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VOCALIZATION BEHAVIOR OF CAPTIVE LOGGERHEAD SHRIKES

(Lanius ludovicianus excubitorides)

by

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June 1995

A thesis submitted to the Faculty of Graduate Studies and Research

in partial fulfilment of the requirements of the degree of

Master of Science

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Suggested short title

VOCALIZATION BEHAVIOR OF LOGGERHEAD SHRIKES

"And Solomon (Sulaiman) was David's (Daud's) heir. And he said: O mankind ! Lo ! We have been taught the language of birds, and have been given (abundance) of all things. This surely is evident favour."

QOR'AN 27:16.

ABSTRACT

Vocalization behavior of captive loggerhead shrikes (Lanius ludovicianus excubitorides)

Mochamad Arief Soendjoto

M.Sc. Natural Resource Sciences

Vocalization behavior of captive loggerhead shrikes was studied at the Avian Science and Conservation Centre of McGill University. In the first stage, calls of two pairs kept in indoor cages were individually recorded not only to catalogue these calls spectrographically and quantitatively but also to use them in identifying the birds sexually. Males vocalized 21 call figures for 16.50% of the observation time and females, 8 call figures for 2.64% of the observation time. Males continuously delivered 1 to 11 bouts with a mean of 7.25 min for a rate of 6.06 bouts/h; females delivered 1 to 9 bouts with a mean of 4.07 min for a rate of 1.27 bouts/h. Males not only vocalized at a higher rate and longer than females, but also demonstrated trill calls which the females did not do. In the second stage, five pairs were paired in large outdoor breeding pens. Their calls were recorded and current visual displays observed in an effort to understand calls related to breeding behaviors. Two new call figures vocalized by males as well as 2 call figures by young shrikes were recorded. Each male demonstrated distinctive calls that differed from those of other males during nest-site selection, nest building and copulation, but similar calls during food offering, aggressive and alarm behavior. Despite the call differences, all males performed similar visual displays during the above activities. Conversely, breeding females gave no calls, other than harsh calls during food offering, food begging, aggressive and alarm behaviors.

RÉSUMÉ

Comportement de vocalisation de la pie-grièche migratrice (Lanius ludovicianus excubitorides) en captivité

Mochamad Arief Soendjoto

M.Sc. Natural Resource Sciences

Le comportement de vocalisation de pies-grièches gardées en captivité a été étudié au Centre de recherche et de conservation des oiseaux de l'Université McGill. La première partie de notre étude avait pour objet de quantifier et de caractériser spectrographiquement les cris de deux paires d'oiseaux maintenus en cages intérieures, pour en identifier les sexes. Les vocalises des mâles comportaient 21 figures de chants produites sur 16.50% du temps d'observation, tandis que celles des femelles n'en comportaient que 8 qui n'étaient produites que sur 2.64% du temps d'observation. Les mâles lançaient des séries de 1 à 11 chants de 7.25 min. en moyenne, à un rhythme de 6.06 séries à l'heure, et les femelles produisaient des séries de 1 à 9 chants de 4.07 min. en moyenne, à un rhythme de 1.27 série à l'heure. Les mâles chantaient plus longtemps et plus fréquemment que les femelles et exécutaient des trilles, ce que les femelles ne faisaient pas. En deuxième partie de l'étude, cinq paires d'oiseaux ont été mis en enclos. Leurs cris ont été enregistrés et leurs parades observées pour comprendre le rapport entre les cris et les comportements de reproduction. Deux nouvelles figures de chants produites par les mâles ainsi que deux autres figures de chants produites par des jeunes oiseaux ont pu être enregistrées. Chaque oiseau mâle avait ses chants distincts durant le choix de l'emplacement du nid, la nidification et l'accouplement, mais les chants des mâles étaient semblables lors de dangers, de la présentation de nourriture ou de comportements agressifs. Malgré les différences de chants, les parades des mâles ne différaient pas. Les femelles ne chantaient pas mais émettaient des sons discordants durant la présentation

de nourriture, la quête de nourriture ou lors de comportements agressifs ou d'alarme.

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I. INTRODUCTION

A. Background

The eastern race of the loggerhead shrike (Lanius ludovicianus migrans) has recently been classified as "endangered" (Johns et al. 1993). Conservation efforts in forms of habitat management (Brooks and Temple 1990; Scott and Morrison 1990; Gawlik and Bildstein 1993; Prescott and Collister 1993; Telfer 1993) and propagation of individuals in captivity, including artificial incubation and hand rearing (Cade 1992; Kuehler et al. 1993) have been proposed and in some cases, are underway.

One of the obstacles of captive breeding efforts has been an inability to distinguish the sexes of this species in a convenient, inexpensive manner. Because both sexes have similar plumage, body shape and size (Coues 1884; Miller 1928; Bent 1965; Bull and Farrand 1992; Scott 1992; Udvardy 1992), sexing individuals for pairing is not easy. While Smith (1973) claimed to be able to recognize the sexes of loggerhead shrikes in the field based on plumage colour, i.e. bluish in males and brownish in females, as well as differing degrees of whiteness in the wings and tail of individual birds, there appears to be much variation in these characteristics and thus, sexing loggerhead shrikes in this manner has not been widely accepted.

Various methods of sexing avian species with similar morphological appearances, such as laparoscopy, DNA fingerprinting, karyotyping of chromosomes, and fecal steroids (see Bird 1987) are available, but can be inconvenient, time-consuming, and/or expensive. For example, sexing shrikes by laparoscopy by an experienced individual can cost at least $100 CDN per bird.

An alternative method might be to examine the relative behavioral patterns of the sexes during the early breeding season, especially differences in songs and/or calls.

Sexual dimorphism in vocalization behavior has been reported in nocturnal (James 1984; James and Robertson 1985; Brooke 1988; Taoka et al. 1989a,b; Taoka and Okumura 1990) as well as diurnal bird species (McLaren 1976; Berger and Ligon 1977; Searcy and Brenowitz 1988; Carlson and Trost 1992; Nuechterlein and Buitron 1992). A few studies have dealt with vocalization behaviors of loggerhead shrikes (see review by Scott 1992) and both sexes of these diurnal, predatory songbirds do sing and/or call (Armstrong 1973; Telfer 1993). Any significant sex-related differences in the types of songs and/or calls related to breeding behavior of loggerhead shrikes are largely unknown, but may prove useful in sexing birds for captive breeding and even for field research.

Indeed, several authors have qualitatively described the calls. Chapman (1904) and Telfer (1993) mentioned that the calls contain unmusical notes. Conversely, Saunders (1935), Bull and Farrand (1992), and Scott (1992) noted that some of their calls were composed of musical double phrases and others were harsh, squeaky, or trill notes. Meanwhile, other authors even have phonetically documented some of their calls either with contextual behaviors and/or situations when vocal communication was produced (e.g. Bent 1965; Cade 1992; Woods 1993) or without clear behavioral descriptions (e.g. Scott 1992; Udvardy 1992; Telfer 1993). No detailed spectrographic and quantitative analyses however, have been conducted on either sex of the loggerhead shrike.

B. Objectives

Overall, this study attempted to record the calls vocalized by captive loggerhead shrikes and also investigated the role of these calls in male-female interactions during breeding. The specific objectives were to catalogue the calls of loggerhead shrikes both spectrographically and quantitatively, to identify characteristics of the calls, and to relate them to specific breeding behaviors. Spectrograms were then analyzed to identify the possibility of sexual dimorphism in calls as well as any variations within the sexes. Subsequently, calls produced during the breeding season were objectively interpreted in order to completely describe the relationship between calls and the associated visual displays during breeding activities.

II. LITERATURE REVIEW

A. The Loggerhead Shrike

1. Status and distribution

Loggerhead shrikes have been the object of research and conservation in recent years because of their scarcity (see Johns et al. 1993). This species is categorized as an endangered species in eastern Canada, and as a threatened species in western Canada by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). Their population in Canada has apparently dropped since the 1900s (Johns et al. 1993). Although the causes are largely unknown (Cadman 1985; Cadman et al. 1987), several factors suggested include pesticide contamination (Busbee 1977), low survival of either fledged juveniles or adults (Anderson and Duzan 1978), collisions with automobiles (Craig 1978; Cadman et al. 1987; Telfer 1993), predation of nestlings and damage of breeding habitat (Scott and Morrison 1990; Tyler 1992), overwintering survival (Brooks and Temple 1990), reduction of hunting perches (Yosef and Grubb 1992), and habitat limitation (Gawlik and Bildstein 1993; Prescott and Collister 1993). Gawlik and Bildstein (1990) did not believe that low reproductive success was the cause of the population decline in the southeastern United States.

This species belongs to the family Laniidae, having 70 species in 9 genera (Perrins and Middleton, 1985). Twelve subspecies, differing either geographically or morphologically, although very little, have been documented. Bent (1965) reported 10 subspecies, i.e. loggerhead shrike (L.l. ludovicianus), migrant shrike (L.l. migrans), white-rumped shrike (L.l. excubitorides), California shrike (L.l gambeli), Nelson's shrike (L.l. nelsoni), island shrike (L.l.anthonyi), Sonora loggerhead shrike (L.l. sonoriensis), Mearns' shrike (L.l. mearnsi), Grinnell's shrike (L.l. grinnelli), and L.l. nevadensis. Their ranges are from southern North America into Mexico (Henshaw 1921; Skutch 1987; Bull and Farrand 1992; Udvardy 1992). Cadman et al. (1987) believed that loggerhead shrikes are not original residents in northeastern North America. They usually migrate from their breeding ranges to the southern United States, wintering primarily in Virginia, northern California and Mexico (Bull and Farrand 1992; Udvardy 1992; Telfer 1993). Shrikes are permanent residents in central California and remain on their territories throughout the year (Craig 1978). Scott and Morrison (1990) believed that the three northern subspecies, migrant shrikes, white-rumped shrikes, and California shrikes, migrate from their breeding areas for winter, whereas others including L.l. mexicanus, are non-migrants. Another subspecies, L.l. miamensis, is apparently a resident in southern Florida (Rand 1957).

2. Habitat requirements and territory

Loggerhead shrikes primarily inhabit open areas with scattered small trees or bushes which can be used as hunting perches (Bent 1965; Peck and

James 1987). They prefer to occupy the relatively tall grass areas (Prescott and Collister 1993). In contrast, a previous study by Gawlik and Bildstein (1990) indicated that breeding areas of this species were habitats dominated by short grasses including pasture, hay fields and residential lawns. This species is often found in areas occupied by thorny vegetation, sharp twigs, barbed wires or other sharp objects. The shrikes use these objects to impale prey or food, since they lack strong toes and sharp talons (Henshaw 1921; Snyder 1951; Bent 1965; Skutch 1987; Cadman et al. 1987; Bull and Farrand 1992; Udvardy 1992; Telfer 1993). Such impaling behavior has led to this species' nickname as 'the butcher bird'.

Bent (1965) believed that the territorial size depended on habitat and availability of food. Territory size ranged from 4.46 to 5.67 ha in grassy areas, but as high as 10.13 to 16.20 ha in semidesert areas. Kridelbaugh (1983) estimated their territory to be 4.6 ha in size. A recent study by Yosef and Grubb (1992) indicated that their post-breeding territories varied from 0.17 to 14.59 ha in size.

3. Breeding behavior

3.1. Mating behavior and nest building

Male loggerhead shrikes approach females to form a potential pair by singing and quivering their wings, whereas females react by fluttering their wings and squawking which are behavioral patterns associated with food-begging (Smith 1973; Craig 1978; Cade 1992). During the non-breeding season each sex has a separate territory, whereas in the breeding season both the male and the female aggressively defend a single breeding territory (Bent 1965; Smith 1973; Haas and Sloane 1989).

Pairs of loggerhead shrikes, being monogamous, erect their nest together (Bent 1965). Both sexes spent 10-12 days to construct it (Kridelbaugh 1983). Gilliard's (1958) study suggested that the male does most of the work. Scott and Morrison (1990) and Cade (1992) found that the female did most of the nest construction with the male providing the nest materials and food. They work together in nest sanitation as well (Kridelbaugh 1983).

They construct their nests 1-2.5 m above ground in dense cover but sometimes up to several metres in trees (Telfer 1993). Trees with thorns, or prickly needles, are preferred for nesting because these may serve to protect nestlings from predators besides facilitating impaling of prey (Kridelbaugh 1983; Gawlik and Bildstein 1990). Kridelbaugh's (1983) study showed that eastern red cedar (Juniperus virginianus), multiflora rose (Rosa multiflora) and osage orange (Maclura pomifera) are often selected as nesting trees. Nests were placed on average 3.2 m high, but the height was influenced by the type of vegetation. The nest site was higher in decidious trees than in multiflora rose. Gawlik and Bildstein (1990) suggested that the nest-site position may be influenced by climatic conditions.

Nests consist of bulky cups well made from twigs, grasses, other plant materials, and some animal hair or feathers (Reed 1904; Bent 1965; Salt and Salt 1976; Kridelbaugh 1983; Peck and James 1987; Telfer 1993). The nest size ranges from 15-20 cm in diameter (Telfer, 1993) and 3-6 cm in depth (Scott and Morison 1990). Peck and James (1987) reported the outside diameter of the nest, the inside diameter, the outside depth, and the inside depth as being 16- 20 cm, 8-9 cm, 7-12 cm, and 5-6.5 cm, respectively.

3.2. Incubation period and hatching

Female shrikes lay an egg a day (Kridelbaugh 1983). In his captive birds, Cade (1992) noted that one female laid an egg between 0900-1100. The clutch size can range from 1 - 7 eggs (Peck and James 1987); 3 - 7 (Kridelbaugh 1983; Brooks and Temple 1990; Tyler 1992); 4 - 6 (Coues 1884; Salt and Salt 1976; Bull and Farrand 1992), 4 - 8 (Udvardy 1992), or 5 - 7 (Telfer 1993). They produce dull white eggs with many light brown and/or grey spots (Chapman 1904; Snyder 1951; Gilliard 1958; Salt and Salt 1976; Bull and Farrand 1992). Shrikes sometimes raise a second brood in a single season (Bent 1965; Peck and James 1987; Tyler 1992; Yosef 1992).

The females usually begin incubation when egg-laying is almost completed. In some cases however, females may initiate incubation with the first or second egg (Kridelbaugh 1983; Cade 1992; Telfer 1993). Bent (1965) stated that both sexes incubate the eggs, although the males may do so just enough to maintain the survival of the embryos (Gilliard 1958). This is contradicted by more recent reports by Applegate (1977). Kridelbaugh (1983) and Cade (1992) that claim that male loggerhead shrikes never incubate, but only participate in feeding the incubating females.

Yosef (1992) reported a polygynous male, but deemed it unusual. The male fed two females during the pre-nesting, incubation, and pre-fledgling periods, but raised his own youngsters in the same manner as a monogamous male.

Hatching occurs asynchronously (Morrison 1980; Kridelbaugh 1983; Cade 1992), usually on the sixteenth day of incubation (Gilliard 1958; Telfer 1993). Different studies, with varying sample sizes, indicated variations in the length of the incubation period, e.g. 10 - 12 (Bent 1965), 16 - 20 (Kridelbaugh 1983), 12 - 16 (Peck and James 1987), 15 - 18 (Scott and Morrison 1990), 16 - 18 (Tyler 1992), and 16 - 19 days (Cade 1992).

