Vocal communication and territoriality during the non-breeding season in a migrant warbler

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The dry forest of Kalakad–Mundanthurai Tiger Reserve is an important habitat for wintering migrant birds. The most common migrant is the greenish leaf warbler, *Phylloscopus trochiloides*. Individuals defend territories, employing simple call notes to advertise territories, and more complex songs during prolonged negotiations of territory boundaries. Playback experiments using recorded calls suggest that individuals respond equally aggressively to territorial intrusions by neighbours as well as strangers, but neighbour recognition cannot be ruled out. Boundary negotiations appear to be costly, and songs may serve as an indicator of a bird's body condition. Vocalizations are important in establishment of territories, which is a prerequisite for over-winter survival. Vocal behaviour thus influences local population dynamics.

THE dry deciduous forests of Kalakad–Mundanthurai Tiger Reserve (KMTR) provide important wintering habitat for migratory bird species during the northern winter season. About one-third of the bird species recorded in the Mundanthurai plateau are wintering migrants. Understanding the population ecology and behaviour of these species is important for our understanding of the local bird communities, as well as the long-term management of the dry forests. One of the most common winter visitors is the greenish leaf warbler, *Phylloscopus trochiloides*, which I studied over five winters[1]. I have previously demonstrated that the local population dynamics of this territorial canopy insectivore is driven by seasonal and annual variations in arthropod abundance, which itself is determined by winter rainfall (NE monsoon)[2]. I also found that individual birds responded to changing food availability by regulating their fat reserves on a diurnal basis: they carry more fat during drier periods with fewer arthropods, and significantly less fat after rains when food is abundant[3].

In this paper I present (i) a descriptive account of non-breeding season vocal communication in *P. trochiloides*, and (ii) results from playback experiments to test for neighbour–stranger discrimination, compared to similar studies in the breeding season in other species[4]. Vocal

communication has been best studied in songbirds[5,6]. The primary focus has been on temperate breeding season vocalizations, particularly on complex songs. Recently, with increasing research on tropical wintering migrants, more is becoming to known about communication outside the breeding season[7–12]. The complexity of avian social organization in the non-breeding season is becoming apparent, with vocalizations playing an important role.

I studied over-wintering *P. trochiloides* in the Mundanthurai plateau in KMTR Tamil Nadu, during 1993–1997. The 15 ha study plot consists of semi-evergreen riverine (gallery) forest (c. 2 ha) and dry deciduous forest (c. 13 ha) – both habitats occupied by *P. trochiloides*[2]. I have previously described the study area, as well as the population ecology and behaviour of *P. trochiloides* in considerable detail[1–3], and will recap those aspects most relevant for the current paper below.

Territoriality

P. trochiloides are solitary and territorial in the non-breeding season, and use calls and songs to regulate territories[1,2,13]. Individuals of both sexes maintain independent territories to secure food resources. During September–December (settlement phase[2]), individuals arrive in the study area, establish territories within the first few weeks, and remain in their territories through mid-March when spring migration begins[2]. The birds undergo their annual complete moult during January–March (moult phase[2]). There is no evidence of non-territorial individuals, although a few birds did wander around for up to 6 weeks during the settlement phase, before disappearing from the study area. The first birds arrive before the onset of winter rainfall (NE monsoon) and occupy the gallery forest, which has the most foliage at that time[2]. Later birds that arrive with or after the start of the NE monsoon occupy the dry forests. Territories along the river tend to be smaller, with much overlap (i.e. higher density), especially during wet years (c. 4.5 birds/ha in January 1993)[2], whereas territories in the deciduous forest are larger, with less overlap even during the wettest year (c. 2.8 birds/ha in January 1993)[2]. This difference in density may affect the social behaviour of *P. trochiloides* as reflected in their vocal behaviour and the frequency of boundary interactions.

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Vocal behaviour

I documented rates of vocalizations and the contexts in which they were used, by following individual colour-banded birds. After locating a known bird I followed it for one minute, recording all vocalizations it made. To ensure independence of observations, I then moved to another bird. I collected such observations throughout the day, although birds were more vocal during early morning. Vocalizations were opportunistically recorded with a Sennheiser K6-P modular microphone and a Sony WM-D6C Professional Walkman cassette recorder. I used the Macintosh program 'Canary' (v. 1.2) to produce sonograms from these recordings.

