.083	0.044	1.89
PFPC	4555	5566	4977	5306	4910	5959	4722	5142	0.097	0.113	0.86

[a] See Methods and Materials.

[b] See Table 6.

[c] This value is based on one measurement only. It was not used in calculations of C.V.'s.

Table 11. Summary of the relationship of date, time of day, and presence of female to spectrographic variables. Figures are mean regression coefficients (see Methods and Materials).[a]

	Independent Variable		
Dependent Variable	Date(d)	Time(hr)	Female Presence
Duration			
DU1	- 0.10	2.77	- 2.05
DU2	0.08*	-0.26	2.90**
DUP	0.32	-1.21	-13.26
Interval			
I12	- 1.38	7.79*	- 2.22
I23	-13.59***	36.66	55.61
I31	22.10	25.89**	-459.89
I13	- 4.10	96.81*	202.45
Low Frequencies			
PF1A	- 4.47*	-18.61***	-79.60
MF1C	- 5.82	- 5.55***	31.63
PF2A	- 5.55***	-26.99***	-71.77
PF2B	- 2.92**	-12.85**	-28.51
High Frequencies			
PF1B	- 2.68	- 7.53	-49.69
MF3	- 0.86	- 5.32	-86.15
Call Frequencies			
PFPA	- 3.60	13.90	- 0.27
MFPB	- 3.50	28.28	-81.57
PFPC	-17.00	74.45	446.85

[a] * $p<0.05$; ** $p<0.01$; *** $p<0.0031$ (=0.05/16 variables)

female presence. I23 becomes shorter with advancing date, while remaining interval variables (I12, I31, and I13) tend to increase with time of day. Low-frequencies decline with both date and time of day, with the exception of MF1C which only declines significantly with time. Although high-frequencies also tend to decline, none of these associations are significant. Frequencies of Pee-ist are not significantly related to date or time, but increase non-significantly with time of day, in contrast to all song frequencies measured.

4.2. Remaining Interval Measurements

Interval measurements with insufficient samples for the analysis of Section 4.1 are given in Table 12, along with the four interval measurements discussed above (I12, I23, I31, and I13). The briefest intervals are those between syllables in the most common sequence (1231231...). The only briefer intervals than those are between S3 and S2 and between Pee-ist and S1. S1 and S3 are also separated by a relatively short interval. Greater intervals occur between repetitions of syllables or before a Pee-ist call. Finally, the interval between the Pee-ist call and S3 is also relatively long.

Table 12. Summary statistics of interval durations.

Interval	Duration (msec)[a]	n
11	2079±1150	84
12	807±209	848
13	1671±999	344
1P	4835±3490	40
21	4556±2120	8
22	---	0
23	1523±844	837
2P	11640±11400	9
31	1115±816	1158
32	542±130	10
33	2472±1510	159
3P	5345±3560	33
P1	1505±656	74
P2	---	0
P3	4149±7850	18
PP	6102±4250	32

[a] $\bar{y}$±s.d.

4.3. Correlations Among Variables

The structures of individual and temporal variation are examined separately in the following sections. In the first section, I investigate covariation among duration, interval, and frequency variables across individuals, and in the second section, I investigate covariation among these variables across dates and times of day.

4.3.1. Structure of individual variation

Correlations among variables based on mean values of each male on frequency, duration, and interval measurements are given in Appendix D. The result of cluster analysis based on these correlations is illustrated in Fig. 35. Some clusters are composed of measurements with an identifying theme. These themes include low-frequency song-syllable variables (PF1A and PF2A), high-frequency song-syllable variables (PF1B, MF3, and PF2B), intervals between syllables (I12, I23, and I31), and Pee-ist frequencies (MFPB and PFPA). Other clusters have only weak identifying themes. These include MF1C, PFPA and MFPB; PF1A, PF2A, and DU2; I31 and DUP; and I31 and DUP.

Some coarser groups are revealed by Principal Components Analysis (Table 13a). The five lowest-frequency variables and DU1 load heavily on factor 1. Factor 2 is well characterized by the three highest-frequency variables.

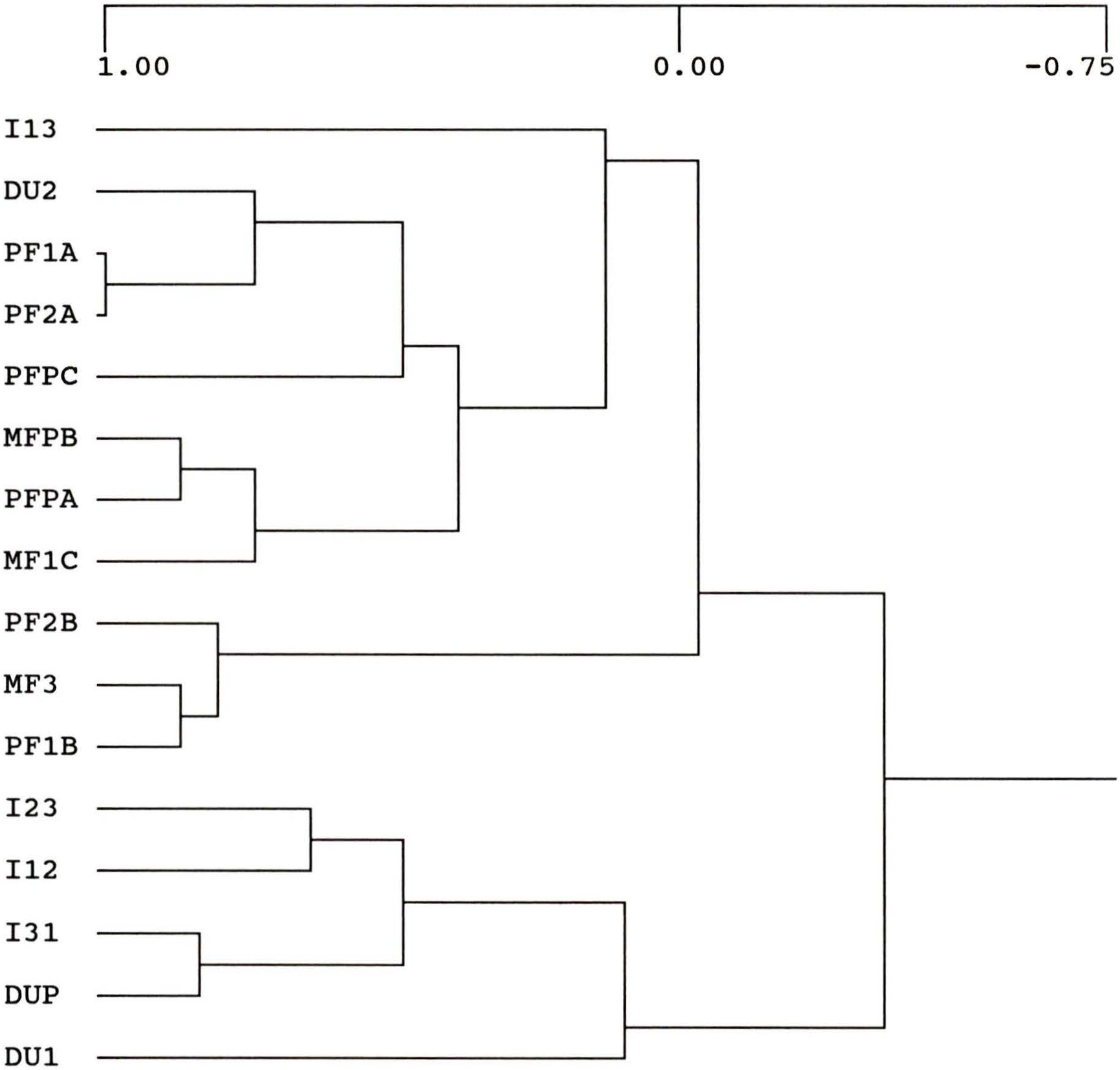

Figure 35. Average-linkage cluster analysis based individual mean values for each variable. The scale shows r (Pearson's product-moment correlation coefficient).