3.3. Development of young shrikes

Young shrikes are essentially altricial birds that completely depend on their parents (Pettingill 1985; Gill 1990). They are fed by their parents in the nest for two to three weeks (Gawlik and Bildstein 1990; Telfer 1993). The growth of young is quite rapid. At two weeks of age the young's weight is almost that of an adult (Telfer 1993). After leaving the nest, the young may return to it for 2 or 3 days. Overall, they depend on their parents for 3 or 4 weeks post-fledging. The male parent trains them to forage and hunt prey items during this period (Kridelbaugh 1983).

To find highly nutritious food during the breeding season, adults attack insects and vertebrate prey more frequently than during the non-breeding season (Morrison 1980; Scott and Morrison 1990). Even though loggerhead shrikes are generally insectivorous, they also eat vertebrate prey like nestling birds, frogs, toads, lizards and small snakes (Gilliard 1958). Furthermore, Bent (1965), compiling various authors' notes, listed myrtle warblers (Dendroica coronata), English sparrows (Passer domesticus), bluebirds (Sialia sialis), mockingbirds (Mimus polyglottos), and chipping sparrows (Spizella passerina) among their prey. Other prey species observed either in the field or in the laboratory include the horned lark (Eremophila alpestris: Wiggins 1962), old-field mice (Peromyscus polionotus: Caldwell 1967), Merriam's pocket mice (Perognathus merriami), green treefrog (Hyla cinera), spring peeper (Pseudacris crucifer: Chapman and Casto 1972), and the grey house mouse (Mus musculus: Kaufman 1973; Busbee 1976). Adults will cannibalize their own young, particularly when they experience difficult environmental conditions (Kridelbaugh 1983).

4. Vocalization behavior

Armstrong (1973) and Telfer (1993) noted that both male and female loggerhead shrikes produce songs and/or calls. To date however, documentation of vocalization behavior of loggerhead shrikes has been quite rare and their songs and/or calls seem poorly understood (Cadman et al. 1987).

Chapman (1904), Saunders (1935), Snyder (1951), Bent (1965), Bull and Farrand (1992), and Udvardy (1992) qualitatively stated that their calls contain a variety of harsh, whistle, scolding and/or trill notes. Other authors phonetically documented vocalization of this species, with or without describing contextual behaviors or visual displays.

Bent (1965) reported some shrikes' calls. Male California shrikes give "*bzeek*" calls when defending their territories or expelling intruders from their mates. Shrikes produce alarm "*schgra-a-a*" calls while fanning their tail, elevating their head and back feathers, depressing their bodies with lowered heads, and opening their bills. Young shrikes vocalize "*tsp*" calls at least an hour after hatching and "*tcheek*" calls they are afraid. Young birds also produce "*screig*" calls that may be used to indicate to the parents where they are. Cade (1992) identified "*mak*" or "*jak*" calls vocalized by females as food begging calls and "*waut*" calls by males as food offering calls. He described their visual displays accompanying these calls. Woods (1993) reported that adults produce "*waa*" calls not only to attract one other during food begging and pre-copulatory behaviors, but to entice the nestlings out of the nest as well. Telfer (1993) phonetically described "*shriek*" as an alarm call and mnemonically explained another alarm call of this species as "a repeated *tink* sound" which when heard sounds like someone tapping two metal objects together. Other authors however, just noted shrikes' calls, i.e. "*bzeee*" and "*queedle-queedle*" (Udvardy 1992), and "*shack-shack*" (Scott 1992) without clearly describing situations in which they were heard.

B. Bird Vocalizations

1. Vocalization and its classification

Vocalizations are sounds produced by the vocal apparatus occurring only in vertebrates (McFarland 1981). In birds this vocal organ is called the syrinx, a unique, elastic membranous structure located at the lower end of the trachea. The bird sings or calls when the air flowing from its air sacs causes vibrations of its syrinx (Greenewalt 1968; Berger 1971; Gordon 1972; Armstrong 1973; Brackenbury 1982; O'Connor 1984; Fedde 1986). Jellis (1977) believed that the interclavicular air sac plays an important role in producing voice and operates as a resonator.

Classifying vocal communication is not easy, due to the enormous diversity of vocalizations, ranging broadly from a repetition of one syllable to a combination voice series (Slater 1983; Pettingill 1985; Gill 1990). Nevertheless, vocal communication in birds is traditionally considered to be calls and songs (Bondesen 1977; Burton 1985; Gill 1990), although their functions do not differ markedly (Armstrong 1965; Berger 1971). Calls consist of short, simple, and unmusical notes and are produced by all ages and/or both sexes of birds. The syllabic number of a call is one or two (monosyllabic or dissyllabic), and rarely more than four or five (Bondesen 1977). On the other hand, songs contain more complex notes with repeated patterns and are commonly melodious (Armstrong 1965; Catchpole 1982; Burton 1985; Pettingill 1985; Gill 1990).

Songs are characteristic of passerine birds and are particularly vocalized by males during the breeding season (Forsythe 1970; Berger 1971; Catchpole 1982; Pettingill 1985). Under natural conditions, male singing only occurs in chaffinches (*Fringilla coelebs*: Kling and Stevenson-Hinde 1977), Cassin's finch (*Carpodacus cassinii*: Samson 1978), zebra finches (*Taeniopygia guttata*: Walters et al. 1991), and indigo buntings (*Passerina cyanea*: Payne and Payne 1993). There are some exceptions. Not all species of the passerine group can sing (Berger 1971) and females may have poor song quality (Seutin 1987). In certain species, both sexes can sing, i.e. barn swallows (*Hirundo rustica erythrogaster*) and cliff swallows (*Petrochelidon p. pyrrhonota*: Samuel 1971). In other species, duets involving two or more individuals and including both sexes can occur, e.g. brown-headed cowbirds (*Molothrus ater*: Brackbill 1961); 9 species of New Guinea birds (Diamond and Terborgh 1968); greater birds of paradise (*Paradisaea apoda*: Dinsmore 1969); aldabra white-throated rails (*Dryolimnas cuvieri aldabranus*: Huxley and Wilkinson 1979); Kenyan black-collared barbets (*Lybius torquatus*: Short and Horne 1982).

Songs and/or calls can be documented spectrographically, qualitatively, quantitatively, phonetically, and/or mnemonically. Berger and Ligon (1977) phonetically and quantitatively described 15 vocalizations of captive pinon jays (Gymnorhinus cyanocephalus). One of them was a single note "*rack*" with an average of 700 Hz in fundamental frequency and another was a short call "*rick*" with an average of 1,160 Hz in fundamental frequency. Skeel (1978) found 10 types of calls vocalized by adult whimbrels (Numenius phaeopus), i.e. low whistle and trill calls on the breeding grounds, and two redundant calls vocalized by chicks from hatching time to one- week old. Skeel (1978) also noted the aerial display song, composed of 20 repeated low whistle calls and three-phrase low trill calls. Meanwhile, Collias (1987) could identify 24 different calls of chicks, hens, and cocks of the red junglefowl (Gallus gallus) in various situations and then developed them in a spectrographic key. Samson (1978) reported that the older males of Cassin's finch had a repertoire of 86 types. Moreover, the yearling males had 97 song types in which 11 were possessed by only the yearling.

2. Vocal function and development

Songs and/or calls are vocally interactive behaviors used by birds to identify each other (Roberts 1969; Burton 1985; Gill 1990). In addition to preventing birds from pairing with the wrong species (Selander 1971), songs and/or calls function to establish territory and announce its possession, drive away other birds from their territory, locate the nest, attract the attention of the opposite sex, synchronize the life cycle, and stimulate females to lay eggs (Armstrong 1965: Slater 1983: Pettingill 1985). Berger (1971) grouped songs serving for mate attraction, dominance of conspecifics, and territorial defence as territorial songs, and songs serving to coordinate birds' activities, particularly a mated pair, as signal songs. A variety of songs that cannot be directly associated with mating activities and territorial defence were grouped as emotional songs.

Burton (1985) believed that in sedge warblers (Acrocephalus schoenobaenus), songs consisting of rambling chatters and trills function in forming a pair. Berger and Ligon's (1977) study described the role of calls in pinon jays. A pair of jays use the "*rack*" calls during nest building and give the "*rick*" calls when collecting nest materials, preening, or sitting quietly. This species also produces both single and double "*racks*" as vocal communication among individuals during foraging. Both McDonald (1989), who experimentally muted male Scott's seaside sparrows (Ammodramus maritimus peninsulae), and Westcott (1992) who studied-ochre-bellied flycatchers (Mionectes oleagineus), found that male songbirds not producing normal songs for their species not only lost their territories, but usually failed to achieve a successful mating. Studies on song sparrows (Melospiza melodia) by Hiebert et al. (1989) reported similar results. Male birds with small repertoires tended to possess smaller territories and spent more time in acquiring territories than those with large repertoires. In great tits (*Parus major*), the better males, defined by having longer strophes, i.e. a number of phrases sung repeatedly in a stereotyped manner as part of a bout, showed less positive drift and demonstrated larger song repertoires. This was associated with longer survival and a higher lifetime reproductive success measured by the number of offspring raised over its lifetime (Lambrechts and Dhondt 1986).

Some species of songbirds are thought to develop their songs early during the first year of their lives (zebra finches: Eales 1985, Clayton 1987, 1988; song sparrows: Marler and Peters 1987). During the sensitive phase, the young songbirds produce subsongs and then complete appropriate songs through hearing the adults' vocalizations, learning, and practicing (Lemon and Herzog 1969; Slater 1983; Kroodsma 1984; Pettingill 1985; Petrinovich and Baptista 1987). The beginning and the end of the sensitive phase however, are poorly known. In zebra finches, for example, the sensitive phase was before 35 days of age (Clayton 1988). A previous study by Eales (1985), however, indicated that the sensitive phase of this species was between approximately 35 - 65 days of age. During that period the young males and females learned their father's songs. On the other hand, other species may learn songs later during their lives (great tits: McGregor and Krebs 1989; European starlings (*Sturnus vulgaris*: Eens et al. 1992). These songbirds continue learning songs and crystallize their songs into a repertoire that is characteristic of the species, sex, or even an individual throughout social interaction and contextual experience during their life (Kroodsma and Pickert 1984). These interactions and experiences affect the timing and the accuracy of song copies by young (Böhner 1983: Eales 1989; Pepperberg 1994). Some species can even modify their songs in their adulthood. European starlings, for instance, were able to modify their repertoires by employing heterospecific imitations learned from other species (Eens et al. 1992). Conversely, in song sparrows there was no evidence that the older the birds get, the larger the repertoire size they have (Hiebert et al. 1989).

3. Sexual dimorphism in vocalization

Songs and/or calls evolve under the environmental selection pressures of either physical or biological factors (Haimoff 1987). When situations change, songs and/or calls are easily modified by birds in a very short time scale (Catton and Gray 1985). Over long distances, during nocturnal behavior, and in dense cover, when visual signals are impaired, songs and/or calls not only serve to help birds communicate each other (Gill 1990), but also serve as a tool for sexual distinction (James 1984).

Sexual dimorphism can be discriminated based on call types or some components of calls and are reported in both nocturnal (British storm petrels Hydrobates pelagicus: James 1984; little shearwaters Puffinus assimilis: James and Robertson 1985; greater shearwaters P. gravis: Brooke 1988; Swinhoe's storm-petrels Oceanodroma monorhis: Taoka et al. 1989a; Leach's storm-petrels O. leucorhoa: Taoka et al. 1989b) and diurnal bird species (whooping cranes Grus americana: Carlson and Trost 1992; eared grebes Podiceps nigricollis: Nuechterlein and Buitron 1992).

Taoka et al. (1989a) found that in Swinhoe's storm-petrels, flight calls of the males differ from those of the females. The male's flight calls are composed of broad-band syllables, whereas the female's calls consist of a harmonic structure. In addition, the number of these calls given by females in flight was greater than those given by males. Conversely, males more frequently gave flight calls on the ground or inside the burrows than females. During a subsequent study using synthetic calls based on the rhythmic components of flight calls of this species, Taoka and Okumura (1990) concluded that the presence or absence of harmonic structure within the frequency component is more important for sex recognition than that of the rhythmic components of calls. Meanwhile, in Leach's storm-petrels, Taoka et al. (1989b) found that the frequency of chatter calls of the male are higher than that of the female. This frequency was measured at the part with the highest value within the fundamental frequency band of each syllable. Carlson and Trost (1992) analyzed guard calls of whooping cranes using discriminant analysis for determinating sex. They found that the result was similar to the result of descriptive statistics. The mean of the main syllable frequency of male calls (946 Hz) was lower than that of female's (1,115 Hz). Nuechterlein and Buitron (1992) reported that in eared grebes, advertising calls could be used to recognize sex. The female calls were higher in frequency than the male's. The duration of calls and intercalls however, was shorter.

III. METHODS

This study consisted of two distinct steps or observation periods (hereafter referred to as stages), both undertaken at the Avian Science and Conservation Centre (ASCC) of McGill University, Ste Anne de Bellevue, Quebec. The first stage, conducted from 12 April to 8 May, 1994, emphasized obtaining call types produced by both sexes, using two pairs of captive-reared loggerhead shrikes of known sex. The specimens were approximately two years old and had produced young during the 1993 breeding season.

The second stage focused on gaining information on the functional context of calls during breeding activities. Due to factors beyond the author's control, these observations were conducted during the laying of the second clutches by five captive shrike pairs, from 20 May to 30 August, 1994 (see Table 1). The sexes of the 3 males and 2 leg-banded females involved were confirmed by either laparoscopy or by their breeding records for the previous spring. All of these birds were two years old and had successfully produced young during the 1993 breeding season.

A. Data Collection

1. The first stage

Each member of each pair was kept in indoor cages measuring 50 x 50 x 65 cm (L x W x H) located in a 6.00 x 2.50 x 2.25 m (L x W x H) observation room. Cages were furnished with barbed wire placed horizontally 25 cm above the floor to provide perching and impaling sites. Both cages were positioned face to face, nearly 90^0 in angle, 1 m in distance, and approximately 45^0 against a 30 x 30 cm observation window. This positioning allowed each member of each pair to see one another and facilitated identification of the caller for the observer looking through a one-way glass window.

To record calls, each of the cages was equipped with a microphone hanging through a hole in the cage's attic with a one-metre mono cable. One cage had a M516 Uher microphone and the other a M517 Uher model. Both microphones were connected to a Sony WM-D6C cassette recorder equipped with headphones by a 3-metre stereo cable. The cassette recorder was controlled from outside of the room. The interior walls of the cages were covered with 3-mm thick carpets to minimize echoing effects.

The recording process for each pair was carried out twice a day (0900-1230 h and 1330-1630 h) after a period of acclimation to the room (8 days for the first pair and 6 days for the other).