Territories are advertised through simple calls–type A (Figure 1) – which the owners utter throughout the winter. Calling rates (number of calls per minute by an individual) are highest (Table 1) during the three hours after sunrise and decline thereafter. Afternoon calling frequencies and rates are higher in the gallery than in the deciduous forest (Table 1). The birds use a second call – type B, a shorter, more sibilant chirp – as a challenge upon detecting an intruder in their territory. The brevity and relative rarity of the type B calls made it difficult to obtain a clean recording for sonograms. The birds also use a song (Figure 2), similar to the breeding season song, but only during face-to-face interactions. Unlike in the breeding season, females also sing. The song involves amplitude modulation, and is generally quiet, often only audible at close range (less than 10 m).

The settlement phase is characterized by frequent intense boundary interactions between individuals. These interactions are stereotypical, with a characteristic progression through various stages of escalation. A typical interaction starts with an individual (intruder) calling (type A) within the territory of another bird (owner). The owner then responds by calling (type A) and rapidly approaching the intruder (typically within a minute). As the owner approaches, it increases its rate of calling and starts using challenge calls (type B). Usually (especially after territory establishment) the intruder retreats at this stage, ending the conflict. If the intruder persists, however, the interaction escalates. Both birds start calling at high rates, using both call types and chasing each other in
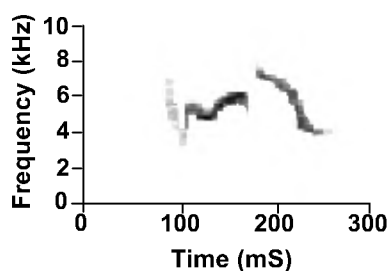
circles. The birds may also start flicking their wings, presumably displaying their wing-bars[14]. The next stage of escalation is when the birds start singing. The combined rate of singing can reach 20 songs per minute – it is difficult to estimate individual rates during these fast interactions. The birds also continue to flick their wings, chase each other and call (both call types) during this peak stage. There is seldom any direct physical contact however, so direct injury costs are low.

An interaction may continue at this escalated stage for several hours, before one of the birds breaks away. In most cases, interaction resumes after a short break when the birds may forage and continues again for several hours. A typical boundary negotiation during the settlement phase involves many such bouts lasting 1–6 days (median = 3 days, N = 37 complete negotiations observed), and on rare occasions, may involve more than two individuals. Such prolonged negotiations appear to be necessary for establishing territory boundaries, as all individuals successful in obtaining a territory over the course of this study (N = 140) were observed to engage in at least one such interaction. In one exceptional case (observed during December 1993–January 1994), the boundary interaction lasted for more than 45 days and appeared to be unresolved well into the birds' moult phase[1,2].

During settlement, on any given day, 40–60% of all birds encountered in the study area may be engaged in boundary negotiations. By the end of December, however, less than 10% of the birds may be so engaged, and fewer still during moult[2]. Interactions become frequent again in late-March, when the forest is drying out, arthropod abundance is decreasing and the birds are preparing to return to the breeding grounds[1,2].

Table 1. Rate of calling in the greenish leaf warbler, *Phylloscopus trochiloides*, in Mundanthurai. Data are from four winters (1993–1997), from the months of October to December. Values are mean (per minute) ± SE Morning refers to a 3-h period after dawn; Afternoon refers to a 5-h period before dusk

Time of day	Riverine forest	N (min)	Deciduous forest	N (min)
Morning	7.3 ± 1.4	215	7.1 ± 2.4	245
Afternoon	2.9 ± 0.4	113	1.1 ± 0.3	95

Figure 1. Example of the call note (type A) used by greenish leaf warblers, *Phylloscopus trochiloides* during the winter in Mundanthurai.
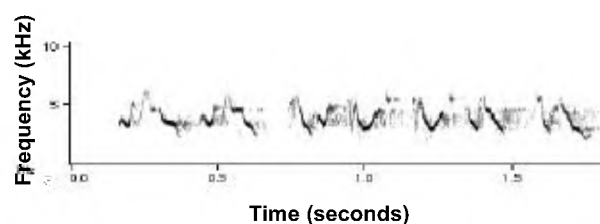

Figure 2. Winter song of *P. trochiloides* in Mundanthurai. Sonogram shows an example of a song from a boundary interaction.