Table 13. Summary of results of Principal Components Analysis (with varimax rotation). Factor loadings are shown for: a. mean individual values; b. mean values from each combination of Date and Time (see text). Bold type highlights loadings of 0.68 or greater.

a.	Factor			
Variable	1	2	3	4
PFPA	**0.939**	-0.205	0.010	-0.236
MFPB	**0.922**	0.079	0.273	0.008
MF1C	**0.890**	0.018	-0.101	0.196
DU1	**-0.863**	-0.456	0.118	0.106
PF1A	**0.708**	0.114	-0.546	-0.431
PF2A	**0.684**	0.069	-0.452	-0.569
MF3	0.034	**0.976**	-0.060	0.053
PF1B	0.130	**0.911**	0.227	-0.285
PF2B	0.114	**0.885**	-0.190	-0.037
I13	0.284	-0.656	-0.488	0.406
DUP	-0.060	-0.544	0.223	**0.705**
DU2	0.253	0.002	**-0.950**	-0.177
I23	0.206	-0.063	**0.926**	0.210
I12	0.075	0.374	0.559	**0.734**
PFPC	0.276	0.080	0.034	**-0.949**
I31	0.095	-0.338	0.431	**0.812**
Variance Explained (%)	28.4	23.9	20.2	22.1

b.	Factor				
Variable	1	2	3	4	5
PF1A	**0.972**	0.097	0.080	0.047	0.113
PF2A	**0.957**	0.026	0.103	0.097	0.236
PF2B	**0.947**	0.014	0.204	0.015	0.016
MF1C	**0.895**	0.213	0.199	0.240	0.122
MF3	**0.726**	0.319	0.533	0.010	0.150
I23	0.564	**0.678**	0.139	0.374	0.235
PFPA	0.218	**0.914**	0.119	0.234	0.141
I12	0.308	**0.841**	0.093	0.155	0.298
PF1B	0.259	**0.791**	0.208	0.321	0.376
DUP	0.305	0.121	**0.933**	0.063	0.015
DU1	0.325	0.476	**0.688**	0.276	0.097
DU2	0.194	0.134	0.199	**0.892**	0.040
PFPB	0.299	0.423	0.054	**0.740**	0.147
MFPC	0.481	0.010	0.405	**0.688**	0.302
I31	0.205	0.001	0.021	0.046	**0.957**
I13	0.241	0.244	0.462	0.495	0.272
Variance Explained (%)	33.0	20.5	13.9	15.8	9.53

Factor 3 is characterized by two temporal variables associated with S2 (DU2 and I23). I12, I31, DUP, and PFPC all load heavily on factor 4.

4.3.2. Structure of temporal variation

Correlations among variables based on mean values at each combination of Date and Time on frequency, duration, and interval variables are given in Appendix D. The result of cluster analysis based on these correlations is shown in Fig. 36. Frequency variables tend to cluster. All song-frequency variables except PF1B form one distinct cluster, and two Pee-ist frequency variables (MFPB and PFPC) form a second. There is some tendency for both duration and interval variables to cluster. Two interval variables (I12 and I23) form one cluster, while two duration variables (DU1 and DUP) form a second.

Results of principal components analysis follow a similar pattern (Table 13b). The five lowest song-frequency variables load on 1; factor 2 is characterized by the two interval variables identified above as forming a cluster (I12 and I23) and by two frequency variables (PF1B and PFPA). Two duration variables load heavily on factor 3. Factor 4 is characterized by the Pee-ist frequency cluster identified above and by DU2. Only I31 loads heavily on factor 5.

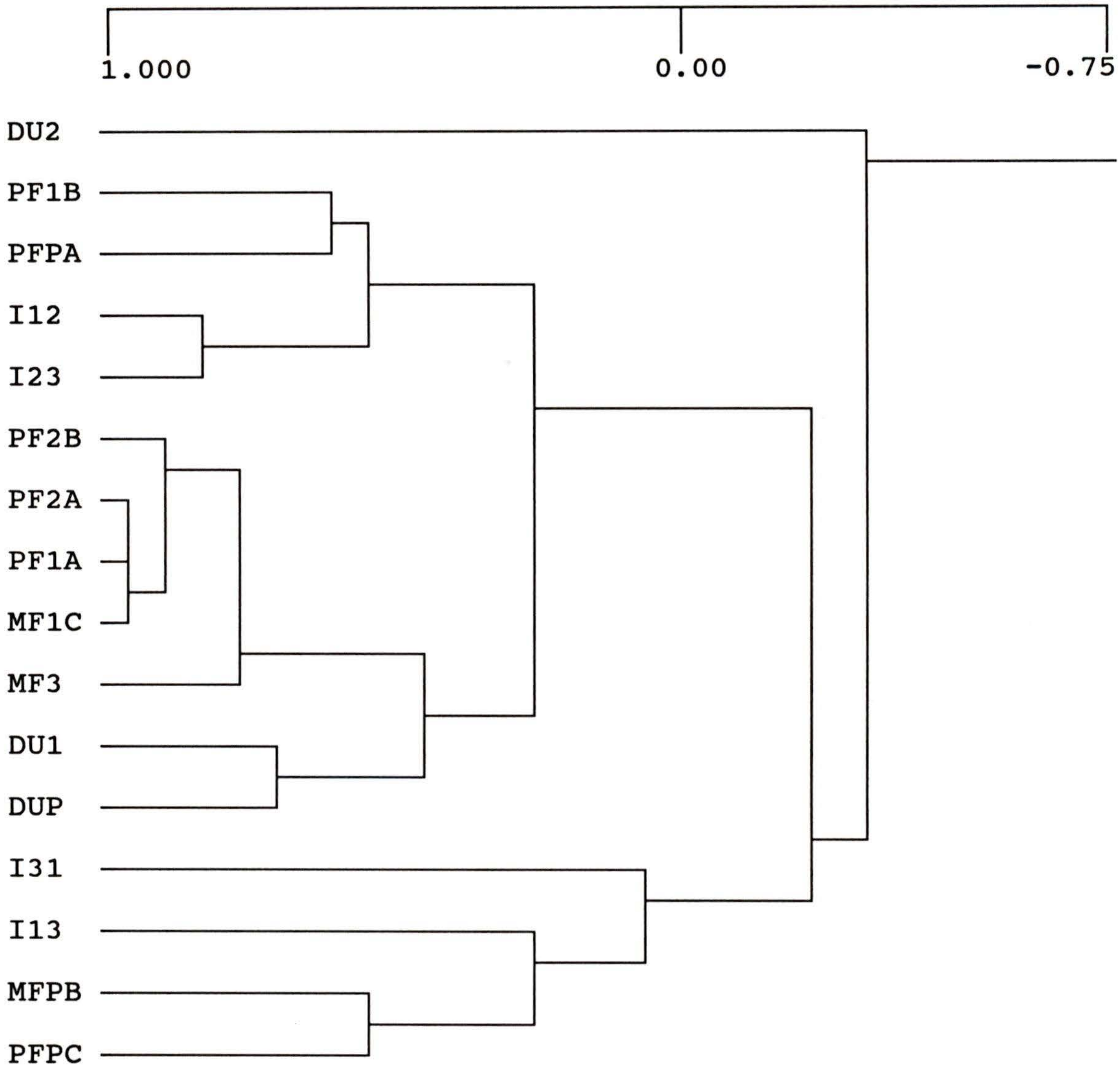

Figure 36. Average-linking cluster analysis based on mean values for variables from each combination of Date and Time. The scale shows r (Pearson's product-moment correlation coefficient).

DISCUSSION

Vocalizations of Empidonax difficilis exhibit individual, temporal, and situational variation in physical structure, incidence, syllable proportions, transition probabilities, frequencies, intervals between syllables, and syllable durations. In light of my observations, I discuss vocal structure, function, and evolution in the species.