Both bout duration and vocal delivery duration were measured with a stopwatch. Call bouts, rather than individuals, were used as samples because of the low number of individuals available for the study. A bout was defined as a series of the same call type consecutively given in a certain time unit which was then referred to as bout duration. Vocal delivery was denoted as a sequence of vocalizations consisting of one or more bouts. The measurement of vocal delivery duration was over if there was a pause between consecutive bouts of more than 10 sec. Call terms used are derived from those reported by Greenewalt (1968), Jellis (1977), Bondesen (1977), and Kroodsma (1982).

2. The second stage

Each pair of loggerhead shrikes used in this stage was housed outdoors in wooden breeding pens (6.5 x 3 x 4-5 m; L x W x H) with wire mesh rooves. Each pen was furnished with leafless hawthorn trees and barbed wire secured to the walls and stuck into the ground to provide perching, nesting and impaling sites. Dog's hair, bush twigs, and hay were provided as nest materials.

Because of a priority by ASCC in 1994 for producing as many shrikes as possible for experimental release, i.e. removal of first clutches to be artificially incubated and the young hand-reared, the microphones were only installed during the second clutch period (see Table 1). Therefore, during the first clutch period some disturbances, i.e. caused by installment and/or placement of the microphones as well as by treatments to obtain aggressive calls, were reduced.

To facilitate distinguishing the sexes during observations, males were marked with blue ink on their breasts. Because the objective was to understand the functional context of the shrikes' calls, i.e. relating them to their breeding behaviors, not only were calls recorded, but also visual displays of the caller during the calling and response of the receiver. To record shrikes' calls initially, each of two breeding pens (pairs 1 and 2) was equipped with a Udix unidirectional microphone hung 2.5 m from the ceiling. Both microphones were connected to a Sony WM-D6C cassette-recorder controlled from outside the breeding pens through 6-m mono cable.

Table 1. Observation schedule during the second-clutch period

Pair	From	To	Comment
1	The day of R (08 June)	The tenth day after R (17 June)	Both sexes disappeared (17 June)
2	Same above	Same above	Female disappeared (17 June)
3	The day of R (21 June)	The seventh day after H (10 August)	All nestlings died (10 August)
4	The day of R (20 June)	(10 August)	The second-clutch eggs were removed (15 July)
5	When nestlings were approximately 12-day old (10 August)	(30 August)	-

Note: 1. R = the first-clutch eggs were removed.
2. H = the day of the first egg of Pair 3 hatched.
3. 20 May - 07 June = observations without recording shrikes' calls

Observations each day comprised 4 to 7 hours between 0900 h and 1800 h through a 60 x 30 cm (H x W) one-way glass window about 4 m above the ground.

On the tenth day of observation, three birds of pairs 1 and 2 mysteriously disappeared (there was no evidence of escape, but predators were strongly suspected). Thus, it was necessary to install the microphones in adjacent, identical pens containing pairs 3 and 4. Despite the setback, the data from pairs 1 and 2 could still be used.

It was of interest to collect data on breeding behavior and vocalizations of breeding pairs reacting to intruders of their own species, as well as others. Thus, on one or two occasions, a strange male held in a wire cage measuring 1 x 1 x 1 m (L x W x H) was introduced for 15 minutes each to all 4 pairs to elicit alarm and aggressive calls. Similar calls were also obtained when shrikes reacted to the visible presence of other birds outside the pen.

B. Data Analysis

To obtain spectrograms, three consecutive calls were randomly selected from each bout and processed using Cornell University's Canary 1.1 program run by LC 520 MacIntosh PC. This PC was equipped with BSR Metrotec equalizer to filter out background noise. A Centris 620 or Color Classic MacIntosh PC was also used for processing the recordings but without an equalizer. Because this program provided many parameter options, spectrograms were standardized by adjusting filter bandwidth of 352.94 Hz, frame length of 256 points, time of 5,752 ms, overlap of 50%, frequency of

86.93 Hz. FFT size of 256 points, window function of Hamming, amplitude of logarithmic, display style of boxy, and clipping level of -130 or -140 dB.

These spectrograms were used to measure the frequency of syllables or calls, their duration, the number of syllables, and the interval between the beginning of two adjacent syllables or calls. Frequency was measured at the part with the highest value within the fundamental frequency of each syllable or call (see Fig. 1A). The fundamental frequency was defined as the lowest frequency that appears on a spectogram or a complex-tone call. Waveforms also were considered for measurement of duration because echoes in some spectrograms were strong and could not be separated from the images of original calls. Also, the duration of aggressive calls and nestling calls was so brief that their frequency could only be estimated.

Spectrograms were also phonetically interpreted to facilitate explanations and were conformed to phonetic interpretations given by previous authors.

Statistical tests were used to examine the possibility of sex discrimination in calls. The calling rate of both sexes was examined with sign test and vocal-delivery duration was examined with Mann-Whitney test. Quantitative variables of calls that were vocalized by both sexes and that were spectrographically similar were classified further using discriminant analysis of the SAS statistics program (see SAS Institute Inc.). Quantitative variables of monosyllabic calls were the highest value of the fundamental frequency and call duration, and those of dissyllabic calls were the highest value of fundamental frequency of each syllable, duration of each syllable, duration of intersyllable, and call duration.

IV. RESULTS

A. Vocalizations

Call structures of captive loggerhead shrikes are relatively simple. Spectrographically, calls of both sexes contain either single (mono-) or double (dis-) syllables. These monosyllabic or dissyllabic calls are repeated in a certain time period, then comprising a bout. Monosyllabic calls contain notes with constant or almost constant frequency (Figs. 4A, 4B, 4D, 6B, 6C), notes with strong harmonic structures (Figs. 4E, 4F, 5A, 6D), or a vibrato note (Figs. 3A-F). Dissyllabic calls contain either two similar-frequency notes (Figs. 4C, 6A), notes with strong harmonic structures (Fig. 5B), different notes (Figs. 1A, 1B, 2A-F, 5C-F), or vibrato-mixed notes (Fig. 1C). In general, the first syllable of a dissyllabic call consists of a frequency-changing note in forms of glissando and stroke, whereas the second one tends to be a constant note. Acoustically, shrikes vocalize whistled, squeaky, trill and harsh calls. Some calls seem similar when perceived by the human ear, but they could be structurally different.

Appendices 1, 2, 3, and 4 show descriptive statistics of call characteristics of male and female captive loggerhead shrikes. Appendices 5 and 6 show bout durations.

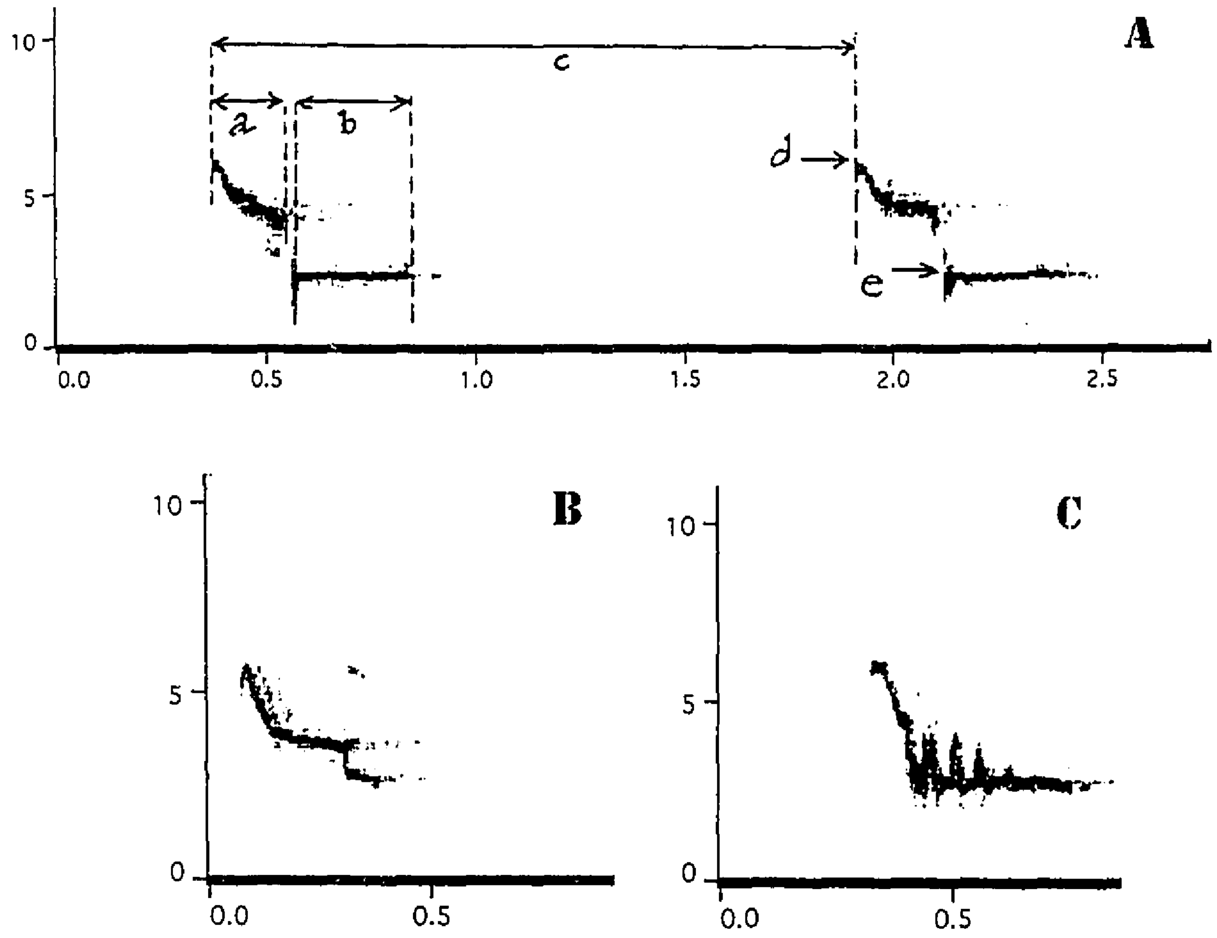

Fig. 1. Spectrograms of male captive loggerhead shrikes' calls: (A) 1M1, *chii-too*; (B) 2M2, *chii-loo*; (C) 8M1, *cree-oop*

Note: 1. Measured parameters are duration of each syllable (a and b), intercall duration (c), and the highest frequency of each syllable (d and e).

2. In all figures, the horizontal axis represents duration (in sec, except for Figs. 4F and 6C in msec) and the vertical axis represents frequency (in kHz).

3. Code: 3M2 = call number 3, vocalized by male number 2.

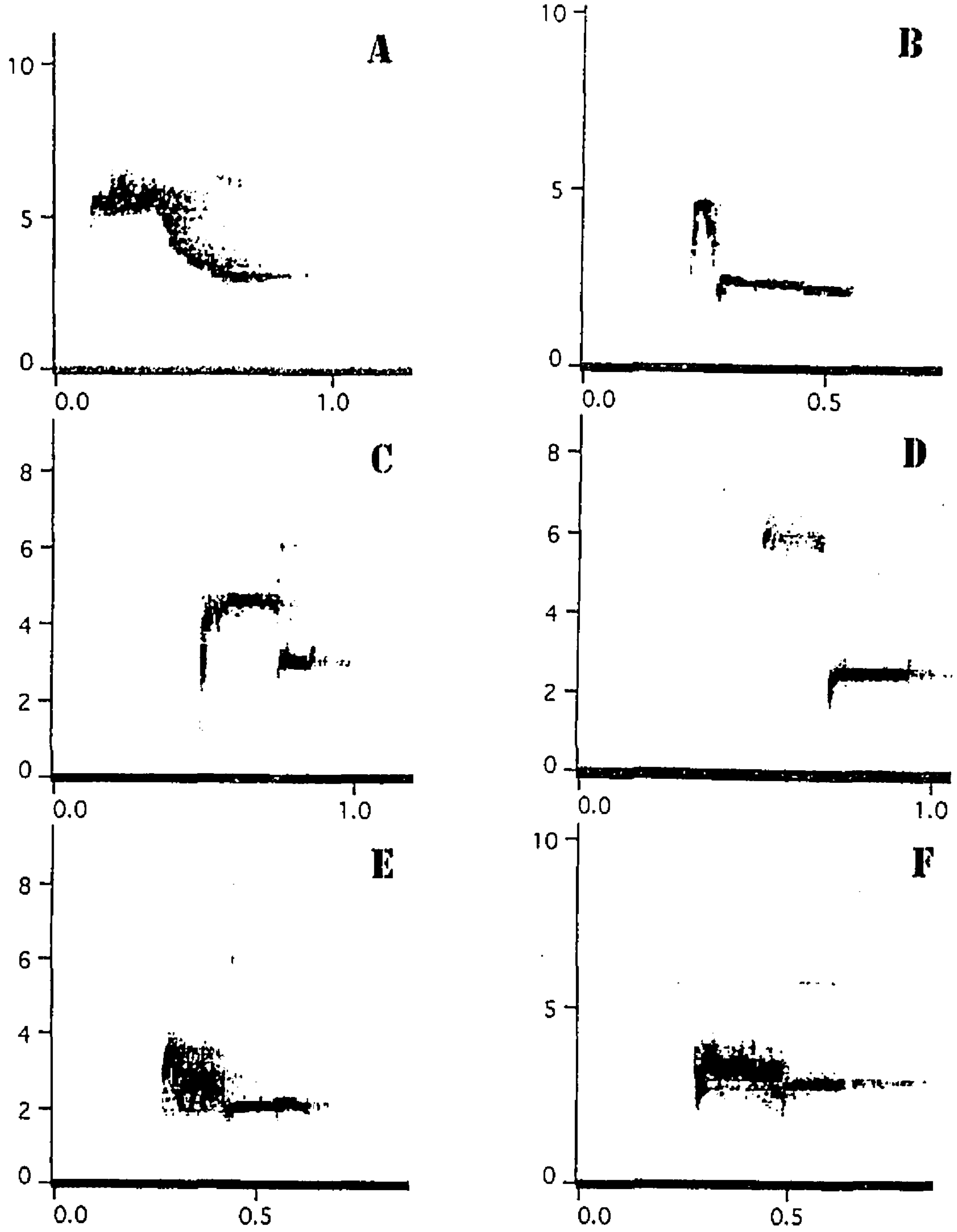

Fig. 2. Spectrograms of male captive loggerhead shrikes' calls: (A) 23M5, *pee-tooy*; (B) 3M2, *pee-oo*; (C) 4M1, *pee-to*; (D) 5M1, *pee-too*; (E) 6M2, *peet-too*; (F) 7M1, *pee-tip*

