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When neighbours are not 'dear enemies': a study in the winter wren, *Troglodytes troglodytes*

H. Courvoisier*, S. Camacho-Schlenker, T. Aubin

Centre de Neurosciences Paris Sud & CNRS UMR8195, Université Paris-Sud, Paris, France

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Owing to the cost of territorial behaviour, territorial animals are able to adjust and modulate the intensity of their response according to their own condition and to the identity of the intruder. In birds, when neighbouring territorial males are well established, they often show a less intense response towards known neighbours than towards stranger conspecific males, a phenomenon known as the 'dear enemy' effect. Through playback experiments performed at the beginning, the middle and the end of the breeding season, we showed that winter wren males were able to discriminate neighbour versus stranger territorial songs despite a partial sharing of syllable repertoire. Surprisingly, males showed a stronger response to neighbours at the beginning of the breeding season and reacted as strongly to neighbour and stranger songs afterwards even if they lived in groups of stable and well-established neighbours. This suggests that neighbours can be as threatening as strangers, probably in both contexts of territorial occupancy and mate attraction, and that interactions between neighbours may depend on multiple factors including ecological constraints, past experiences and mating systems.

Many animals defend from conspecifics an area, called a territory, which can hold different kinds of resources such as food, nest sites or mates. Territorial defence may be costly for individuals that spend time and energy fighting conspecifics instead of feeding or courting/guarding mates, with the risk of being injured or even killed. As a consequence, the intensity and nature of territorial behaviour can vary according to characteristics of the resident (for example, physical condition or breeding status) and according to the potential threat the intruder may represent (for example related to its potential condition or motivation, its previous intrusions or its degree of familiarity; Marler & Slabbekoorn, 2004; Temeles, 1994). In many songbird species, resident males can vocally discriminate between unknown/stranger intruders and neighbour intruders (living in adjacent territories), and also between different neighbours (Stoddard, 1996). The possibility to discriminate different categories of individuals requires both that the signals produced by the intruders show some particularities and that the resident can decode and remember such particularities.

Songbirds defend their territories by adopting specific postures, by approaching the potential intruder and by singing territorial songs, which have been learned from one or several tutors. As a consequence of the learning process and genetic mixing, territorial songs can vary between distinct populations (Krebs & Kroodsma, 1980; Mundinger, 1982), potentially and ultimately leading to speciation (Toews & Irwin, 2008). Geographically close birds, such as neighbours with adjacent territories, share more song elements (syllables, sequences of syllables or complete song types) than more distant ones (Mundinger, 1982). Repertoire sharing is known to be one factor involved in the regulation of social and spatial relationships among neighbours (McGregor, 2005) as shared song types (defined as the exact same renditions of the same syllables in the same order) enable neighbours to use matching/nonmatching singing strategies during countersinging interactions (Beecher & Campbell, 2005; Beecher, Campbell, Burt, Hill, & Norby, 2000; Mennill & Ratcliffe, 2004; Todt & Naguib, 2000) and seem to influence territorial settlement (Beecher, Campbell, & Norby, 2000; Naguib, 2005). However, very few studies have directly linked song sharing or microgeographical variation of songs, that is, microdialects, to neighbour/stranger (N/S) discrimination. In the skylark, *Alauda arvensis*, a bird with a long and versatile song, Briefer, Aubin, Lehongre, & Rybak (2008) and Briefer, Rybak, & Aubin (2013) showed that short sequences of syllables shared by neighbours could support the 'group signature', since, in a playback experiment, a male would respond to a modified stranger song (to which the 'shared sequence' of the neighbourhood was added) as if it was a neighbour song. Similarly, in the white-crowned sparrow,

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* Correspondence: H. Courvoisier, Centre de Neurosciences Paris Sud & CNRS UMR8195, Université Paris-Sud, Bat 446, 91405 Orsay Cedex, France.
E-mail address: helene.courvoisier@u-psud.fr (H. Courvoisier).

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Zonotrichia leucophrys, a species with a discontinuous singing style, singing one short song type specific to each dialectal zone, the N/S discrimination seems to rely on a group of a few syllables (Nelson & Poesel, 2007).

The winter wren is a common and sedentary forest songbird in Europe living in stable groups of two to seven adjacent neighbours (Armstrong, 1955). Each male has a moderately complex repertoire of four to seven different stereotyped song types, each composed of 17–27 different syllables (Camacho-Schlenker, Courvoisier, & Aubin, 2011). During the breeding season, males engage in intense sessions of singing and countersinging, during which they repeat several times the same song type before shifting to another one. Macro- and microgeographical variations in the song have been described and neighbours exhibit a high degree of song sharing (Camacho-Schlenker et al., 2011; Catchpole & Rowell, 1993; Kreutzer, 1974a; Kroodsma, 1980). Camacho-Schlenker et al. (2011) showed that song repertoire similarity (in terms of both song type sharing and syllable sharing) decreased with increasing distance between individuals. Neighbours share 90% of their syllable repertoire and 90% of their song types, whereas males living 2 km apart still share 50% of their syllable repertoire but no song type at all, highlighting a key role of the syntax as already suggested by Van Horne (1995).