1. Use of Vocalizations in Breeding

Male movements within territories at different stages of the breeding cycle has not previously been described. Prior to the female's arrival, males move frequently, primarily near the periphery of their territories. During nest construction and incubation, males extend their territories away from the nest and sing there. Periodically during these stages males return to the nest area and call until receiving a response from their mates. This description of male behaviour during nest construction contradicts Sakai's (1988) observations that males are quiet and remain near the nest during incubation. In agreement with my findings, Davis et al. (1963) reported exchanges of Pee-ist calls between mates during incubation and brooding. The male movements that I observed suggest certain functions of the associated vocalizations (see Section 2).

This study provides the first detailed analysis of the use of long distance vocalizations (song and Pee-ist) over the breeding cycle of _E_. _difficilis_. Males sing extensively through the morning prior to the arrival of the female and during nest building and incubation, but sing very little during courtship or after the chicks hatch. This is contrary to the descriptions of Davis et al. (1963), who observed that unmated males sing through the day, and that mated males sing at dawn only. These different observations suggest that geographic variation in singing behaviour exists. Further studies of vocal and breeding behaviour at other locations are needed to test this possibility.

Descriptions of the uses of calls at different stages of breeding have been given. I have presented original descriptions of Ti-ti-ti, Weet-weet-weet, Seet, and Rasp calls in this species. Conversely, I did not observe certain vocalizations described by Davis et al. (1963): alarm notes ('Tsit') or 'Pik-pik-pik'. These authors' observations on the use of vocalizations also differ from mine. First, they make no reference to the use of Pee-ist calls in vocal exchanges between neighbouring males. Second, they state that males never use Tsip calls. However, my observations support theirs (a) on the use of Chrrip in aggressive situations and in vocal exchanges between mates near the nest, and (b) on behaviour during courtship, including displacements, short chases, call exchanges, foraging in close proximity, and attacks on other flycatchers.

Behaviour associated with feeding the young is elaborate. Davis et al. (1963) also noted vocal exchanges between mates while females were on the nest, and found that females usually leave the nest when males approach with food [contra Sakai (1988)]. Unlike Davis et al. (1963), however, I did not observe lengthy exchanges of Pee-ist calls between mates while the female was on the nest. The complex behaviour of males feeding the young while the female is brooding has not previously been described. As in this study, Davis et al. (1963) observed the male feeding the nesting female.

Polygyny has not previously been described in difficilis. Limited polygyny has been described in three species of Empidonax: the Acadian, Least, and Willow Flycatchers (Mumford, 1964; Prescott, 1986; Briskie and Sealy, 1987). No estimate can be made of the frequency of this behaviour or of its effect on male and female fitness, based on the small sample in my study.

The lengths of breeding stages in Davis et al. (1963) and Sakai (1988) are close to my estimates. This is surprising because both those studies took place in California, where a longer breeding season would be expected. Dates for each stage in my study are slightly earlier than those in Sakai (1988; see my Table 5). More northerly nesting birds, therefore, may finish breeding earlier simply by starting earlier.

My study confirms the observations of Davis et al. (1963) and of Sakai (1988) that females build the nest and incubate and brood the young by themselves, while both sexes contribute equally to feeding the young. Also in agreement with Davis et al., I observed an instance of a female ceasing to feed fledglings sooner than did the male. I agree with those authors' suggestion that females cease to feed the young in order to renest. Renesting after a successful brood has been previously noted by Williams (1943) and Davis et al. (1963). Renesting after unsuccessful completion of a brood was previously reported by both Davis et al. (1963) and Sakai (1988).

2. Constraints on and Functions of Vocalizations

In this section, I make inferences about function based on observed patterns of individual, temporal, and situational variation.

2.1. Individual Variation

The primary function of individual variation is recognition, as discussed in the Introduction (Section 3.2.1). Three observations suggest that recognition, not only of conspecifics but of individuals, would be advantageous in this species. First, neighbouring males frequently exchange calls. Individual recognition of voice in these exchanges would allow males to identify other males as neighbours. Because neighbours probably present less threat to territories, the ability to recognize neighbours allows less energy to be spent defending territories (Falls, 1982). Second, mates both participate in raising the young. Activities associated with raising young are better coordinated if mates recognized each other individually. For example, it is to the brooding female's advantage to leave the nest only in response to her mate's Pee-ist calls and not to those of other conspecific males. Third, fledglings call in response to Pee-ist or Tsip calls. It is advantageous to the fledglings to call only in response to their parents, since any additional calling renders them more susceptible to predation.

The three observations given above only suggest that individual recognition would be advantageous in this species. They do not provide evidence for the existence of individual recognition. Two further observations, while not conclusive, suggest the existence of individual recognition in this species. First, aggression between mates declines as the breeding season progresses due, perhaps, to increasing familiarity with each other's vocalizations. An alternative explanation for lesser aggression between mates is declining hormone levels as the season progresses. The facts that males continue to sing and that renestings occur until at least July suggest, however, that hormone levels do not decline strongly in May and June. Second, males approach to near the nest, call until receiving a response, and only then approach the nest to feed the young. The length of time that this process takes suggests that males identify themselves as individuals and not just as conspecific males before approaching.

The potential bases for individual recognition have been demonstrated by this study. Substantial individual variation (ratio among/within C.V. > 1.0) occurs in syllable proportions, transition probabilities, frequencies, syllable durations, and intervals between syllables. As well, considerable qualitative differences among birds in physical structure of vocalizations have been described. Recent research has suggested that birds are less perceptive of variation in whole-song features, such as sequence, than they are of features of single notes or syllables, such as frequency or duration (Kreutzer, 1990; Weary, 1991). Weary (1991) stated that this perceptual ability allows rapid identification of an individual, since only a few notes then need to be heard. Also, it allows more accuracy, since more repetitions of the former are heard in a given period of time. In either case, this suggests that, of the features found to vary among individuals in difficilis, syllable proportions and transition probabilities are unlikely bases for individual recognition.

The suitability of a particular feature as a basis of individual recognition depends also on how perceptive birds are to variation in that feature. Dooling (1982) suggested that birds can perceive changes of 1-2% in frequency and 10-20% in temporal features. If this is true of Empidonax, individual recognition is unlikely to be based on syllable duration or on intervals between syllables. Many of the mean values of each bird on these measurements are well within 10% of one another (Table 11). Studies of perceptual abilities therefore suggest frequency to be a reasonable basis of individual recognition. Most of the mean frequency values of each bird differ from those of the other birds by more than 2%.

2.2. Temporal Variation

Three general approaches to inferring the function of temporal and situational variation were presented in the Introduction (Section 3.2.2). Most of the following inferences about function are based directly on the situations or the time in which vocalizations or certain variants were observed. As well, some inferences are based on the message-meaning model of Smith (1977). That is, I infer function (or the 'message') from the association of vocalizations with other behaviour of the signalling bird.

The daily pattern of gradual decline in song output from early morning until around noon, when song ceases altogether, is the most striking pattern of temporal variation in this species. This pattern is common among birds (Kacelnik, 1979), and various theories have been advanced to account for it. Morton (1975) and Henwood and Fabrick (1979) have suggested that many species of birds sing only at dawn because air turbulence due to daytime warming restricts the distance at which vocalizations can be heard later in the day. Kacelnik (1979) proposed that birds sing at dawn because foraging efficiency, due to low light levels, is low at that time. Two other theories were reviewed by Kacelnik and Krebs (1983). The first holds that birds sing at dawn because the mobility of invertebrate prey is low in the early morning. The second suggests that high overnight mortality of territory holders gives challengers a high probability of finding empty territories in the morning and thus obliges territory holders to advertise their presence at that time. These theories are not mutually exclusive, and one or all may apply to my observations, particularly since the observed song pattern may have evolved in an environment different from the present one. Some of the theories, however, appear to be more likely than others, based on the circumstances observed. Air turbulence may not be a factor in this study because daytime heating within the forest environment on the Queen Charlotte Islands is slight. Similarly, limited foraging efficiency due to low light levels may not explain the pattern of song in this case because the birds continue to sing at high levels until well after full daytime light levels are in effect. I made no observations to support the 'territorial challenge' theory. For example, there was no obvious tendency towards greater numbers of border exchanges in the early morning. Beyond that, as will be argued below, the primary function of song in this species appears to be mate attraction and not territorial defence. The fourth theory, that of food availability, therefore is the most likely explanation of the diurnal pattern of singing in this population. Decline in singing was mirrored by an increase in insect activity levels over the morning from near nil at dawn.