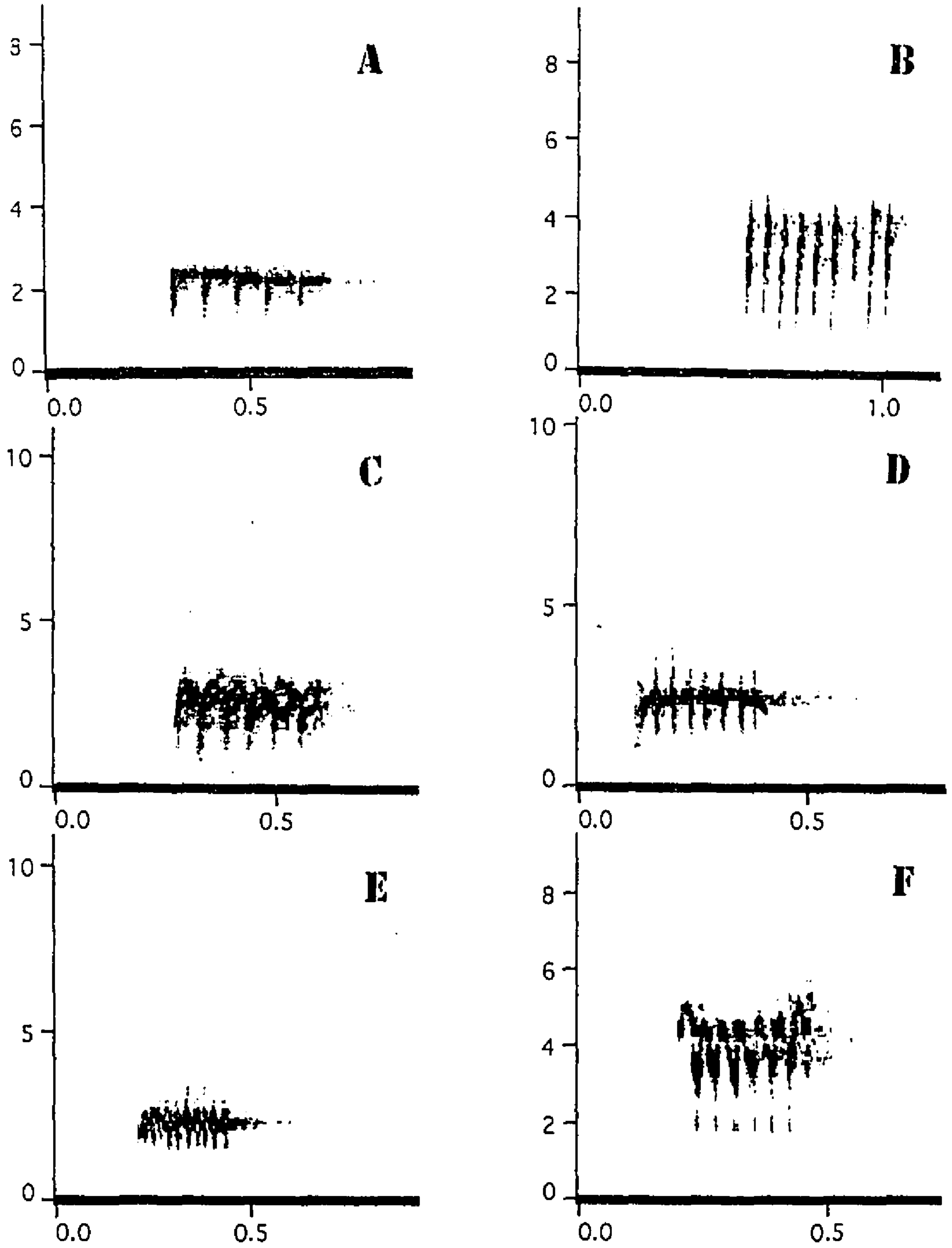

Fig. 3. Spectrograms of male captive loggerhead shrikes' calls: (A) 9M1, *pree-lee-lee*; (B) 10M2, *pree-wee-wee-wuut*; (C) 11M1, *pree-wee-weep*; (D) 12M1, *pree-weep*; (E) 13M2, *pwp*; (F) 14M1.2, *creek*

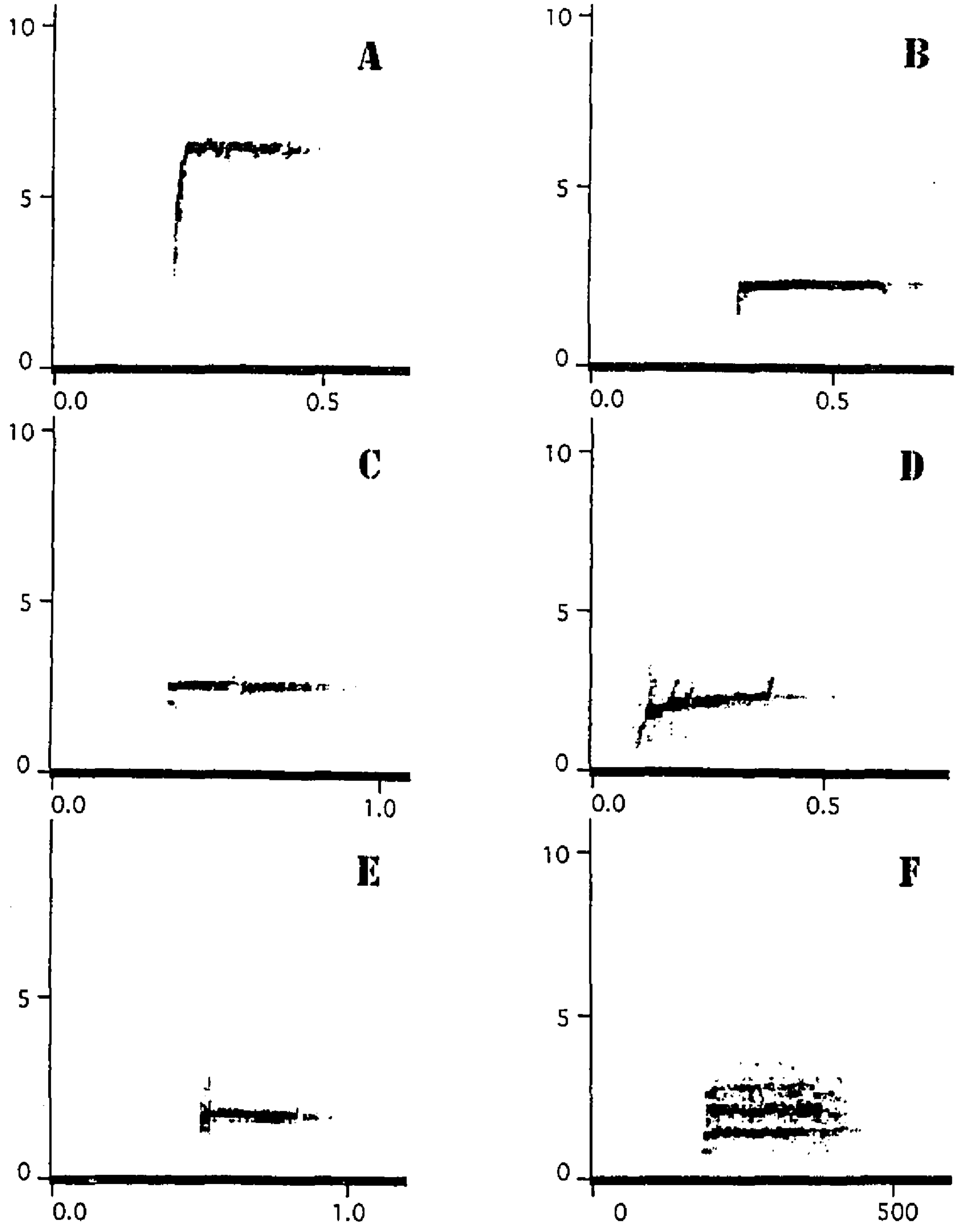

Fig. 4. Spectrograms of male captive loggerhead shrikes' calls: (A) 15M2, *peet*; (B) 16M1.2, *peep*; (C) 22M4, *peep-peep*; (D) 18M1.2, *quick*; (E) 17M2, *wuuk*; (F) 19M1.2, *shack*

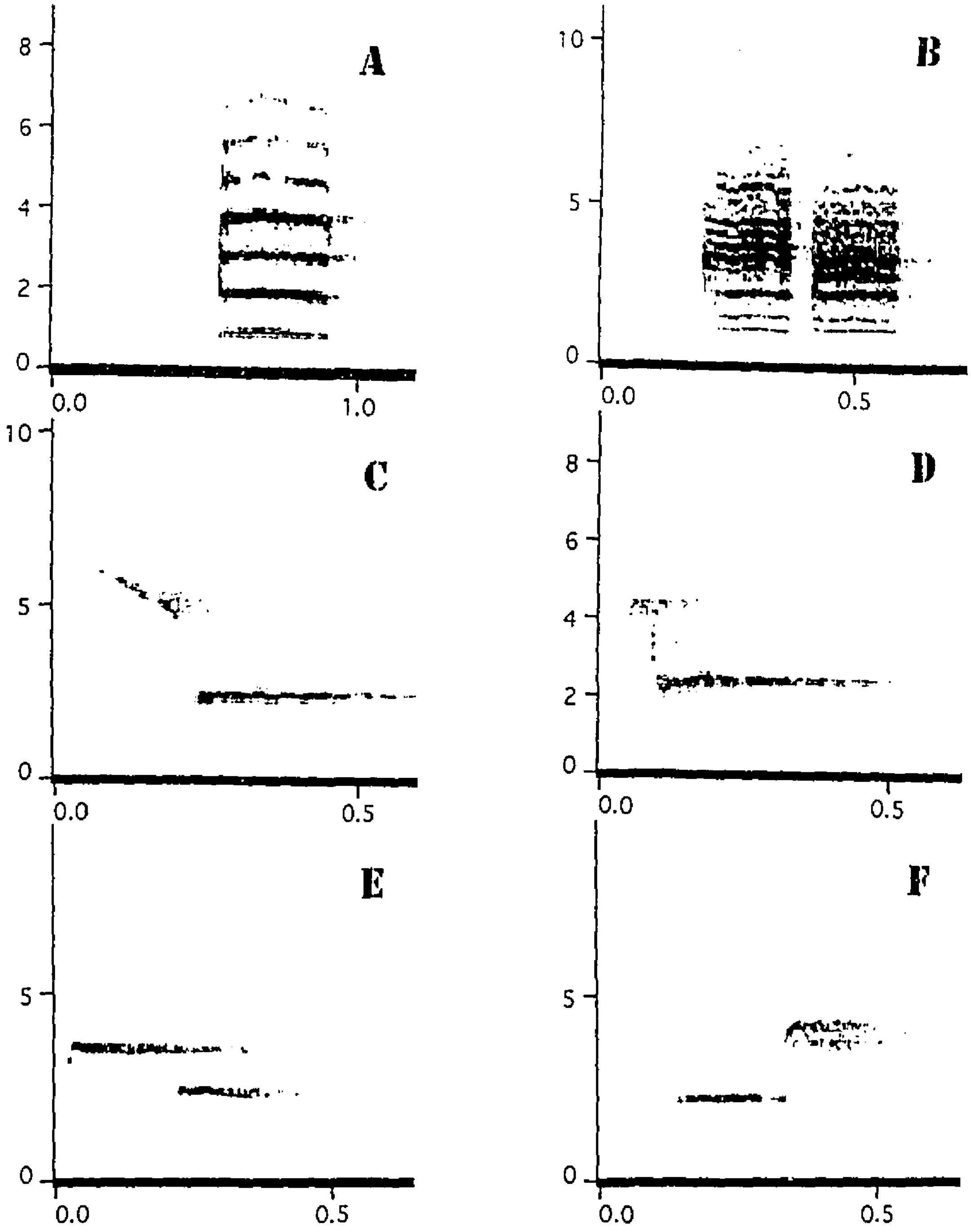

Fig. 5. Spectrograms of male captive loggerhead shrikes' calls: (A) 20M1, *shaack*; (B) 21M1, "*shack-shack*"; and spectrograms of female captive loggerhead shrikes' calls: (C) 1F2, *chii-too*; (D) 2F2, *pee-oo*; (E) 3F2, *peet-too*; (F) 4F2, *qu-chick*

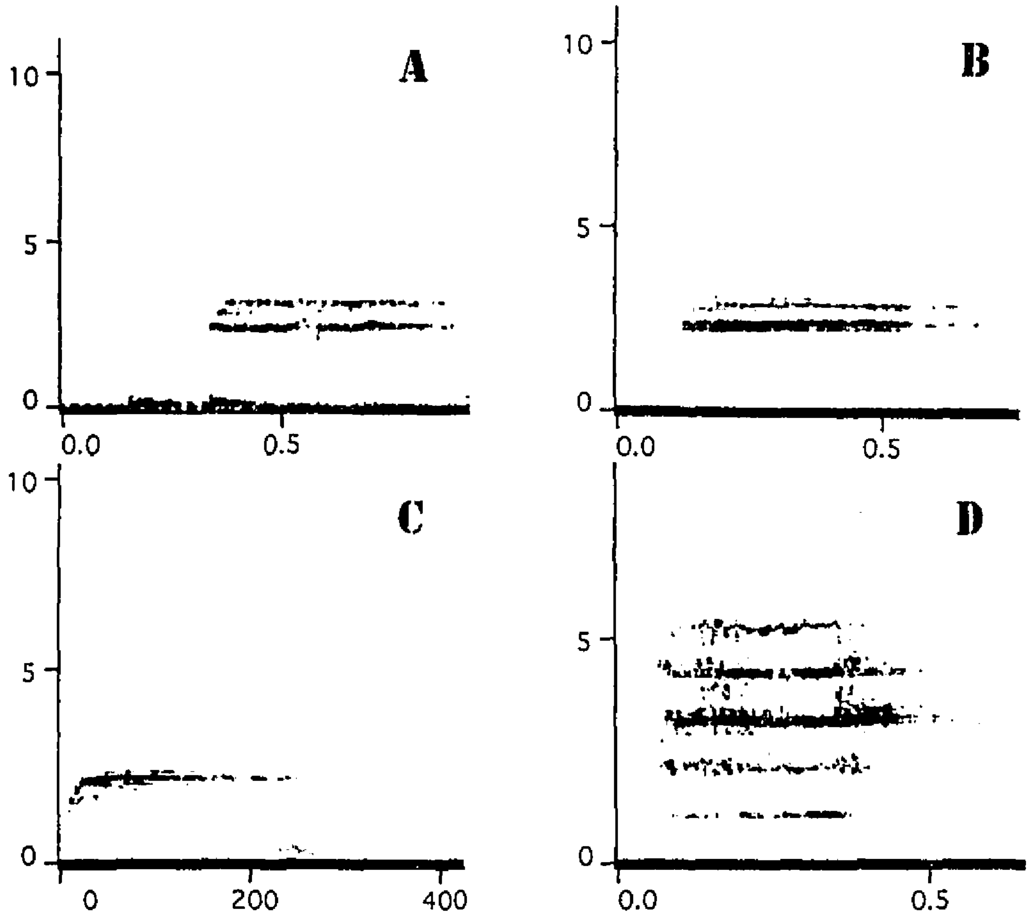

Fig. 6. Spectrograms of female captive loggerhead shrikes' calls: (A) 5F1, *peep-peep*; (B) 6F1, *peep*; (C) 7F2, *quick*; (D) 8F1, *shaack*

1. Whistled calls

a. *Chii-too* structures

Chii-too structures are dissyllablic and consist of 4 structural variations (for males, see Figs. 1A-C, 2A; for a female, Fig. 5C). Each structure starts at a glissando curve, followed by a downward curve with smooth continuous frequency changes, finally terminating at either a staccato curve, a curve of approximately constant frequency, or a staccato curve mixed with trill. The frequency gap between the end of the glissando and the staccato, the pause between both syllables, and the duration of each syllable or call cause structural and variable variations.