Playback experiments

Temeles[15], in a review of playback experiments in territorial contexts, suggested that territory owners may respond more aggressively towards intruding strangers than known neighbours in a breeding territory, but not in a feeding-only territory. In a breeding territory, strangers pose a greater threat since they may take over both territory and mate, whereas established neighbours who have already tested the owner's ability to hold the territory, may only sneak occasionally to steal a mate. In a feeding-only territory, all intruders impose an equal cost in terms of stolen food, therefore an owner may respond equally aggressively towards all intruders[15,16]. The winter territorial system in *P. trochiloides* presents an opportunity to test this idea, and I used playback experiments for this test.

I used playback of recorded calls[8,16] to test for any differential response from territory owners towards their neighbours and strangers. I only used recordings of type A calls since these represent the natural situation for the start of any owner–intruder interaction.

For each trial (all conducted before 11 a.m.), a target owner was presented with playback of a 3-minute sequence of calls from either a neighbour, or a stranger. Strangers were individuals recorded at least three territories away from the owner, hence unlikely to have been heard before. Only one type of playback (neighbour or stranger) was presented on any given day to any particular target owner; all owners were subjected to both neighbour and stranger playbacks. Trials were conducted after locating target individuals in their territories, when they were not engaged in any social interactions, with the speaker at about 15 m from the bird. The speaker was placed just inside the territory boundary shared with the neighbour in question, for both neighbour and stranger playbacks. Target individuals received the neighbour/stranger playbacks in random order and within a period of 3 days. I conducted these playbacks during late-November to December, i.e. after most territory boundaries were established, but before the birds started moulting[2]. During each trial, I recorded the time it took the target owner to give the first response call (latency to call), the time to approach the speaker (latency to approach), and the distance (horizontal) at closest approach. I used paired *t*-tests to compare mean responses.

I attempted playback experiments with 24 different colour-banded individuals during the winters of 1993–1994, 1994–1995 and 1996–1997. These birds could not be sexed in the field since the species is sexually monomorphic. In 13 individual cases (i.e. 26 potential trials), the experiment was interrupted by the appearance of one of the target bird's neighbours, followed by interactions among the two birds. The small sizes of the territories – typically less than 40 m across – made it difficult to avoid calling in such non-target individuals during

playback. In a normal response to playback, the target bird approached and flew around directly above the speaker, uttering both call types and apparently searching for the intruder – but very rarely did the bird fly down to the speaker. When a neighbour also flew in, both individuals engaged in a direct interaction, sometimes escalating to the level of singing and wing-flicking displays, and ignored the playback from the speaker. In 3 cases, playback appeared to trigger prolonged interactions lasting several days, similar to those seen during initial territory establishment. Trials disrupted by such interference from neighbours were excluded from further analyses.

In the remaining 11 sets of (clean) trials, the target's response did not differ between neighbour and stranger playbacks for any of the measured response variables – latency to call, latency to approach, closest approach distance (Figure 3). Time of day and season (represented by Julian day) had no effect on the response to neighbours and strangers. In four cases when the target bird did not fly directly over the speaker (i.e. closest distance > 0 m), the bird did not utter call type B, but this happened with both neighbour's and stranger's calls.
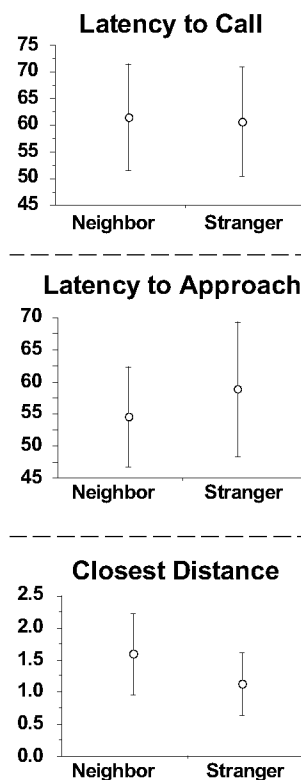

Figure 3. Results from playback experiments with *P. trochiloides* at Mundanthurai with mean ± SE for three response variables: (Top panel), Latency to call; (Middle panel), Latency to approach and (Bottom panel), Closest distance of approach. Responses to neighbours and strangers were not significantly different in paired *t*-tests for all three variables.