A number of other song features vary with time of day. In summary, vocalizing rate, low-frequencies, and song complexity[8] decline as the day progresses. High vocalizing rates, frequencies, and song complexities have frequently been linked to situations that would be presumed to increase excitation, for example in territorial encounters (Becker, 1982). Since daily declines in song output are concurrent

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8. Declining song complexity is a function of declining proportions of syllable 2 in the song.

with variation in syllable proportions, frequencies, and intervals (Fig. 14), it is reasonable to suggest that this variation provides a means of sending a graded signal, intermediate between the extremes of song and no song. I argue below that the primary function of song is to attract a mate. Declining frequencies and increasing intervals may therefore indicate a reduced tendency to interact with females. Pee-ist frequencies do not decline with time of day, suggesting that declining frequency is not a general phenomenon, but one related specifically to the message of song.

Frequency characteristics of vocalizations also tend to decline with date. I suggest that declining frequency is a reflection of the fact that it becomes increasingly less profitable to attract a mate as the season progresses. There are two reasons why it is less profitable to attract a mate later in the season. First, one mate has likely already been attracted. Second, the opportunity to successfully raise a brood declines as food supplies diminish and the end of the summer nears. It therefore is again reasonable to suppose that variation in frequency with date provides a means of sending a graded signal, intermediate between song and no song. A final change in song characteristics with date is the decreased interval between S2 and S3. The function of this variation is unclear.

2.3. Situational Variation

In this section I speculate on the function of vocalizations, based on patterns of variation among situations. It must be emphasized that definitive statements about vocal function (sensu Smith, 1977) hinge on systematic observations of the responses of recipients (Kroodsma and Byers, 1991).

2.3.1. Song

Variation in song production by stage of breeding (Fig. 14) suggests that the primary function of song is to attract a mate and not to defend territories. Song production declines precipitously upon attraction of a mate and, when it resumes during nest construction and incubation stages, males relocate their song territories away from the nest. Furthermore, males resume singing if a nest has been destroyed during the brooding stage. If territorial defence is the primary function of song, males would be expected to sing at locations and at times when territorial defence is necessary--near the nest and during nest construction and incubation. Two other observations support mate attraction as the primary function of song. At the only territory (A2) where I could hear the male singing when I was near the nest, I observed the female attack her singing mate. If the function of male song is territorial defence, it would not benefit the female to attack her singing mate. It is, however, to the female's advantage to prevent the male from attracting a second mate. The second observation, one made a number of times, was that singing males switch to calls, primarily Pee-ist, whenever a neighbouring bird is audible. If territorial defence is the primary function of song, males would be expected to continue to sing after detecting potential intruders.

The fact that the primary function of song appears to be mate attraction does not preclude territorial defence as a secondary function. The effect of song on a passing male's proclivity to challenge for a territory is not known. As well, the individual distinctiveness of song revealed by this study suggests that song may identify individuals so that aggression between neighbours may be avoided.

2.3.2. Pee-ist

There appear to be two main functions of Pee-ist calls. The first function is territorial defence. As mentioned above, Pee-ist is the primary vocalization in border exchanges between neighbouring males. As well, production of Pee-ist does not change drastically with stage of breeding (Fig. 14). This suggests that the function of Pee-ist calls on the song portion of the territory does not change with stage of breeding. Since territories are maintained throughout the breeding season, this in turn suggests that Pee-ist functions in territorial defence. Numerous observations of males approaching the nest with Pee-ist calls before going to the nest suggest that identification of self and of location may be other functions of Pee-ist calls. Such identification in turn facilitates coordination of feeding the young.

The association of Pee-ist calls with movement, often without any other apparent stimulation, suggests that Pee-ist calls provide a message about the probability of flight.

2.3.3. Tsip

Tsip vocalizations are used by females in much the same manner as males often use Pee-ists--near the nest and in exchange with their mates. This suggests that Tsips are also used to identify self and location. Since females are capable of producing Pee-ist calls, the similar functions of Pee-ists and Tsips poses the question of why females do not also use Pee-ist calls on a regular basis. One possibile explanation is that females are frequently on the nest. Pee-ist calls have greater amplitude than do Tsips and thus render the caller more easily located, making Pee-ists a poor choice for nesting females.

Tsips and Pee-ist calls are used by parents as they approach fledglings. These calls appear to stimulate the chicks to vocalize, making them more easily located.

2.3.4. Other calls

Chrrips are associated with aggression between mates, between neighbours, and between males and other species of birds. This suggests that Chrrips send a message about willingness to interact aggressively to defend territory, offspring, or self. The harsh tone and relatively low frequency of Chrrips also suggests that they function in aggression (Morton, 1982).

As with Pee-ist calls, Ti-ti-ti calls are associated with movement. They thus may provide a message about the probability of flight. As well, Ti-ti-ti calls are sometimes used in border exchanges and in courtship, suggesting a willingness to interact somewhat less than that indicated by Chrrips. Their spectrographic similarity to Chrrip calls (Figs. 9 and 10) supports this contention.

It is difficult to speculate on the function or message of Weet-weet-weet, Zeet, or Seet calls, since these were rarely heard. The fact that they were heard primarily during courtship, however, suggests that they are used while the bird is excited or aggressive.

The most obvious function of the chicks' Sip vocalization is to solicit food. This is supported by the fact that calling rates are high when a parent is present and feeding the chicks. Given the increased mobility of fledglings as they grow older, a second function of Sips must be to enable adults to locate fledglings. Rasp vocalizations appear to be given by chicks as they are being fed. The function of this behaviour is unclear.

3. Extent and Sources of Variation

A description of variation in vocal characteristics of one population of *E. difficilis* has been provided. This description may now serve as a basis for comparisons with other populations and for choosing appropriate techniques for population surveys. In this section, I provide recommendations for these. As well, I discuss how variation described here compares with previous descriptions of this species and others.

3.1. Comparison with Other Populations

3.1.1. Recommendations for comparisons of populations

Where significant variation due to date, time, or presence of the female has been detected, the best option is to take measurements from different populations at approximately the same date, time, and stage of breeding. Because it would be time-consuming to determine whether a female is present every time a male is recorded, it is fortunate that there is apparently little effect of the female's arrival on vocal characteristics (Table 11).

Despite that, taking measurements at the same time and date for a large number of populations may not be practical. A second strategy is to adjust measurements for the different times and dates that they were taken. This is straightforward in the case of spectrographic variables for which regression coefficients have been determined (Table 11). Regressions were not done for proportions of syllables or for transition probabilities, and therefore, adjustments to these for time of day or date can only be approximate. Proportions of syllables and transition probabilities did not vary with date, and therefore, it is only necessary to ensure that these measurements are taken at the same time of day. Doing so is practical for most research.

Low-frequencies declined significantly with time of day and with date as much as 27 Hz per hour and 5.5 Hz per day (Table 11). Given the approximately 7 hours per day (0500 to 1200) and the range of 70 days (early May to mid July) in which the birds sing, these rates would result in maximal declines of 190 and 385 Hz respectively. Johnson (1980) reported ranges in population means of frequency measurements of up to 1500 Hz across the geographic range of _difficilis_ (including _occidentalis_). Temporal variation would not need to be considered to distinguish populations differentiated by 1500 Hz. For less strongly differentiated populations, however, temporal variation of low-frequencies must be considered.

Intervals increased with time of day as much as 97 msec per hour. I23 declined significantly by 14 msec per day. At these rates, intervals would increase by 680 msec over a day and decrease by 980 msec over a breeding season. Johnson (1980) reported ranges in population means of interval measurements of 280 and 350 msec, so the effect of temporal variation must be considered in comparing any populations of _difficilis_.