Calls in Figs. 1A and 1B differ little in frequency. In Fig. 1A, the glissando begins at 6.00 ± 0.19 kHz and comes down to approximately 4.50 kHz, before going to a staccato of 2.63 ± 0.06 kHz. In Fig. 1B, the beginning of the glissando is 5.76 ± 0.18 kHz and the ending is approximately 4.00 kHz. The staccato is 2.85 ± 0.15 kHz. The marked difference however, is in the duration of the syllable and of the call. The glissando duration of Fig. 1A is 0.179 ± 0.008 sec and the staccato, 0.302 ± 0.017 sec. The short pause (approximately 0.019 sec) occurs between both syllables. Call duration is 0.500 ± 0.019 sec. On the other hand, the glissando duration of Fig. 1B is 0.248 ± 0.015 sec and the staccato 0.064 ± 0.005 sec, which is almost one-fifth of that in Fig. 1A. There is no pause between both syllables. Call duration is 0.313

± 0.015 sec. The call of Fig. 5C vocalized by the female resembles the male's call in Fig. 1A.

The call in Fig. 1C consists of the glissando as the first syllable followed by a trill that seems to be the beginning of the second syllable before ending with the staccato. The glissando is 6.09 ± 0.10 kHz in frequency and 0.075 ± 0.004 sec in duration. The staccato is 2.45 ± 0.12 kHz in frequency and including the trill, it lasts 0.339 ± 0.012 sec in duration. Unlike Figs. 1A, 1B, 1C, the beginning of the first syllable of Fig. 2A is like a staccato followed by a glissando and then comes down to a staccato in the second syllable. Due to little frequency gap and an unclear pause, the duration of each syllable is not easy to measure. Even though this call is spectrographically similar to a monosyllabic call, acoustically it is a dissyllabic call. In some spectrograms, dissyllabic call images obviously appear at the second harmonic.

b. *Pee-oo* structures

The first syllable of the *pee-oo* structure is a stroke curve and the second one is a staccato. The stroke is higher in frequency than the staccato and is more or less one-fourth of the duration of the staccato. Both sexes vocalize these structures (male: Fig. 2B; female: Fig. 5D).

c. *Pee-too* structures

Unlike *chii-too* and *pee-oo*, both syllables of *pee-too* structures are either a staccato or at least staccato-like (males: Figs. 2C-F; females: Figs. 5E, 5F). The first syllable may be higher or lower in both frequency and duration than the second one. In some calls (Figs. 2E, 2F), the bandwidth of the first syllable is wider than that of the second one.

d. *Peep* structures

These structures include monosyllabic calls, *peep*, *peet*, *quick*, as well as a dissyllabic call: *peep-peep*. *Peep* (Fig. 4B) is a pure-tone call and *peep-peep* (Fig. 4C) is a modification of *peep,* i.e. vocalized twice in rapid succession. Both calls are similar in the frequency and duration and there is a pause between both syllables of *peep-peep*. In females however, *peep* (Fig. 6B) and *peep-peep* (Fig. 6A) contain harmonic structures. *Peet* (Fig. 4A) and *quick* (Figs. 4D, 6C) are almost pure-tone calls. The *peet* call is high in pitch and is heard as almost a mouse-like sound in nature. This squeaky call begins at frequency of roughly 2.50 kHz and in an extremely short time, climbs to a constant frequency of 6.68 ± 0.07 kHz and a duration of 0.242 ± 0.009 sec.

2. Trill calls

Trill calls (Figs. 1C, 3A-F) contain vibrato notes, i.e. notes with rapid alternation of frequencies. These vibrato calls are distinguishable by the human ear. It is noteworthy that only males used these calls. Trill calls range from 2.58 ± 0.04 to 6.09 ± 0.10 kHz in their frequencies and from 0.286 ± 0.025 to 0.456 ± 0.020 sec in duration. Seven phonetic interpretations are found: *cree-oop*, *pree-lee-lee*, *pree-wee-wee-wuut*, *pree-wee-weep*, *pree-weep*, *purp*, and *creek*. The *cree-oop* call (Fig. 1C) is considered as one of the dissyllabic *chii-too* variations. *Pree-wee-wee-wuut* consists of repeated pulses with a wide frequency band. To the human ear, this call is heard as a gurgling trill. *Pree-wee-weep*, *pree-weep*, and *purp* seem to be structurally similar. The number of elements or the speed in vocalizing these elements causes variations among them. *Creek* is heard as almost a cricket-like sound.

3. Harsh calls

Harsh calls are complex frequency or complex tone calls characterized by strong harmonic structures. There are two basic structures of harsh calls, i.e. *shack* (Figs. 4E, 4F, 5A, 6D) and "*shack-shack*" (Fig. 5B). "*Shack-shack*", phonetically referring to Scott (1992), is essentially *shack* vocalized twice in rapid succession. Based on the fundamental frequency, duration of call and tone intensities that are represented by a function of coloring density on the spectrograms, *shack* structures could be heard as *wuuk* (Fig. 4E), *shack* (Fig. 4F), and *shaack* (Figs. 5A, 6D). The *wuuk* call (1.82 ± 0.03 kHz, 0.224 ± 0.012 sec) was higher in fundamental frequency but shorter in duration than *shack* (0.91 ± 0.02 kHz, 0.256 ± 0.014 sec), *shaack* (1.05 ± 0.10 kHz, 0.366 ± 0.023 sec) and "*shack-shack*" (1.08 ± 0.06 kHz, 0.417 ± 0.017 sec). *Shack*, *shaack* and "*shack-shack*" were nearly the same in fundamental frequency, but *shack* was a little shorter in duration than *shaack* and "*shack-shack*", respectively.

4. Vocal-delivery duration

During the first observation period (49.08 h for both pairs), the males spent 16.5 percent (8.10 h) of the time in vocalization activities, and females only 2.64 percent (1.30 h). The difference between the calling rate of males (mean= 6.06 bouts/h) and females (mean= 1.27 bouts/h) was statistically significant (Sign test, χ^2= 18.05, P< 0.001). Males delivered 1 to 11 bouts and females 1 to 9 bouts. Each bout lasted an average of 0.99 ± 0.65 to 2.40 ± 0.67 min for males and 1.07 ± 0.51 to 2.54 ± 2.75 min for females (see Appendices 5 and 6). Vocal delivery duration of the males (mean= 7.25 min, SE= 1.32, R= 0.82-19.84, n= 67) was longer than that of the females (mean= 4.07 min, SE= 1.80, R= 0.17-10.09, n= 19). This difference between the sexes was statistically significant (Mann-Whitney test, U= 48.3, P= 0.0004).

5. Call discrimination

There are seven call types vocalized by both sexes that are spectrographically similar. These calls are monosyllable (Figs. 4B/6B, 4D/6C, and 5A/6D) and dissyllable (Figs. 1A/5C, 2B/5D, 2E/5E, and 4C/6A). These calls were analyzed further using discriminant analysis to determine whether they could be used to discriminate sex. The results are summarized in Table 2.

Monosyllabic calls in Figs. 4B and 6B are used as examples to explain the table. If calls were sexually grouped for the discriminant analysis, then 95.45 percent of the 22 male call samples were classified as male calls and 4.55 percent as female calls. For the 6 female call samples, 100 percent were classified as female calls. The differences of call variables between sexes were statistically significant (Mahalanobis distance, F=35.70 or P=0.0001).

If calls for Figs. 4B and 6B were not grouped, then 77.8 percent of 9 call samples vocalized by male number 1 could be classified by discriminant analysis as calls belonging specifically to male number 1 and the remainder, i.e. 22.2 percent, could also belong to other birds. For male number 2, 84.6 percent of his 13 call samples pertained specifically to him, while 15.4 percent could also be relegated to other birds. Of 6 call samples vocalized by female, 100 percent were classified as female calls.

Table 2. Summary of discriminant analysis of spectrographically similar calls vocalized by both sexes of captive loggerhead shrikes

Call Figs.compared (individual samples vocalizing (N))	Bout samples (n)	Classification (%)	F (value; probability)
4B vocalized by M (M=2), 6B vocalized by F (F=1)	Grouped sexually M=22 , F=6	M=95.45, F=100	35.70 ; 0.0001
	Not grouped M1=9, M2=13, F1=6	M1=77.78, M2=84.62, F1=100	22.03; 0.0001
4D vocalized by M (M=2), 6C vocalized by F (F=1)	Grouped sexually M=18, F=2	M=94.44, F=100	23.54 ; 0.0001
	Not grouped M1=11, M2=7, F2=2	M1=63.64, M2=57.14, F2=100	8.69; 0.0001
5A vocalized by M (M=1), 6D vocalized by F (F=1)	M=7 F=16	M=71.43 F=56.25	1.26 ; 0.3063
1A vocalized by M (M=1), 5C vocalized by F (F=1)	M=12 F=5	M=100 F=100	12.13 ; 0.0004
2B vocalized by M (M=1), 5D vocalized by F (F=1)	M=18 F=6	M=100 F=100	33.64 ; 0.0001
2E vocalized by M (M=1), 5E vocalized by F (F=1)	M=21 F=5	M=100 F=100	14.39 0.0001

Table 2 (continued)

4C vocalized by M (M=1), 6A vocalized by F (F=1)	M=11 F=12	M=100 F=100	35.41; 0.0001

Note:

1. Variables for monosyllabic calls: highest value of fundamental frequency (HV), duration (DUR) of call; variables for dissyllabic calls: HV of syllable 1, HV of syllable 2, DUR of syllable 1, DUR of syllable, DUR of intersyllable, DUR of call.
2. M1 = Male number 1, M2 = Male number 2,
   F1 = Female number 1, F2 = Female number 2.

However, there appears to be some variability with these classifications. For instance, of 7 call samples of the male shown in Figs. 5A and 6D (Table 2), 71.4 percent were classified as male calls and the remainder, i.e. 28.6 percent, as female calls. Of 16 call samples of the female, 56.3 percent were classified as female calls and the remainder, i.e. 43.7 percent, as male calls. There was no statistical difference between the sexes. Thus, compared to calls of Figs. 4B and 6B and Figs. 4D and 6C, calls of Figs. 5A and 6D were less useful for distinguishing between the sexes.

Meanwhile, variables of all dissyllabic calls can classify 100 percent of the samples to male or female as the difference between sexes was statistically significant [Mahalanobis distance, F values vary but $P<0.0005$]. Thus, compared to monosyllabic calls, dissyllabic calls involving more variables may be more useful for sexing. To select one or more specific dissyllabic calls that can be used for sexing would require further statistical analysis on a larger sample size or possibly, playback experiments. Because of the spectrographic similarity however, the differences in variables can explain variations of calls both within and between sexes. Thus, it is possible to use trill calls as a sex discrimination tool in loggerhead shrikes because these calls are vocalized only by males.

B. Calls Related to Breeding Behaviors

1. Visual displays

In the first stage, visual displays of the caller and reaction of the receiver were not investigated because of their confinement in relatively small cages with no physical contact and logistical difficulties in observing any behavioral patterns in detail. It is interesting to note however, that when calling and perching on the barbed wire, the caller did direct its attention toward the resident of the opposite cage. The receiver reacted by either sitting quietly on its perch and looking toward the caller or jumping around in the cage. What calls cause these opposite reactions is not known.

In the second stage using paired shrikes in spacious breeding pens, calls associated with breeding behaviors and possibly accompanied by displays, occur at various stages, i.e. nest site selection, nest building, food offering, food begging, as well as aggressive, alarm and copulatory behaviors. Calls were generally produced by the males. Few calls were produced by females, other than harsh calls during food begging, food offering, and aggressive or alarm calls.

Visual displays simultaneously were composed of wing fluttering, tail fanning, and head bobbing or partly just involved wing fluttering or feather fluffing. In head bobbing, the bird stretched its neck and moved its head up and down. Displays and wing flutterings appeared to be responsible for causing up and down movements in spectrogram images from calls issued during these behavioral patterns (see Figs. 8, 9 and 10).

2. Nest site selection and nest building

To my knowledge, there have been no previous reports dealing with calling behavior of loggerhead shrikes during nest site selection and nest building. Notably in this study, only the males vocalized during these activities. When using these vocalizations, the males always directed their attention toward the females. Males only seemed to display when the females were looking toward them.

Each male of the observed pairs issued somewhat different calls specific to it (see Table 3), but performed visual displays that were similar to other males. Prior to nest building (in this study, after the first clutches of eggs were removed), the male called and displayed at two or three different sites. Likely

Table 3. Calls of male captive loggerhead shrikes during breeding activities

Call in activity	Pair 1 M3.F2	Pair 2 M4.F3	Pair 3 M2.F5	Pair 4 M5.F4
Nest-site selection: Mean ± SE (in min.) Range min-max. Records (n)	Fig. 5B *"Shack-shack"* 0.84±0.71 0.17-1.85 6	Fig. 2C *Pee-to* 0.79±0.33 0.35-1.45 9	Fig. 3B *Pree-wee-wee-wuut* 1.18±0.28 0.30-2.28 22	Fig. 2A *Pee-tooy* 1.56±0.72 0.43-3.27 10
Nest building: Mean ± SE (in min.) Range min-max. Records (n)	Fig. 3C *Pree-wee-weep* 0.87±0.51 0.60-1.77 6	Fig. 4C *Peep-peep* 1.52±0.32 0.35-1.90 11	Fig. 3B *Pree-wee-wee-wuut* 1.04±0.27 0.17-2.97 29	Fig. 2A *Pee-tooy* 1.40±0.33 0.35-2.30 18
Copulation attempts/ copulation	No data	Fig. 3A *Pree-lee-lee*	Fig. 3B *Pree-wee-wee-wuut*	Fig. 2A *Pee-tooy*

Note: 1. For example: M3.F2 = male number 3 paired with female number 2
2. SE is at confidence interval of 95%

the male was offering the female a choice of sites suitable for nesting, but it is not known for certain who actually chooses the final site. After a nest site was selected, the male only called and displayed at that site and no longer at the other sites. The male may then produce calls that differ from those during nest site selection behavior, e.g. "*shack-shack*" during nest site selection behavior and *pree-wee-weep* during nest building (heard from the male of pair number 1), but the displays remain similar. Next, the male brought nest materials to the site, followed by calling. The female responded to this invitation by moving closer and also bringing nest materials. Not all nest building activity is accompanied by calling and displaying.