Functions and costs of singing

Bird songs have been studied extensively in the breeding season and some patterns are clear[5,6]. Generally, males do most of the singing. The song usually has two functions: mate attraction aimed at females; and territorial aimed at other males. Further, males sing more or less continuously throughout the early parts of the breeding season, at least until they have successfully mated[8,17]. In wintering *P. trochiloides*, both sexes sing, and songs appear only during highly escalated territorial interactions. Songs may, therefore, be costly and may serve as an indicator of the bird's quality (body condition). While the energetic and physiological costs of singing to birds are still unclear[18], singing interactions do appear to be costly in wintering *P. trochiloides*. First, singing is accompanied by various other activities – rapid flight and wing flicking – which are likely to be energetically expensive. Second, prolonged singing interactions also impose a significant time cost, in terms of lost time for foraging and other activities. This may have important repercussions on the birds' overall energy budget[3]. I only have suggestive evidence for such costs – eight individuals captured while engaged in prolonged boundary interactions had no visible subcutaneous fat, although four of them were captured in the afternoon, when most birds carry visible fat loads[3].

The non-breeding season simplifies the context in which to study the functions of vocalizations: the absence of mating or breeding simplifies the functional interpretations of calls and songs. The use of calls as the primary territorial signals shows that even such simple vocalizations can suffice for functions such as territory advertisement. Song, in this case, appears to serve more as a signal of a bird's body condition or potential to engage in a prolonged contest and is used by both males and females[9,19–23].

My playback experiments suggest that *P. trochiloides* may not discriminate between neighbours and strangers during winter, in accordance with Temeles[15]. Yet, this interpretation must be tempered by the low sample sizes, and consequent lack of statistical power in this study. One cannot completely rule out neighbour recognition, and some differential response that I was unable to detect[4]. Territorial interactions decline in intensity with time, and prolonged singing contests cease almost completely once two individuals agree on a territory boundary. Once territories are established, neighbours generally respect these boundaries and retreat upon hearing the owner's calls. This suggests that neighbours may indeed be getting to know each other and this familiarity reduces the costs of contests[13,24–26]. As floaters are rare, most birds only encounter their neighbours on a regular basis, increasing the opportunity for some form of vocal recognition. Alternatively, the rarity of strangers may also make vocal recognition unnecessary. Birds are also constantly testing their boundaries and neighbours – I often observed birds flying into a neighbour's territory, giving a single call and flying back into their own territory. If a territory owner disappears after settlement (as seen in at least four cases), neighbours generally expand their territories into the vacant space. As such, any incursion into a bird's territory is likely to be by a neighbour attempting to expand its territory, so the owner should respond aggressively to any calls.

The vocal behaviour of passerine migrants during the non-breeding season is only recently being studied[8–10,12,27], and this is the first such study in India. In territorial species, vocalizations, often complex and diverse, play an important role in the establishment and maintenance of territorial boundaries, as I have described for *P. trochiloides*. In *P. trochiloides*, obtaining and maintaining a territory is the first important step towards ensuring over-winter survival[1,2]. Vocal behaviour thus influences individual fitness, as well as local population dynamics, by determining territorial success. The vocalizations of most Indian songbirds, although quite diverse and fascinating, remain poorly studied. The resident and migrant passerines of our region span the entire gamut of vocal behaviour from stereotyped songs (e.g. cuckoos, leaf warblers) to life-long learning and mimicry (e.g. drongos, mynas, reed warblers). The ground is therefore fertile for testing and advancing the theoretical framework of acoustic communication in birds, developed mostly in northern temperate regions. Such studies will also help us develop a deeper understanding of and appreciation for the bird species inhabiting the region, and provide greater motivation for conserving them.

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