The only significant temporal variation in duration measurements was in DU2, which increased by 0.078 msec per day. This rate represents a maximal increase of 5.5 msec over the breeding season. Johnson (1980) did not measure the duration of S2. However, the range in population means for DU1 is reported to be 56 msec. Assuming geographic variation in DU2 to be similar, temporal variation in DU2 is probably not a serious concern.

I found no significant temporal variation in high-frequencies or Pee-ist frequencies. Given the large effects found of date and time of day on Pee-ist frequencies (Table 11), it would nevertheless be prudent to consider temporal variation when making Pee-ist frequency measurements.

Significant variation with time of day was found in the probabilities of transitions 12, 13, 1P, 3P, P1, and PP, and in the proportions of S2 and the Pee-ist call (Fig. 16 and Table 7). No studies in geographic variation of such measurements have been done. However, the very large changes in transition probabilities and in syllable proportions with time of day strongly suggests that it would be prudent to consider temporal variation in comparing populations (Fig. 16, Table 7).

Only one measurement was significantly related to female presence. DU2 increased by 2.9 msec after the arrival of the female. Given the geographic variation in DU1 reported by Johnson (1980; see p.139), this is not likely to seriously affect geographic comparisons.

Levels of individual variation affect the sample size needed to compare populations. Sample sizes required to detect the difference between this population and one that varies from this one by 10% on a given measure are shown in Table 14. Power and significance level are set at 0.9 and 0.05 respectively. For each class, the most variable measurement was chosen as the basis for calculation. See Methods and Materials for details of the calculation.

Sample sizes required for each class of measurement suggest that it may be impractical to compare populations on measures of intervals, transition probabilities, or syllable proportions. Restricting population comparisons to the least variable measure within each category would reduce the necessary sample size somewhat.

3.1.2. Comparisons with variation found in other studies

Johnson (1980) reported levels of variation among

Table 14. Minimal sample sizes required for comparison of two populations, based on levels of individual variation found in this study. See Methods and Materials for description of technique and assumptions.

Measurement Category	n
Duration	21
Interval	80
Song frequencies	14
Call frequencies (PFPA, MFPB only)	16
Transition probabilities (12, 23, 31 only)	139
Syllable proportions (1, 2, 3 only)	151

individuals comparable to those presented here (Table 10). One exception to that is among-individual variation in MF1C, which in Johnson's study is considerably higher than variation found in other frequency measurements. In five of six variables, variation among individuals is somewhat less in this study than in Johnson (1980). This is likely because Johnson made one measurement per individual of each variable, while I made up to thirty-six per individual for frequency and duration measurements and up to one hundred per individual for interval measurements (see Methods and Materials). Also, I ensured that measurements of birds were from comparable dates and times, while Johnson (1980) apparently did not.

Variation among individuals in transition probabilities or in syllable proportions has not previously been documented in this species. Temporal or situational variation in any difficilis vocal feature has also not previously been reported.

In agreement with most other studies of avian vocalizations, variation among individuals is greatest in intervals, less in durations, and least in frequencies (Miller, 1986), (Tables 10, 15). As Miller (1986) suggested, this likely reflects constraints on the mechanisms or control of vocal production. For example, variation in frequency is limited by body size, while variation in temporal features is under no such constraint.

Table 15. Summary of variation in vocal characteristics among individuals in selected species. Where more than one measurement of a type was reported, the average coefficient of variation is given.

Study	Coefficient of Variation Duration	 Interval	 Frequency
Nonpasserines			
Nuechterlein, 1981 Western Grebe (*Aechmophorus occidentalis*)	0.401	0.634	0.099
Miller, 1986 Least Sandpiper (*Calidris minutilla*)	0.041	0.086	0.025
Passerines (Sub-oscines)			
Present--Pacific -slope Flycatcher	0.078	0.154	0.054
Payne and Budd, 1979 Acadian Flycatcher (*Empidonax virescens*)	0.135	---	0.057
Passerines (Oscines)			
Gaddis, 1985 Mountain Chickadee (*Parus gambeli*)	0.224	0.284	0.068
Konishi, 1964 Dark-eyed Junco (*Junco hyemalis*)	0.366	0.256	0.070
Marler and Tamura, 1962 White-crowned Sparrow (*Zonotrichia leucophrys*)	---	---	0.082

Additionally, temporal measurements are subject to twice as much measurement error as are frequency measurements, since they require the identification of two points on a spectrogram.

Comparisons of variation in vocal characteristics with that of other studies, especially of other species, are difficult to make because of differences in procedure. Measurement error varies among species because the vocalizations of some species produce spectrogram traces with more sharply defined edges than do others. Nevertheless, a brief sampling of the literature suggests that variation in _difficilis_ vocalizations is less than in oscines (Table 15). Vocal learning is common in oscines, including the genera represented in Table 15 (Kroodsma and Baylis, 1982). Conversely, studies by Kroodsma (1984) on Willow and Alder Flycatchers and by Payne and Budd (1979) on Acadian Flycatchers suggest that vocalizations are innate in _Empidonax_. As well, a study on Eastern Phoebes (_Sayornis phoebe_) suggests that vocalizations are innate in the family Tyrannidae and perhaps in all suboscines (Kroodsma, 1985). Learning of vocalizations in oscines adds an extra dimension of variation among individuals in oscines (Kroodsma, 1982; Mundinger, 1982). Variation in Least Sandpipers, for which vocal learning has not been reported (Kroodsma and Baylis, 1982), is less than in _Empidonax_ (Table 15). Reasons for this difference are unclear, but it suggests some vocal learning in Empidonax.

learning in Empidonax. High variation found in Western Grebes (Table 15) may be due to the poorly defined edges of spectrographic traces produced from vocalizations of this species and the corresponding difficulty in measurement.

3.2. Population Surveys

In the procedure described by Emlen (1977) for conducting a population survey along a transect, cue frequency is used to adjust the number of times that vocalizations are heard from different individuals while walking a transect. Cue frequency is the proportion of samples of a certain length of time in which a cue is expected to be heard. Emlen (1977) recommended that song be used as the cue during the breeding season. Two observations from this study suggest that song would be a more accurately determined cue than would calls. First, early in the morning during pre-female and nesting stages, there is less variation among individuals in song production than there is in Pee-ist production at any time (Table 3). Second, song performances are more continuous than is production of any of the calls, which are often produced in bouts in response to specific stimuli.

Stage of breeding strongly affects song production, and therefore the current stage of breeding must be known.

Variation among individuals in breeding chronology precludes using date as a simple guide to stage of breeding (Table 5). Only prior to the arrival of the female are all males at the same stage of breeding, and I therefore recommend that population surveys of <u>difficilis</u> be conducted at that stage. The first female of this study was not apparent until May 10, and therefore Queen Charlotte Island populations should be surveyed in the first week of May. The relatively low level of variation among individuals in song production early in the morning suggests that surveys conducted within three hours of sunrise would be most accurate (Table 3).

Values represented in Fig. 14 are proportions of time spent vocalizing per hour long sample, and are therefore not directly translatable to cue frequency (see above for definition). Cue frequencies may, however, be estimated from information in Fig. 14 and from the amount of time that a surveyor spends in each territory.[9] The proportion of time spent singing prior to the arrival of the female is 89% (Fig. 14), and therefore if a surveyor spent as much as ten minutes in a territory, the cue frequency would approach 100%. Conversely, if a surveyor spent a short time in each territory, cue frequency would be closer to 89%.

In summary, transect counts will produce the most accurate estimates of <u>difficilis</u> populations in early spring

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[9] Time to walk across a territory depends on its size. Territories of this study averaged approximately 150m in length (Fig. 2).

and within three hours of sunrise. Cue frequencies used to adjust these counts will be 89 to 100%, depending on the rate of surveying.

4. **Structure of Variation**

Functions and extent of variation have been discussed in Sections 2 and 3 respectively. In this section, I examine phenomena underlying this variation among individuals or times. I first discuss how spectrographic measurements (interval, duration, and frequency) are intercorrelated. Second, I discuss how variation in transition probabilities is related to variation in syllable proportions, chi-statistics (indicating tendency to produce a transition beyond the proportions of syllables in the sample), and intervals between syllables. As well, I briefly discuss the effect on transition probabilities of the syllable preceding the transition.