Some typical interactions at this stage follow: on 21 June, 1994 at 10:32 AM, approximately 10 min after the first clutch was removed from pen 4 (male number 2, female number 5), the female returned to the nest, inspected it, and then left the nest. Next, the male came to the nest, stood in it, and called *pree-wee-wee-wuut*. During this calling, he always directed his attention toward the female. When the female looked toward him, he displayed by fluttering his wings, fanning his tail, stretching his neck, and bobbing his head up and down. His beak was pointed up and then down, almost touching the nest. However, when the female stopped watching him, he fluttered his wings slowly, stopped bobbing, and eventually ceased all visual displays. The female continued to ignore his calls. She perched on the tree branch about 2 m from the old nest, preened, and did not attempt to come closer to him. The male then stopped, flying away to another perch. He called *pree-wee-wee-wuut* for 0.43 min. Two days later at 11:37, the male called *pree-wee-wee-wuut* and displayed on a rafter 15 cm below the roof and 4.5 m in height. The rate of his calls and displays seemed to be a bit faster than before, especially when the female approached within approximately 20 cm of him. He stopped, after calling and displaying for 1.83 min, flew to the site below the old nest, and dismantled the down part of the old nest. He flew again with the old nest material in his beak, approached the female to within 10 cm, and repeatedly touched this material to her body. The female took the nest material in her beak and flew to another perch. Then she threw the nest material away in deliberate fashion. After another attempt by the male, she directly refused the material and moved away from him. The male responded by placing the material near where she perched. On 26 June at 09:46, the male called *pree-wee-wee-wuut* and displayed on the edge of the nest after creating a 5 cm pile of nest materials, mostly grass, roughly 30 cm above the old nest site, and forming a nest cup. Basically his display was similar to the former nest site selection display. The female responded by bringing small twigs to the nest site. The male stopped calling after 0.33 min and flew from the nest. The female moved to the centre of the pile of nest materials, scratched about in them, crouched, rotated her body opening one or both wings to the side, and pecked at several materials and arranged them on the edge of the nest. She did this for approximately 2 min and then moved to a tree branch 2 m below the old nest. Five min later, the male returned to the nest site, calling *pree-wee-wee-wuut* for 0.52 min. He stopped when the female ignored him. In this case, the male did not switch his call figure when he changed perching sites.

3. Food offering

The structure of the food offering call has complex tones and was vocalized by both sexes while bringing food in their beaks. The male produced *shack* calls with no wing fluttering (Fig. 7) when offering food to a female laying or incubating the eggs, to nestlings that were still in the nest, and to fledglings that were not able to take food by themselves yet. The male vocalized 1 to 6 *shack* calls when the receiver did not immediately respond to his offer. If the receiver immediately responded by taking food from his beak, he did not vocalize. The females also produced similar *shack* calls without displays, when offering food to young.

Meanwhile, the behavioral patterns in which the male produced calls while fluttering his wings (Fig. 8) occurred during the nest building period, during the egg-laying period and when the female temporarily left the nest. The male continuously called and fluttered his wings even from a distance, then flew or moved closer to the female so that he could give her his food. Of the 29 courtship feeding observations, 24 records were followed by copulation attempts. These behavioral patterns by the male appear to induce the female to copulate.

4. Food begging

Food begging calls were harsh *shack* calls or complex-tone calls and were vocalized either by the female (Fig. 9) or by young shrikes (Fig. 14) while fluttering their wings. These calls are phonetically and spectrographically similar to food offering calls by the male. The female produced food begging calls during egg-laying, incubation or on perching sites just after leaving the nest. Only one instance was recorded where food begging calls were consecutively followed with courtship feeding and copulation. Cade (1992) reported food begging calls by his female as "*mak*" or "*jak*" and the response call by the male, while transferring food to the female, to be "*wuut*".

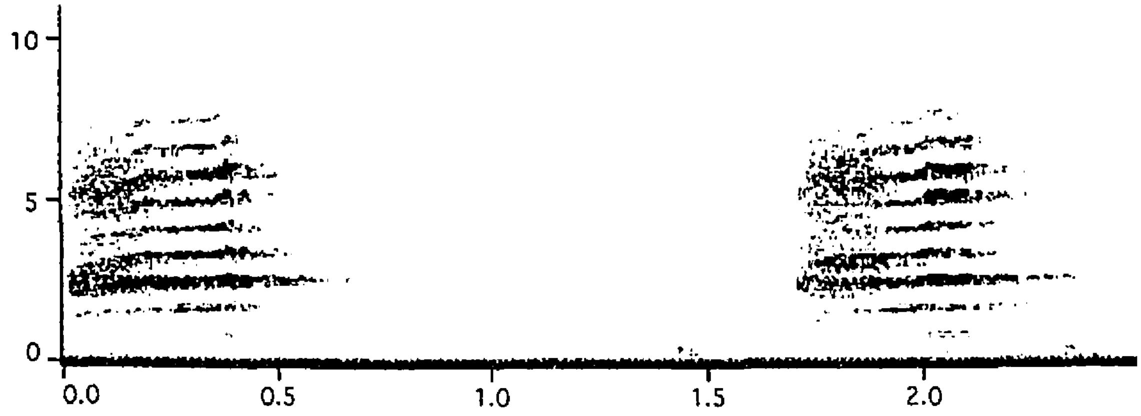

Fig. 7. Food-offering calls vocalized by male captive loggerhead shrikes without display

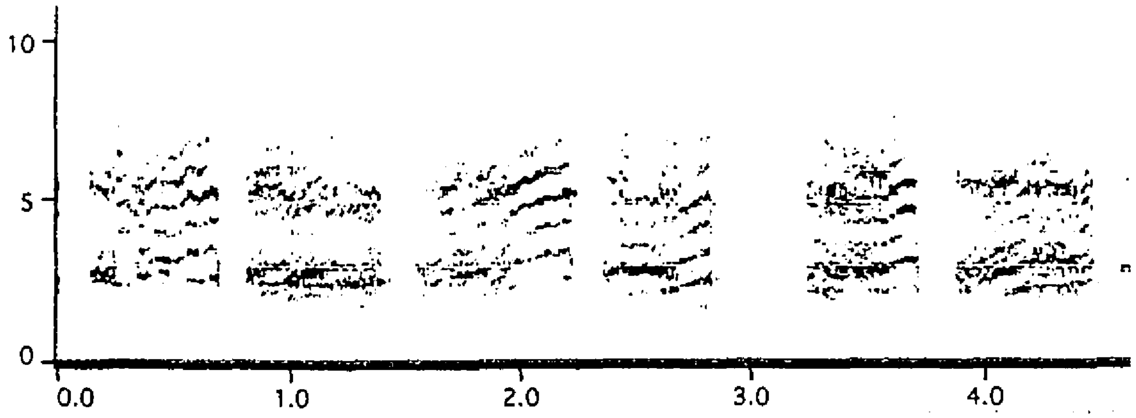

Fig. 8. Food-offering calls vocalized by male captive loggerhead shrikes with display

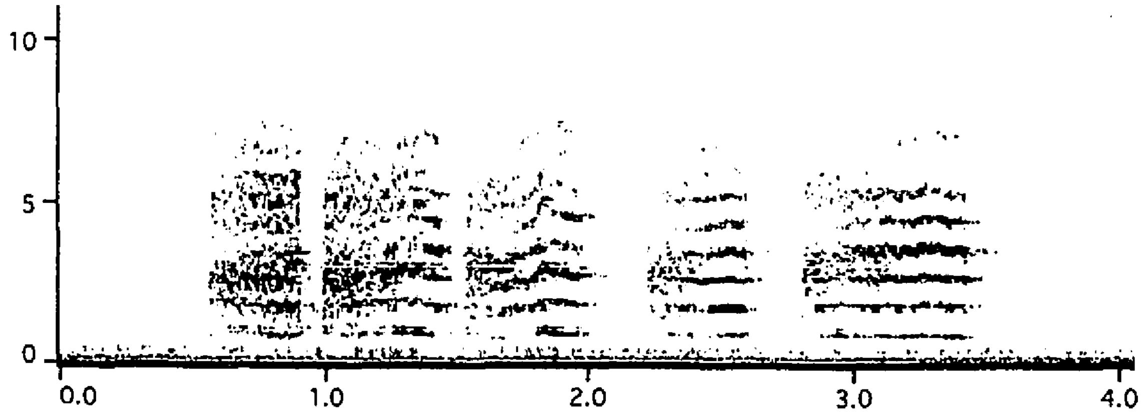

Fig. 9. Food-begging calls vocalized by female captive loggerhead shrikes with display

5. Copulation

Copulations were quick and mostly took place either in the morning or in the afternoon. Of 24 copulation attempts, 11 were considered to be successful. After the female took food offered by the male, the male mounted her from the back while fluttering his wings and calling. After the copulation ended, the female remained on her perch and flapped her wings. Occasionally after copulation, the male attempted to retake food from the female.

Each male gave *shack* calls that were similar to other males during courtship feeding, but issued his own distinct calls during copulation attempts or copulation (see Table 3). Ten copulations which were accompanied with two consecutively similar calls (*pee-tooy* in Fig. 10 and *pree-lee-lee* in Fig. 11) were recorded. There was only one record in which a copulation was accompanied with three consecutively similar *pree-wee-wee-wuut* calls.

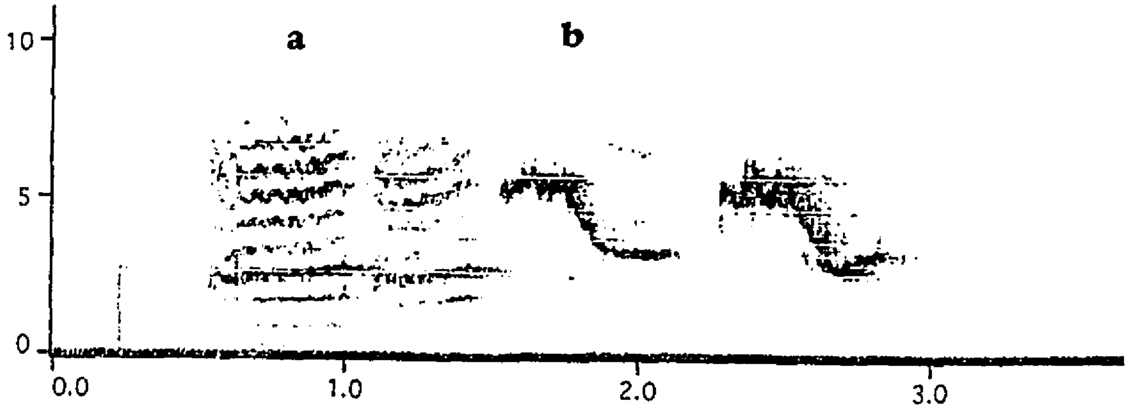

Fig. 10. Courtship feeding calls (a) followed with copulation *pee-tooy* calls (b). These calls vocalized by male captive loggerhead shrike of pair 3.

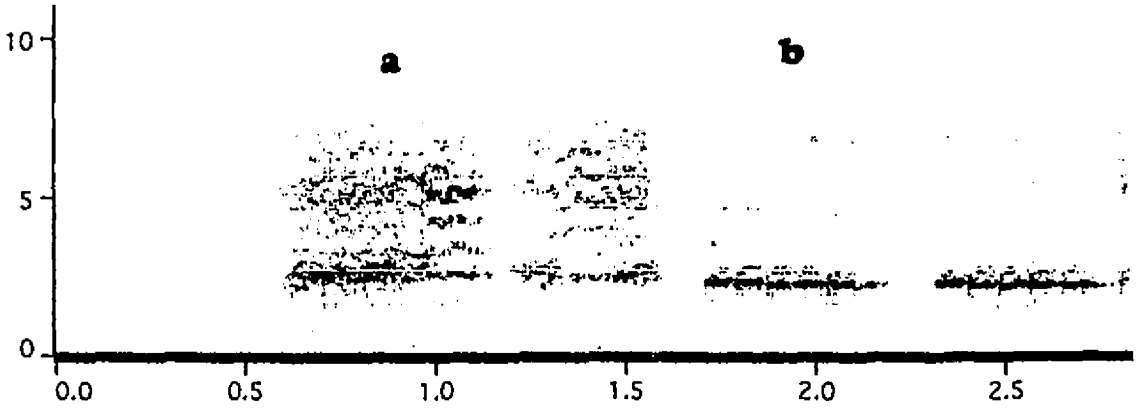

Fig. 11. Courtship-feeding calls (a) followed with copulation *pree-lee-lee* calls (b). These calls vocalized by male captive loggerhead shrike of pair 2.

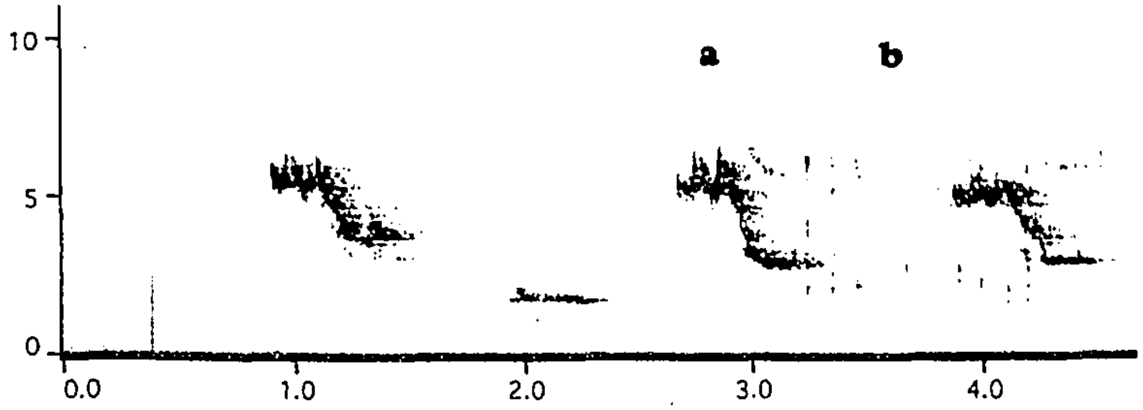

Fig. 12. Copulation-attempt calls by male captive loggerhead shrike (a) followed with aggressive calls by female captive loggerhead shrike (b)

6. Aggressive and alarm calls

Telfer (1993) mnemonically described aggressive calls as "a repeated *tink* sound, like that made by tapping two pieces of metal together" and concluded that it functioned as an alarm call. Aggressive calls seem to be harsh in their nature and their spectrogram is so thin that their duration is not easy to measure. This call is estimated to be fewer than 6.5 kHz in frequency and more or less 0.020 sec in duration. Aggressive calls are vocalized:

1) by the female when refusing to copulate (see Fig. 12b). In one case she immediately turned her back away, directed her face toward the incoming male, lowered her body, and opened her wings widely.

2) by the male when chasing the female in flight.

3) by the male, when flying fast about 5 cm in front of the one-way window observation which functioned as a mirror to him. These aggressive calls resembled "*bzeek*" (Bent 1965) or "*bzeee*" (Udvardy 1992) and lasted approximately 2 sec in duration.

4) by the male, when faced with a strange male shrike introduced to the pen. He attempted to attack the caged shrike by moving in close. When perching on the cage or staying on the ground near the cage, his attention was always directed toward the opponent. His posture was almost horizontal with the body lowered and the wings opened, and his tail flicked up and down.

5) by both sexes while hovering within 1 m of the nest when a human intruder approached their nest containing eggs or nestlings.

6) by both sexes, when watching a hawk perched on the peak of a 7-metre electricity pole about 8 m outside the pen. They vocalized entirely aggressive calls for nearly 20 min continuously, flew around and moved from one high perching site to another, always keeping the hawk in sight and fluffing their feathers. Similarly, both sexes produced aggressive calls when starlings and sparrows passed above the pen or perched on the wire roof of the pen.

When watching the hawk, aggressive calls were also followed by alarm calls (Fig. 13). Like food offering and food begging calls, alarm calls are complex tones. These calls were vocalized with high intensity and with a long duration. Bent (1965) described alarm calls as "prolonged jaylike notes, *schgra-a-a*" and Telfer (1993) referred to them as a *shriek*.

7. Calls vocalized by young shrikes

"*Tsp*" and "*screig*" were vocalizations made by young shrikes. Both names were given phonetically by Bent (1965). Nestlings vocalized "*tsp*" approximately 6.5 kHz in frequency and extremely short in duration (Fig. 15), while pointing up and always opening their beak. When nestlings vocalized the "*tsp*" call collectively, it was very noisy in the breeding pens. Noisy vocalizations for altricial nestlings facilitate parents to locate their nestlings, but could also invite predators (Redondo and De Reyner 1988). They stopped calling when parents brooded them or put food in their beaks. Thus, "*tsp*" calls can be associated with food begging and the demand for brooding. Fledglings issued "*screig*" calls that were also complex tones (Fig. 16) while sitting on the edge or close to the nest or walking around on the ground. They also produced these accompanied by fluttering their wings when begging for food (Fig. 14). For the human ear, these two calls, i.e. "*tsp*" and "*screig*", can be used to determine the difference between nestlings and young birds that have fledged or are ready to fledge.

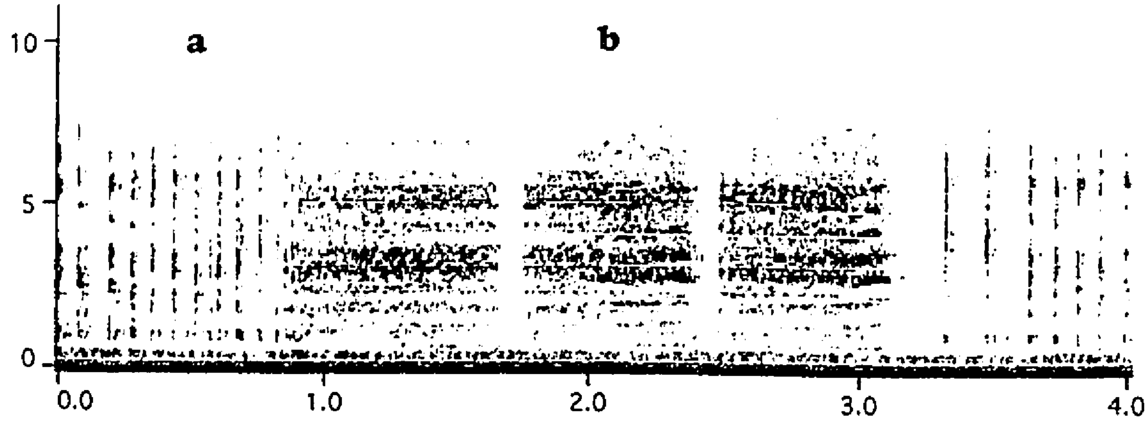

Fig. 13. Aggressive calls (a) and alarm calls (b)

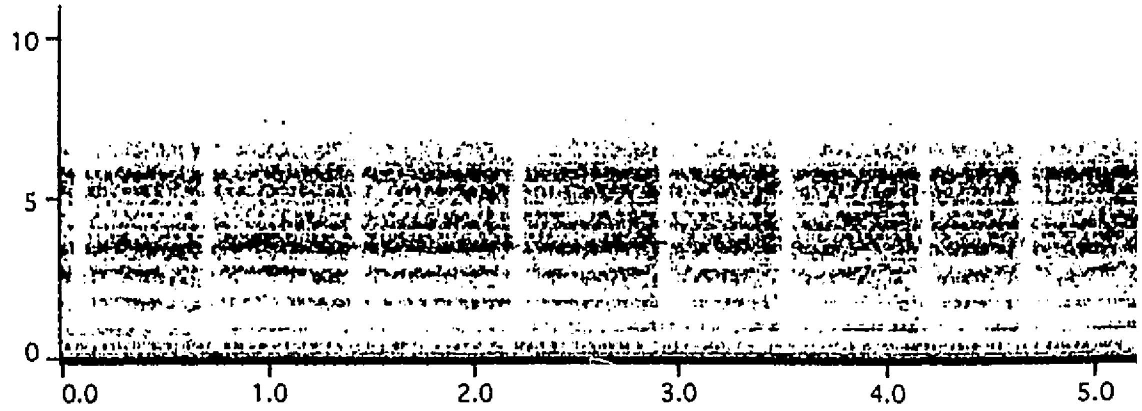

Fig. 14. Food-begging calls vocalized by young shrikes

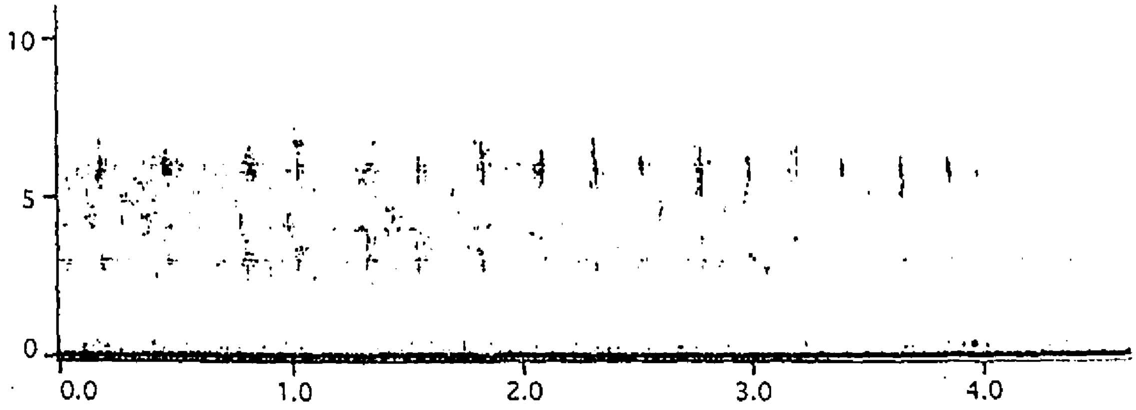

Fig. 15. "*Tsp*" calls vocalized by nestlings

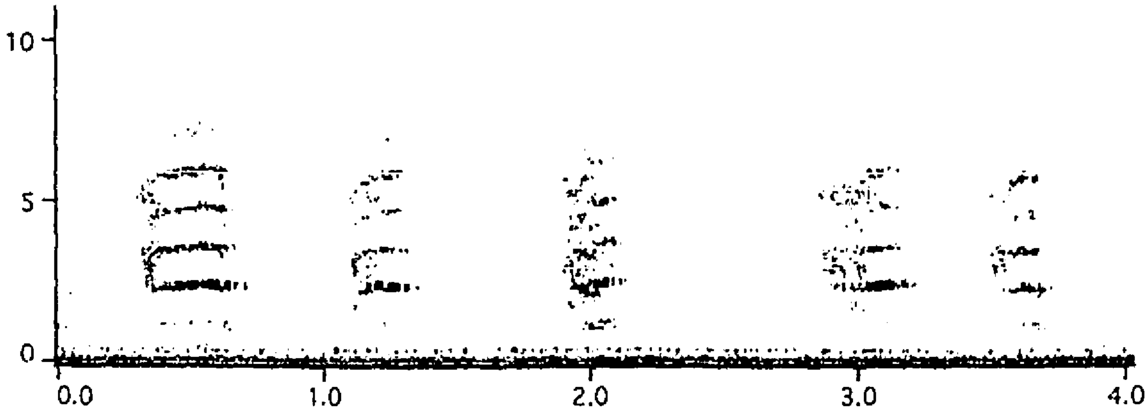

Fig. 16. "*Screig*" calls vocalized by fledglings

V. DISCUSSION

A. Vocalizations

This study indicates that loggerhead shrike calls contain no more than two notes ranging from a pure tone or frequency to complex tones or frequency-changing notes. In contrast, Scott and Morrison (1990) reported that males' songs were composed of not only repeated double-note but of triple-note calls as well. The kind of note they were referring to was however, not further explained. Acoustically, calls of this species are generally whistled, trill, squeaky, or harsh sounds, as described by Chapman 1904, Saunders 1935, Snyder 1951, Bull and Farrand 1992, and Scott 1992.

Both sexes vocalize some spectrographically similar calls, in spite of the little differences in frequency and duration (compare the males in Figs. 1A, 2B, 2E, 4B, 4C, 4D, 5A with the females in Figs. 5C, 5D, 5E, 6A, 6B, 6C, 6D, respectively; and see Table 2). Discriminant analysis could likely classify those calls sexually if the individual sample size had been larger and if many variables could be measured. On the other hand, males demonstrated three remarkable differences from females in their vocalizations. Males demonstrated trill calls that females did not do, and they consistently vocalized a higher calling rate and longer call than females.

Bent (1965) mentioned that the trill songs vocalized by the male in the spring vary in pitch, rhythm, and quality. In some avian species, one or both sexes can vocalize trill calls in spite of different structures. In those cases where only one sex issues trill calls, this can be used for sex identification. In boreal chickadees (Parus hudsonicus: McLaren 1976), only the male produces trill calls. These calls, normally preceded by musical calls, are aggressive calls. Conversely, in pinon jays (Berger and Ligon 1977), only the female vocalizes trill calls and these calls are thought to be non-aggressive calls. In male red-winged blackbirds (Agelaius phoeniceus), songs consisting of short introductory notes and a longer, rapid trill call are useful for promoting sexual differences and stimulate females maximally (Searcy and Brenowitz 1988).

Besides trill calls, a higher calling rate and longer vocal delivery in male loggerhead shrikes studied indicates that males in general are much more active in calling than females. This confirms Bent's (1965) view stating that male loggerhead shrikes frequently vocalize songs and/or calls, but females do so briefly.

In male-female interactions, male shrikes may demonstrate trill calls primarily to indicate their sex, and then vocalize actively and longer not only to attract females but also to show off their repertoire in terms of either the number of calls or the figures of calls. By doing so, the males might be counterbalancing sexual selection, by giving females the opportunity to first recognize them as being of the opposite sex and also indirectly announcing individual quality. In addition, males can use their repertoires to express different behavioral patterns (Smith 1959), to counter other males' songs, to drive away male neighbours as a result of a Beau Geste effect (Krebs 1977), and to minimize the rate of habituation of the listeners (Yasukawa 1981). By achieving the latter via a larger repertoire, males would benefit by countering other males' songs in dense populations (male-male interaction) and to overcome competition for mates (male-female interaction) (Kroodsma 1977). Thus, call repertoires play an important role in male-male interaction during territorial establishment and maintenance as well (Kroodsma 1976). However, how mates are chosen in loggerhead shrikes is still unknown. It is possible that female loggerhead shrikes might choose their mates based on call repertoire.

In the red-winged blackbird, the male with the larger repertoire more effectively repels intruders from his territory (Yasukawa 1981). Hiebert et al. (1989) found that the male song sparrow with the larger repertoire tended to spend less time floating before acquiring his territory, to hold a larger territory and for a longer period, and to have a greater relative annual and life time reproductive success than the male with a smaller repertoire. Males that did not demonstrate their songs early in the breeding season failed to establish territories and to attract mates, whereas those which did not do so in the middle of the breeding season lost their territories or mates (McDonald 1989, Westcott 1992).

In the great tit, Lambrechts and Dhondt (1986) found similar results. The better singers, i.e. male great tits issuing songs with longer strophes, less positive drift, and larger repertoires, possessed longer survival and produced more offspring that survive during their lifetime. Lambrechts and Dhondt (1986) defined a strophe as a number of phrases sung repeatedly in a stereotyped way. A number of strophes sung repeatedly and separated by silent period were termed a bout. Lambrechts and Dhondt (1986) then defined drift as the changes of singing rate within each strophe. This drift was expressed in a regression curve between total phrase length - in this case, length of phrase plus interphrase pause - and phrase rank. There was no further explanation about phrase rank. Drift was positive when the singing rate reduced.

Call repertoires of males may help the female, primarily during pair formation, to choose her mate (Miller 1979, McDonald 1989, Wescott 1992). She uses the males' songs as an indicator of genetic fitness (Searcy 1979) and even for male age estimation (Loffredo and Borgia 1986). For example, Hiebert et al. (1989) concluded that female song sparrows respond more strongly to males with larger repertoires.

Practically speaking, frequency of calling was used for determining sexes of captive loggerhead shrikes prior to the use of laparoscopy. Using frequency of calling alone, the sexes of 11 of 14 (78.6 percent) captive loggerhead shrikes determined by laparoscopy were correctly identified. At that time, trill calls were not used for sexing. It is highly likely that a combination of the trill calls issued only by males and frequency of calling can be a useful technique for sexing monomorphic loggerhead shrikes in field and laboratory.

Calls of loggerhead shrikes also vary on an individual basis within the sexes based on frequency and duration. For example, calls in Figs. 3F, 4B, 4D and 4F by male number 1 and 2 are spectrographically and phonetically similar, but they are different with respect to frequency and duration (see Table 2 for discriminant analysis of Figs. 4B and 4D; also Table 6 for a mean of frequency and duration). A similar phenomenon likely exists with the females.

Calls vary structurally within and among individuals as well. The call structure in Fig. 1A for male number 1 varied somewhat with that same male's call structure in Fig. 1C. The call structure varied again with male number 2 in Fig. 1B and again in Fig. 2A by male number 5.

Since members of this species are morphologically similar, variations in frequency and duration of calls, as well as call structure may promote recognition of individuals. Weary and Krebs (1992) reported that individuals of avian species recognize each other based on distinctive repertoires, variations, or qualities of songs and/or calls. Brooks and Falls (1975) observed that white-throated sparrows (Zonotrichia albicollis) use variations in terms of note patterns, duration of notes, intensity of pitch, changes of pitch, or note interval as individual recognition. Brooks and Falls (1975) and Krebs (1977) believed that those factors may vary among individuals, but are relatively consistent within individuals. This feature may be useful for maintaining a pair bond in male-female interactions. Even though pair bonds may be maintained better by combining both vocalization and visual signals than by vocalizations alone, vocalization may play an important role for a female to recognize her mate when visual signals are absent (Miller 1979, James 1984).

This study also found that loggerhead shrikes produce a bout of two different calls vocalized alternately and on rare occasions, i.e. a mixed bout. For example, a shrike would alternate between *shack* and *pee-too* calls, generally only three or four times, within a bout. A typical bout might be as follows: several *pee-toos*, a *shack*, a *pee-too*, a *shack*, a *pee-too*,a *shack*, a *pee-too*, and then a string of *shacks*. This mixed bout however, was categorized as a pure bout when calculating bout duration.

B. Calls Related to Breeding Behaviors

It was not too difficult to interpret call functions in their contextual behavior, when observing the males and females frequently vocalizing similar calls in certain activities, e.g. food offering, food begging, aggressive and alarm calls. On the other hand, it was difficult to interpret calls made by males which were different from the above during those same activities. This difficulty can apparently occur when interpreting the activities of individuals who possess high call repertoires in terms of differences in call types, variations, qualities or a sequence of call delivery, as Weary and Krebs (1992) stated. It is not easy to determine the meaning of calls to the receiver in these cases (Catchpole 1982). In cases like this, displays accompanying calls tend to function much more in conveying a message than just calls alone. Bondesen (1977) noted that in open range birds, calls and visual displays are an effective communication system for both defending territories and for courtship behaviors during the breeding season.