4.1. Spectrographic Measurements

Cluster and Principal Components analyses reveal correlations among frequency measurements across individuals (Fig. 35, Table 13a). Birds can therefore be characterized by the pitch of their voice. This is not surprising since a prime determinant of pitch is size of the vocal tract, which is characteristic of each bird. Stronger correlations are found among subsets of frequency measurements. A high correlation between PF1A and PF2A and spectrographic similarities between E1A and E2A suggest that E1A and E2A are identical elements. That is, S1 and S2 appear to have been formed through the combination of one element (E1A/E2A or some precursor) with different elements. Moderately high correlations among high-frequency song measurements (MF1B, PF2B, and MF3) show that the tendency to have a generally high, medium, or low voice is particularly strong among the high-frequency variables. Finally, the moderate correlation between PFPA and MFPB suggests that there is no relationship between the frequency of either of the points represented by these variables and the difference in frequency between these points.

Weak correlations among duration and interval measurements across individuals reveal that birds cannot be characterized by rate of singing (Fig. 35, Table 13a). Thus, for example, a long mean interval between two syllables in a given bird does not suggest a long mean interval between other syllables in that bird. I can suggest no reason for the moderately high correlation between measurements DUP and I31.

Moderately strong correlations among low-frequency measurements (PF1A, MF1C, PF2A, and PF2B) across times indicate that dates and times of day can be characterized by pitch (Fig. 36, Table 13b; see also Table 11). With the partial exception of MF3, remaining frequency measurements vary independently. Moderate correlations between DU1 and DUP and particularly between I12 and I23 suggest that dates and times of day may be characterized generally by rate of singing.

Correlations across times among song variables suggests that the mechanism underlying temporal variation operates on the whole song and not just on certain elements or syllables. I have suggested that declining frequencies and increasing intervals as the day progresses provides a message about tendency to interact with females (Section 2.2). Correlations among interval variables and among song frequency variables found in this study suggest that this message is provided by the whole song. Conversely, generally low correlations between song and Pee-ist variables suggest that Pee-ist provides a different message.

4.2. Transition Probabilities

4.2.1. Individual variation

Variation in transition probabilities (Table 8) reflects variation in probabilities of syllables as a function of time since production of the first syllable (Figs. 19, 23, 27, 31). For example, birds A1N, A3, and A7 follow S3 with S1 relatively infrequently and have corresponding low probabilities of S3 at relatively brief intervals after S1 (Fig. 27). As well, low probabilities for transition 13 in birds A2 and A4 accord with a tendency to not follow S1 with S3 until a relatively long period of time after S1 (Fig. 19). However, variation among birds in transition probabilities is not always explained by corresponding variation in probabilities as a function of interval, as presented in Figs. 19, 23, 27, and 31. For example, birds A2, A3, and A4 follow S1 with S2 considerably more frequently than do the remaining birds, and despite that, only A2 follows S1 with S2 at particularly long intervals after the production of S1 (Fig. 19). How then do A3 and A4 manage to follow S1 with S2 so often, despite their typical profiles for the S1-S2 transition? Since S2 follows S1 most commonly after brief intervals, I would expect a brief mean interval between S1 and S2 in A3 and A4. Table 10 shows this to be so. In summary, variation in transition probabilities among birds is a function both of probabilities of syllables as a function of time since the preceding syllable and of mean intervals between those syllables.

Transition probabilities (Table 8) correspond to both syllable proportions (Table 6) and chi-values (Table 9). Thus, bird A4 follows S2 with S1 a high proportion of time and has a high proportion of S2 within its song and a high chi-value for transition 12. As well, the tendencies of birds A2 and A4 to not follow S1 with S3 corresponds well to low proportions of S3 and low chi-values for transition 13 in those birds. However, the relative contribution of variation in syllable proportions and chi-values to variation in transition probabilities varies among birds. For example, like birds A2 and A4, bird A3 tends to not follow S1 with S3. Despite that, A3 has a high proportion of S3 in its song. A low probability for transition 13 in this bird is a reflection of a low chi-value (Table 9).

The relative contribution of variation in syllable proportions and chi-values to variation in transition probabilities also varies among transitions. For example, variation among birds in probabilities of transition 31 is not related to variation in syllable proportions (compare Table 6 with Table 8, particularly for birds A4 and A7). Correlations between transition probabilities and syllable proportions and between transition probabilities and chi-values are given in Table 16. These correlations provide a measure of the relative contribution of syllable proportions and chi-values to variation among individuals in transition probabilities. In summary, transition probabilities are a reflection both of syllable proportions and chi-values, but the strength of these relationships varies among both birds and transitions.

Table 16. Summary of the association between transition probabilities and syllable proportions and between transition probabilities and chi-values for various intervals.

Transition	Transition-Syllable[a]	Transition-Chi-value[b]
11	0.724	0.989
12	0.985	0.937
13	0.766	0.990
1P	0.648	0.535
21	-0.058	0.890
23	0.397	-0.106
2P	0.657	-0.369
31	0.599	0.970
32	0.003	0.141
33	0.898	0.988
3P	0.753	0.590
P1	0.406	0.980
P3	0.799	0.976
PP	-0.698	0.883

[a] Correlation between transition probability and proportion of the second syllable in the transition.
[b] Correlation between transition probability and chi-value for that transition.

4.2.2. Temporal variation

Variation in transition probabilities by time of day (Fig. 16) corresponds well to probabilities in syllables as a function of time since production of the first syllable (Figs. 20, 24, 28 32). For example, lower probabilities for transition 12 as the day progresses are reflected in lower probabilities of S2 at shorter intervals after production of S1 (Fig. 20).

Variation in transition probabilities by time of day (Fig. 16) also corresponds well to proportions of the second syllable in a transition (Table 7). Thus, significant variation in probabilities for transitions 12, 1P, 3P, and PP reflects variation in proportions of S2 and Pee-ist calls. Variation in transitions 13 and P1, however, is not explained by variation in proportions of second syllables in these transitions. Changes in these transitions correspond to changes in chi-values (Fig. 17). That is, an increase and a decrease, respectively, in probability of transitions 13 and P1 reflect corresponding changes in predilection for these transitions. Some variation among dates in probabilities of syllables as a function of time since production of the first syllable has been identified (Figs. 21, 25, 29, 33). In no case did this result in significant variation in transition probabilities among dates. This is not surprising, since variation among dates shown in Figs. 21, 25, 29, and 33 is minor.

4.2.3. Variation with preceding syllable

Transition probabilities as a function of the syllable preceding a transition have been documented in Fig. 34. Clearly, the probability of occurrence of a given syllable usually depends on the identity of the preceding two syllables. In other words, there is evidence of second-order Markov chains (Chatfield and Lemon, 1970).

5. Definition of a Song in Empidonax difficilis

Thus far, I have described song components and the sequence in which they occur. That is, song in difficilis consists of three syllables that are produced in a more or less predictable order.[10] How these syllables are arranged to form a song remains to be determined. Is the song, for example, S1-S2-S3 or is it S3-S1-S2? Alternatively, a song, in the form of a recognizable and organized unit, does not exist in this species.

Identification of the start and end of a particular song is based primarily on relative lengths of intervals between song components (Armstrong, 1973). For example, in

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[10] I do not consider Pee-ist calls to be part of song because song is frequently given with few or no Pee-ist calls and because Pee-ist calls are not arranged into a sequence within song to the same extent that S1, S2, and S3 are. Moreover, the intervals before and after a Pee-ist call tend to be long (Table 13).

the sequence ABCABCABC..., BCA would be identified as a song if the interval between A and B were generally longer than were other intervals. By this reasoning, Davis et al. (1963) determined that a song in difficilis was generally S1-S2-S3 (using terminology of the present study), while Johnson (1980) thought that the song was usually S3-S1-S2. Comparison of mean lengths of intervals 12, 23, and 31 (Table 11) provides evidence for Johnson's view: the interval between S2 and S3 (1485 msec) is larger than either of the other two (821 and 1037 msec). These interval lengths differ considerably less from each other than do intersong and intersyllable lengths typically found in bird song. Marler and Isaac (1960a,b) and Thompson (1972), for example, reported intersong intervals that are a magnitude or more larger than intersyllable intervals. There may therefore be insufficient basis to conclude that S3-S1-S2 is a song.