Calls seem to be unnecessary in some cases, but can play an important role in other cases, for example to attract the attention of a receiver. In food offering, the male does not call if the female immediately takes food from his beak. The food on the beak apparently acts as a visual signal which directly stimulates the receiver to react. On the other hand, the male will call when the female does not respond to his offered food. Without the calls, he cannot relay his message to his mate or youngsters for a quick response.

A similar situation is seen in nest site selection. During calling, the male's eyes were always directed toward the female. The male only displayed when the female paid attention to him. His displays became faster and more urgent when she reacted by coming closer to him. In these cases, the calls function to attract the attention of the receiver. Thus, the displays function not only to indicate his location but to indicate the meaning of his invitation as well.

In all cases, the male shrike took the initiative in nest site selection, nest building, copulation, and food offering prior to copulation. Each male gave his own specific calls in the first three behavioral patterns. Otherwise, all males issued the same harsh calls during aggression and alarm, as well as during food offering and courtship feeding. This suggests that in male-female interactions, each male facilitates his identification to his mate through his calls and thus, controls the female's breeding activities. Otherwise, in situations where individual recognition is not too important, each male can transfer his messages by issuing similar harsh calls that can be understood not only by pair members but by conspecific members as well. These messages can be accentuated and defined to the receiver by accompanying behavioral patterns and visual displays, e.g. sudden movements, repeated fast flight from one site to another, wing fluttering, or horizontal posture accompanied with fluffing feathers. The alarm call, an important anti-predator behavior in many species of birds and mammals, is a good example. This call can function as a warning of danger not only for members of a pair (East 1981) but also for genetic relatives, including non-descendent kin (Hoogland 1983).

During observations of breeding pairs, the females produced no other calls besides harsh calls during food offering to young, food begging, aggressive, or alarm behaviors. This is contrary to the results of the first stage where females produced several types of calls, some of which were spectrographically and phonetically similar to those of the males. This can be explained based on territorial occupation. During the breeding season, a pair of shrikes occupy the same territory. In nest site selection, the male appears to give his mate the opportunity to choose the nest site. Calls produced during the nest site choice thus function to announce and indirectly defend their territory. In other words, using his calls the male takes over territorial defence. Conversely, during the non-breeding season, males and females occupy separate territories that each has to defend. Armstrong (1973) proposed that during this season female shrikes use their calls to defend their territories.

Overall, there is much more to learn about vocalization behavior in loggerhead shrikes, captive and free-ranging. Like much scientific investigation, this study generated a number of unanswered questions. Does the female shrike select a mate based on his call repertoire? Which affects the female's choice more: the number of calls or types of calls? Are there other types or variations in loggerhead shrike calls? In the field, data collected might be much more variable because shrikes face more complex problems on a daily basis, such as mating competition, predator attacks, and lessened availability of food, nest materials and/or nest sites.

VI. CONCLUSION

This study spectrographically and quantitatively described the calls of captive-raised loggerhead shrikes as well as relating their calls to breeding behaviors. Their calls consisted of whistled, harsh, trill sounds with variations in structure, frequency, and duration. Males gave trill calls that are not issued by females and they also vocalize more actively than females. When males and females were paired in the breeding pens, each male gave distinctive calls that were different from other males' calls in nest-site choice, nest building, and copulation, but emitted similar harsh calls during food offering, aggression and alarm. All males however, exhibited similar visual displays during all the behavioral patterns mentioned above. Thus, visual displays and vocalization play an important role in transferring and explaining the message of the callers.

As to whether loggerhead shrikes use trill calls as sex recognition and whether they vary their calls for individual recognition and pair-bond maintenance, further study is required to examine these hypotheses.

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Appendix 1. Descriptive statistics of dissyllabic calls of male captive loggerhead shrikes

CF: Bs	Syllable 1 duration (sec)	Syllable 1 frequency (kHz)	Syllable 2 duration (sec)	Syllable 2 frequency (kHz)	Call duration (sec)	Intercall duration (sec)
1A n=12	0.179±0.008 0.144-0.240	6.00±0.19 5.55-6.77	0.301±0.017 0.226-0.360	2.63±0.06 2.44-2.94	0.500±0.019 0.414-0.560	1.943±0.260 1.392-3.310
1B n=8	0.248±0.015 0.230-0.281	5.76±0.18 5.48-6.03	0.064±0.005 0.054-0.075	2.85±0.15 2.68-3.02	0.313±0.015 0.295-0.343	1.913±0.167 1.432-2.643
2B n=18	0.060±0.002 0.050-0.074	4.66±0.05 4.34-4.80	0.267±0.018 0.134-0.314	2.52±0.04 2.40-2.78	0.329±0.018 0.192-0.374	1.573±0.152 0.930-2.428
2C n=5	0.252±0.033 0.210-0.294	4.99±0.18 4.70-5.32	0.156±0.036 0.124-0.210	3.55±0.09 3.43-3.71	0.417±0.058 0.344-0.484	1.759±0.167 1.557-2.113
2D n=14	0.159±0.014 0.123-0.210	6.34±0.12 6.05-6.73	0.211±0.016 0.162-0.290	2.73±0.03 2.59-2.89	0.396±0.017 0.350-0.460	1.874±0.288 1.315-3.650
2E n=21	0.167±0.005 0.136-0.193	3.70±0.03 3.51-3.98	0.190±0.008 0.153-0.227	2.30±0.04 2.17-2.62	0.362±0.010 0.299-0.481	1.675±0.176 1.029-2.800
2F n=4	0.213±0.041 0.194-0.233	3.61±0.66 3.22-4.14	0.155±0.064 0.112-0.221	3.14±0.26 3.01-3.45	0.368±0.076 0.243-0.451	1.572±0.281 1.350-1.686
1C n=13	0.075±0.004 0.069-0.085	6.09±0.10 5.81-6.45	0.339±0.012 0.317-0.360	2.45±0.12 2.12-2.82	0.414±0.040 0.335-0.455	1.720±0.197 1.314-2.487
5B n=12	0.177±0.011 0.151-0.209	1.10±0.06 1.00-1.20	0.194±0.012 0.167-0.267	1.08±0.06 0.99-1.20	0.417±0.017 0.365-0.451	1.444±0.330 1.234-2.003
4C n=11	0.204±0.010 0.180-0.220	2.69±0.05 2.60-2.75	0.217±0.011 0.190-0.228	2.68±0.05 2.58-2.80	0.467±0.015 0.458-0.480	1.910±0.129 1.630-2.480
2A * n=28	-	5.97±0.08 5.42-6.21	-	3.43±0.11 3.08-3.86	0.584±0.010 0.542-0.620	1.685±0.118 0.988-2.547

Note: 1. CF = Call Figure; Bs = Bout samples

2. In each box, the upper of pair of numbers is Mean ± SE at confidence coefficient 99%; and the lower is minimum and maximum values (range) on data.

3. * = this call consisted of two syllables, but duration of each syllable was not measured

Appendix 2. Descriptive statistics of monosyllabic calls of male captive loggerhead shrikes

CF; Bs	Call duration (sec)	Call frequency (kHz)	Intercall duration (sec)
3A n=21	0.381 ± 0.039 0.300 - 0.652	2.58 ± 0.04 2.46 - 3.01	1.725 ± 0.148 1.262 - 2.978
3B n=18	0.456 ± 0.020 0.356 - 0.502	4.16 ± 0.06 3.92 - 4.32	1.841 ± 0.111 1.523 - 2.767
3C n=5	0.331 ± 0.034 0.281 - 0.400	3.07 ± 0.10 2.94 - 3.22	1.899 ± 0.464 1.241 - 2.765
3D n=13	0.309 ± 0.017 0.250 - 0.385	2.86 ± 0.13 2.56 - 3.37	1.796 ± 0.333 1.214 - 4.005
3E n=4	0.286 ± 0.025 0.276 - 0.309	2.85 ± 0.05 2.80 - 2.91	1.955 ± 0.706 1.675 - 2.950
3F; Data M1&M2 combined, n=27	0.287 ± 0.011 0.224 - 0.410	5.16 ± 0.23 4.56 - 5.88	1.757 ± 0.117 0.962 - 2.476
M1 only, n=14	0.278±0.009 0.224-0.410	4.82±0.25 5.16-5.88	1.692±0.203 1.518-2.235
M2 only, n=13	0.297±0.022 0.234-0.302	5.52±0.12 4.56-5.06	1.828±0.133 0.962-2.476
4A n=10	0.242 ± 0.009 0.205 - 0.257	6.68 ± 0.07 6.60 - 6.80	1.614 ± 0.198 1.305 - 2.299

Appendix 2 (continued)

4B; Data M1&M2 combined, n=22	0.330±0.016 0.267-0.411	2.31±0.06 2.11-2.55	1.443±0.147 0.974-2.450
M1 only, n=9	0.324±0.022 0.267-0.409	2.39±0.05 2.18-2.55	1.434±0.191 0.974-2.450
M2 only, n=13	0.334±0.025 0.272-0.411	2.25±0.07 2.11-2.48	1.449±0.246 1.100-1.754
4E n=15	0.224±0.012 0.200-0.265	1.82±0.03 1.74-1.89	1.640±0.114 1.321-1.976
4D; Data M1&M2 combined, n=18	0.287±0.014 0.230-0.326	2.46±0.06 2.25-2.68	1.552±0.079 1.248-1.941
M1 only, n=11	0.284±0.021 0.230-0.325	2.43±0.09 2.25-2.66	1.558±0.104 1.268-1.941
M2 only, n=7	0.291±0.024 0.259-0.326	2.49±0.12 2.35-2.68	1.542±0.188 1.248-1.876
4F; Data M1&M2 combined, n=22	0.256±0.014 0.208-0.316	0.91±0.02 0.82-1.00	1.451±0.167 0.915-2.234
M1 only, n=12	0.251±0.020 0.208-0.310	0.92±0.03 0.86-0.98	1.316±0.182 0.915-2.116
M2 only, n=10	0.261±0.027 0.215-0.316	0.90±0.04 0.82-1.00	1.512±0.255 1.090-2.234
5A n=7	0.366±0.023 0.334-0.404	1.05±0.10 0.92-1.16	1.741±0.289 1.337-2.365

Appendix 3. Descriptive statistics of dissyllabic calls of female captive loggerhead shrikes

CF; Bs	Syllable 1 duration (sec)	Syllable 1 frequency (kHz)	Syllable 2 duration (sec)	Syllable 2 frequency (kHz)	Call duration (sec)	Intercall duration (sec)
5C n=5	0.155±0.006 0.144-0.168	6.03±0.11 5.89-6.12	0.277±0.015 0.256-0.295	2.53±0.10 2.48-2.65	0.446±0.025 0.428-0.471	1.418±0.276 1.175-1.892
5D n=6	0.061±0.006 0.049-0.071	4.47±0.10 4.39-4.55	0.373±0.013 0.350-0.391	2.54±0.07 2.49-2.69	0.436±0.011 0.410-0.462	1.736±0.312 1.247-2.100
5E n=5	0.180±0.015 0.160-0.193	3.55±0.10 3.46-3.62	0.183±0.007 0.171-0.193	2.50±0.09 2.40-2.59	0.370±0.022 0.355-0.390	1.455±0.299 0.996-1.960
5F n=3	0.206±0.050 0.180-0.219	2.42±0.29 2.36-2.51	0.252±0.013 0.240-0.268	4.19±0.37 4.00-4.36	0.460±0.012 0.450-0.468	1.958±0.475 0.987-1.326
6A n=12	0.211±0.010 0.200-0.221	2.48±0.04 2.38-2.59	0.223±0.010 0.200-0.259	2.49±0.01 2.48-2.56	0.452±0.020 0.406-0.496	1.573±0.391 1.233-2.659

Appendix 4. Descriptive statistics of monosyllabic calls of female captive loggerhead shrikes

CF; Bs	Call duration (sec)	Call frequency (kHz)	Intercall duration (sec)
6B n=6	0.371 ± 0.033 0.333 - 0.405	2.54 ± 0.09 2.45 - 2.72	1.635 ± 0.097 1.422 - 2.018
6C n=2	0.185 ± 0.017 0.170 - 0.200	2.33 ± 0.64 2.30 - 2.38	1.245 ± 0.393 0.912 - 1.475
6D n=16	0.345 ± 0.023 0.260 - 0.480	1.04 ± 0.04 0.98 - 1.15	1.707 ± 0.214 1.086 - 2.376

Appendix 5. Bout duration (in minutes) of each call of male captive loggerhead shrikes

Call Fig. : Bout samples	Mean ± SE	Min. and max. range
1A, n=12	2.40 ± 0.67	1.35 - 4.01
1B, n= 8	1.72 ± 1.14 **	0.65 - 3.75
2B, n=18	1.71 ± 0.41	0.72 - 2.84
2C, n= 5	2.03 ± 2.42 **	0.62 - 3.63
2D, n=14	1.58 ± 0.78	0.50 - 3.88
2E, n=21	1.50 ± 0.25	0.96 - 2.58
2F, n= 4	1.83 ± 3.57 **	0.77 - 3.12
1C, n=13	1.97 ± 0.63	0.83 - 3.13
3A, n=21	1.72 ± 0.39	0.82 - 3.10
3B, n=18	2.14 ± 0.68	0.32 - 4.56
3C, n= 5	1.86 ± 1.34 **	1.23 - 2.82
3D, n=13	2.00 ± 0.68	0.76 - 3.45
3E, n= 4	1.01 ± 0.70	0.88 - 1.37
3F, n=27	1.71 ± 0.37	0.67 - 3.63
4A, n=10	1.57 ± 0.65	0.73 - 2.90
4B, n=22	1.85 ± 0.45	0.38 - 3.92
4E, n=15	1.78 ± 0.61	0.72 - 3.60
4D, n=18	1.04 ± 0.39	0.22 - 2.11
4F, n=22	1.35 ± 0.36	0.82 - 2.78
5A, n= 7	1.60 ± 0.86	0.62 - 2.37
5B, n=12	0.99 ± 0.65	0.22 - 2.82

Note: ** Small sample size and/or wide data range cause SE ~ mean or SE > mean.

Appendix 6. Bout duration (in minutes) of each call of female captive loggerhead shrikes

Call Fig. ; Bout samples	Mean ± SE	Min. and max. range
5C, n= 5	2.54 ± 2.75 **	1.25 - 4.80
5D, n= 6	1.50 ± 1.30 **	0.53 - 2.43
5E, n= 5	1.71 ± 2.07 **	0.67 - 3.33
5F, n= 3	1.39 ± 6.86 **	0.62 - 2.77
6A, n=12	1.28 ± 0.52	0.10 - 2.06
6B, n= 6	1.28 ± 0.92	0.58 - 1.92
6C, n= 2	1.32 ± 6.05 **	1.22 - 1.41
6D, n=16	1.07 ± 0.51	0.22 - 2.17