Variability in interval lengths provides a second source of evidence for determining the structure of song. Since song is defined, in part, as sequences of vocalizations arranged into a recognizable structure, it is reasonable to expect that intervals between syllables of a song will be less variable than intervals between songs. Variation in interval 23 is slightly greater than that for intervals 12 or 31, both within- and among-individuals. This pattern of variation supports Johnson's S3-S1-S2 arrangement of syllables, although here again the differences in variability are not large.

It is also reasonable to expect that the first utterance after an interruption in singing will typically be the beginning of the song. Production of a Pee-ist call represents one such interruption, and S1 is clearly the preferred song syllable after a Pee-ist call (Fig. 15). This supports the S1-S2-S3 sequence favoured by Davis et al. (1963).

The evidence, based on interval lengths, interval variability, and first vocalization after an interruption, is contradictory. Because of this, there is little basis for defining any sequence (of any length) of _difficilis_ vocalizations as a song. As is true of the use of subspecies in taxonomy (see Introduction), categorization inhibits full description and appreciation of variation. One consequence of that is found in Johnson (1980). On the basis of his S3-S1-S2 conception of _difficilis_ song, Johnson chose to not measure the interval between S2 and S3. There is enough documentation of variation in this thesis to conclude that S1-S2-S3 and S3-S1-S2 are both typological representations of _difficilis_ song. No evidence exists to suggest a correspondence between any song that we might define and the way the birds perceive or produce vocalizations. This provides further reason to not designate a song in this species.

6. Evolution of Empidonax difficilis Vocalizations

6.1. Evolution Within the Genus

The pattern of evolution of vocalizations within *Empidonax* is difficult to discern for two reasons. First, as I have described in the Introduction, relationships among *Empidonax* species are generally unclear. There is no indication of a strong relationship, for example, among those species endemic to western North America (Cordilleran, Dusky, Gray, Hammond's, Pacific-slope), and thus it is difficult to determine whether the multi-syllable song repertoire common to these developed in an ancestor or evolved separately in each species. Second, vocalizations can evolve rapidly since they are free of biological constraints that apply to morphological change (Payne, 1986). For example, the effect of vocal change on function is much less than the effect of change in wing span on flying. In spite of these difficulties, I offer two observations that might have a bearing on *Empidonax* vocal evolution.

The first observation is that of trace levels of polygyny in *difficilis*. As described in the Introduction (Section 3.1), research has either suggested that polygyny should strengthen sexual selection or that it should weaken it (Kroodsma, 1977; Catchpole, 1980; Catchpole and McGregor, 1985; Loffredo and Borgia, 1986). Ornate or exaggerated characteristics are usually the result of strong sexual selection (West-Eberhard, 1983), but there appears to be no trend toward particularly simple or complex song among the four species of *Empidonax* now known to be polygynous. Song in Least, Willow, and Acadian Flycatchers consists of one syllable, comparable in complexity and length to S1 of *difficilis* (Johnson, 1963; Payne and Budde, 1979; Kroodsma, 1984), while *difficilis* song consists of three syllables. By that measure, the song of *difficilis* is among the most complex found in *Empidonax*. Variation in song complexity among species of *Empidonax* is not related simply to sexual selection. Two caveats apply to this conclusion. First, polygyny has been found at only trace levels in *Empidonax*, and the effect of such levels of polygyny on strength of sexual selection is uncertain. Second, three of four documented cases of polygyny in *Empidonax* have been provided within the last five years, and therefore the distribution of polygyny in *Empidonax* is probably not fully documented. For these reasons, conclusions about the relationship between polygyny and vocal characteristics in *Empidonax* are tentative.

The second observation that might have a bearing on *Empidonax* vocal evolution is that all *Empidonax* species with multi-syllable song are endemic to the western third of the continent and have overlapping breeding ranges there

(Farrand, 1983). No other area contains so many Empidonax species, suggesting that song complexity may have evolved under selection for species isolation and may be maintained by it.[11]

6.2. Evolution Within the difficilis Species Complex

The difficilis complex consists of E. difficilis, E. occidentalis, and E. flaviventris (Johnson, 1980). Based on morphological and vocal characteristics, Johnson drew conclusions about the evolution of this group and of the taxonomic status of its members (see Introduction, Section 1). In this section, I review the findings of this study that have some bearing on those conclusions. Criticisms of his methods have been presented in the Introduction of this thesis. As well, on the basis of variation found in this study, I have argued that consideration must be given to temporal and individual variation in vocal characteristics before populations are compared (Discussion: 3.1.1).

This study corroborates Johnson's finding that song of coastal difficilis populations is characterized by higher frequencies and frequency spreads than song of interior occidentalis or insulicola populations (Table 17). However, frequencies reported herein are higher than those given in

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[11] Evidence for song complexity evolving in complex song environments is equivocal. Miller (1982) reviewed this issue.

Table 17. Geographic comparisons of interval, frequency, and frequency spread measurements of _E_. _difficilis_/ _occidentalis_ vocalizations.

Measurement	Channel[a] Islands	Coastal[a,c]	Interior[a,c]	QCI[b]
Frequency (Hz)				
MF1C	4191	4880-5067	3800-4443	5101
PF2B	4900	5400-5417	3900-4200	5638
MF3	5282	5960-6108	5100-5733	6387
Freq. Spread (Hz)				
Freq. Spread S1	3964	4000-4333	2086-2267	4900
Freq. Spread E1C	2036	2300-3367	767-1150	3500
Duration (msec)				
DU1	258	202- 227	255- 257	291

[a] Johnson (1980)
[b] Present study
[c] excludes measurements from populations in southern Oregon and in northern California near zone of contact between _difficilis_ and _occidentalis_

Johnson (1980). This is surprising since Johnson's measurements do not show a trend toward higher frequencies in northern populations. Of the three frequency measurements given by Johnson, only MF1C is highest in the most northerly population of that study (Bellingham, Washington). High frequencies reported here are not the result of small size, since Queen Charlotte Island birds are not significantly smaller than birds of other coastal populations (Johnson, 1980). Johnson speculated that the low-high-low pattern in clinal variation of a number of traits, including song frequency, corresponds with the cool-warm-cool weather pattern going from the Channel Islands to the Pacific Coast and to the Rocky Mountains. The frequencies reported here cast some doubt on that interpretation since the Queen Charlotte Islands are cooler than either the Channel Islands or the Rocky Mountains.[12] Like Johnson (1980), I found large frequency spreads in coastal <u>difficilis</u> populations. As with frequencies, frequency spreads found in this study are higher than any in Johnson (1980), in this case conforming to a trend apparent in Johnson's data towards larger frequency spreads in northern populations. Finally, a long duration for S1 found in this study is opposite to the trend in Johnson's data.

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12. Mean Daily Temperature, May: Massett, British Columbia (Queen Charlotte Islands): 8.9 °C; Avalon, California (Channel Islands): 15.7 °C; Twin Falls, Idaho (Rocky Mountains): 12.7 °C. (Source: Willmott et al., 1981)

Not only is the value of 291 msec larger than any measured in coastal populations in Johnson (1980), but it is also larger than values reported by him for insulicola or occidentalis. Because of the echo at the end of each song syllable in my recordings, some error is introduced into the measurement of durations (see Methods and Materials). Presumably the same measurement error was present in Johnson's recordings and, as I specifically took it into account, I do not feel that measurement error accounts for the difference between our findings.

Individual variation in spectrographic form of the three song syllables and of the Pee-ist call has been documented. Variation in the spectrographic form of song syllables falls within the range of variation exhibited by spectrograms of coastal birds given in Johnson (1980), although some spectrograms presented here contain features similar to those of interior or Channel Island birds. For example, while S1 spectrograms are clearly of the coastal type, E1B in birds A1N and A3 is similar to that of interior birds in having a blunt peak and rounded ascending portion (see descriptions of coastal, interior, and Channel Island forms in the Introduction). The steeply rising E1C of bird A1N is also similar to that of interior birds. S3 spectrograms in this study can also be identified as coastal, in this case by a slight rise in frequency. The frequency of S3 in birds A1N and A4, however, rises almost as much as it does in some interior spectrograms of Johnson (1980). S2 is also of the coastal form, in this case with no exception.

The numerous instances of interior traits in bird A1N are not matched by interior-like frequencies or interval durations in this bird (Table 10). Frequencies in this bird are above average, and DU1 is very near the mean of the seven birds.

Unlike song, Pee-ist spectrograms presented here differ from any given by Johnson (1980). Relatively slight frequency modulation, particularly in the terminal portion of the call, distinguishes the calls analyzed in this study from any of those presented in Johnson (1980). The terminal portion of this call rises from 2.5 to 3 kHz in coastal birds (Johnson, 1980) and from 0 to 1.5 kHz in this study. Of the 20 coastal spectrograms presented by Johnson, the terminal portion of one of the two from Vancouver, B.C. rises the least--by slightly less than 2 kHz. Since this is the most northerly location for which a Pee-ist spectrogram is provided in Johnson's study, the possibility of a north-south cline in this trait exists. Quantitative measurements of Pee-ist call frequencies are required to confirm this.

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APPENDIX A

Definitions of frequency, interval, and duration measurements made in this study.

Song Variables:

PF1A - peak frequency of E1A

PF1B - peak frequency of E1B

MF1C - frequency of middle part of E1C

PF2A - peak frequency of E2A

PF2B - peak frequency of E2B

MF3 - frequency of middle part of S3

I12 - interval between S1 and S2

I23 - interval between S2 and S3

I31 - interval between S3 and S1

I13 - interval between S1 and S3

DU1 - duration of S1

DU2 - duration of S2

Pee-ist Variables:

PFPA - peak frequency of first part of Pee-ist

MFPB - frequency of middle part of Pee-ist

PFPC - peak frequency of last part of Pee-ist

DUP - duration of Pee-ist

APPENDIX B

Date and time since sunrise of each tape recording used for analysis of frequencies, syllable durations, and intervals between syllables.

Bird	Date	Time Past Sunrise (hr)
A1N	May 13	2.00
	May 7	4.43
	May 13	9.20
	June 1	2.60
	June 2	4.65
	May 27	6.90
	June 29	2.07
	July 7	4.12
A1S	May 7	5.20
	May 20	1.16
	May 25	5.28
	May 24	7.65
	June 10	1.69
	June 4	4.37
	June 1	8.44
A2	May 21	1.95
	May 7	2.26
	May 24	10.98
	June 2	2.53
	June 2	5.33
	June 5	9.32
	June 29	2.54
	July 1	4.60
	July 4	8.30
A3	May 21	2.97
	May 7	3.21
	May 22	5.21
	May 28	2.28
	June 1	4.05
	May 30	7.33
	June 10	2.09
	June 10	4.25
	June 10	7.09

Bird	Date	Time Past Sunrise (hr)
A4	May 14	2.20
	May 11	3.55
	May 14	6.51
	May 31	1.67
	May 31	3.70
	May 31	6.88
	June 10	3.57
A5	May 14	7.05
	May 25	2.95
	May 27	3.96
	June 2	7.06
	July 3	3.04
	July 9	4.19
	July 3	5.92
A7	May 26	1.50
	May 25	3.92
	May 21	6.07
	June 12	1.74
	June 12	4.14
	June 12	6.95
	June 26	2.66
	June 26	4.58
	June 26	8.82

APPENDIX C

Date and time since sunrise of each written recording used for analysis of syllable proportions and transition probabilities.

Bird	Date	Time Past Sunrise (hr)
A1N	May 5	1.99
	May 5	3.39
	May 9	7.78
	June 5	1.65
	June 6	4.30
	May 26	6.41
	July 4	2.28
	July 7	3.75
	June 26	6.06
A1S	May 3	1.52
	May 3	3.25
	May 3	6.12
	May 19	0.63
	May 18	3.93
	May 22	7.77
	June 7	1.63
	June 4	4.53
	May 31	7.43
A2	May 3	1.98
	May 3	3.65
	May 3	8.13
	May 22	1.55
	May 23	3.22
	May 24	9.65
	June 4	2.45
	June 4	4.57
	June 4	7.63

Bird	Date	Time Past Sunrise (hr)
A3	May 6	0.93
	May 6	3.62
	May 6	5.96
	May 28	2.77
	May 19	3.64
	May 29	6.40
	June 10	2.04
	June 10	4.25
	June 10	7.32
A4	May 15	2.40
	May 15	4.79
	May 15	6.64
	May 31	1.72
	May 29	4.47
	May 31	6.77
	June 10	3.63
A5	May 14	7.19
	May 31	1.55
	May 27	4.15
	June 2	7.46
	July 3	3.37
	July 9	3.77
	July 6	6.18
A7	May 26	1.29
	May 25	4.28
	May 21	6.80
	June 8	1.70
	June 8	4.02
	June 12	7.39
	June 29	1.90
	July 5	3.61
	June 26	8.82

APPENDIX D

Pearson's product-moment correlations among variables based on mean values from each bird. Each correlation is multiplied by 1000 to clarify the presentation.

	DU1	DU2	DUP	I12	I13	I23	I31	MF1C	MF3	MFPB	PF1A	PF1B	PF2A	PF2B	PFPA	
DU1	---															
DU2	-354	---														
DUP	400	-339	---													
I12	- 89	-653	417	---												
I13	- 4	471	509	-223	---											
I23	- 49	-859	333	656	-201	---										
I31	233	-534	829	722	303	559	---									
MF1C	-731	269	- 71	173	290	95	251	---								
MF3	-491	55	-577	376	-555	- 71	-317	94	---							
MFPB	-813	- 16	065	250	109	439	157	695	60	---						
PF1A	-777	773	-545	-528	230	-440	-559	609	155	502	---					
PF1B	-551	-125	-636	268	-745	145	-454	5	871	275	196	---				
PF2A	-737	703	-579	-594	150	-387	-617	540	89	510	984	213	---			
PF2B	-502	227	-412	191	-529	-294	-384	55	796	195	281	782	243	---		
PFPA	-723	268	- 83	-173	264	137	- 11	795	-205	854	732	- 9	756	- 21	---	
PFPC	-358	206	-686	-622	-389	125	-746	51	11	275	589	379	717	179	484	---

Pearson's product-moment correlations among variables based on mean values from each combination of Date and Time. Each correlation is multiplied by 1000 to clarify the presentation.

	DU1	DU2	DUP	I12	I13	I23	I31	MF1C	MF3	MFPB	PF1A	PF1B	PF2A	PF2B	PFPA	PFPC
DU1	---															
DU2	611	---														
DUP	702	-198	---													
I12	565	-321	60	---												
I13	30	-294	294	-107	---											
I23	479	-504	- 68	847	-178	---										
I31	- 73	-107	- 50	228	274	120	---									
MF1C	447	13	454	384	-334	525	-332	---								
MF3	660	-231	646	583	154	590	-026	817	---							
MFPB	231	-614	-225	316	288	449	211	-306	- 73	---						
PF1A	364	-122	349	357	-209	573	-355	949	799	-285	---					
PF1B	515	132	185	590	-407	439	-431	566	524	- 51	419	---				
PF2A	411	-130	405	268	-340	464	-421	932	703	-392	963	398	---			
PF2B	460	-264	463	326	-109	494	-180	839	794	-375	927	292	925	---		
PFPA	350	-262	-318	672	-166	548	-067	- 86	68	565	-125	636	-195	-198	---	
PFPC	250	-402	-579	-148	265	- 51	-176	-664	-584	564	-490	-313	-501	-497	366	---

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Title of Thesis: Vocalizations and nesting behaviour of the Pacific-slope Flycatcher, *Empidonax difficilis*.

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January 13, 1992
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