In this study, by using playback experiments, we asked whether male winter wrens could discriminate between neighbour song (song type shared with neighbours) and stranger song (unknown song types of males living 2 km apart) even if neighbour and stranger birds could share 30% of their syllable repertoire. Since the N/S discrimination can vary along the breeding season (Briefer, Rybak, & Aubin, 2008; Hyman, 2005), we repeated the experiments at the beginning, the middle and the end of the breeding season.

METHODS

Study Areas and Subjects

The experiments were conducted during the breeding seasons of 2010 and 2011, between 0830 and 1300 hours, in the woods surrounding the University of Paris 11 (France) on a total of 23 different males grouped in seven neighbourhoods. Individual territories of about 50–100 m diameter were assessed by careful observations of each bird's positions, movements and singing behaviours. As the nests of the winter wren are very cryptic, the breeding status of the males could not be systematically determined. However, a first clutch was usually observed by the end of April, followed by a second clutch in June.

Song Recording and Broadcast Signals

Songs were recorded using a Marantz PMD690 digital recorder connected to a Sennheiser ME67 microphone (frequency response 40–20 000 Hz). To remove unwanted noises, song files were filtered (band-pass 3–9 kHz) using Avisoft SASLab v.5.1. (R. Specht, Avisoft, Berlin, Germany) and their amplitudes were normalized at 90%.

For playback experiments, each male was tested with two different types of signals broadcast near the border of its territory to mimic a territorial intrusion: (1) a neighbour song = a song recorded from an adjacent neighbour few days before the experiment; (2) a stranger song = a song recorded few days before from a male living 2–4 km away.

As illustrated in Fig. 1, broadcast neighbour and stranger songs shared on average 30% of individual syllables for the three periods of the breeding season (syllable repertoire similarity, Hultsch & Todt, 1989: beginning: 0.29 ± 0.05, $N = 23$; middle: 0.30 ± 0.04, $N = 21$; end: 0.30 ± 0.08, $N = 21$; Kruskal–Wallis test: $H_2 = 0.52$, $P = 0.773$). However, these shared syllables are found in a different order and mixed with unshared syllables leading to different song types. As neighbours share most of their song types, the 'neighbour' song type was shared between neighbours and was thus sung by the target male. The 'stranger' song type was not sung either by the target male or by its neighbours.

Signals used for the playback experiments contained two repetitions of the same song (mean duration = 3.8 ± 0.6 s) separated by a 6 s silence to fit the natural rhythm of song production of the species.

Playback Procedure

Songs were broadcast using a Marantz PMD660 digital recorder connected via a 10 m cable to a Megavox Pro mega-6000 loudspeaker

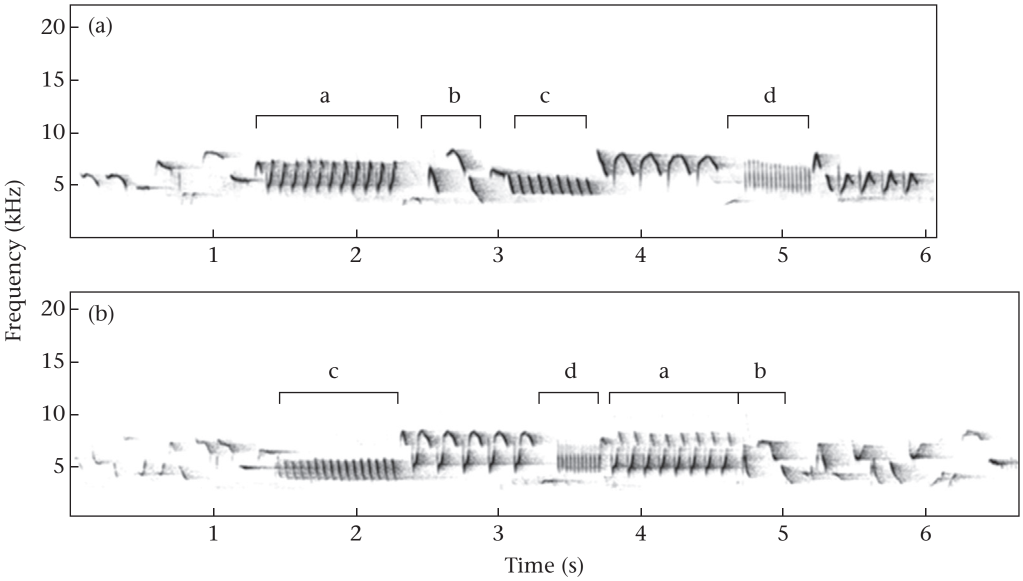

Figure 1. Examples of song types sung by (a) a neighbour and (b) a stranger. Several shared syllables (a–d) can be observed. They are rearranged in a different order and mixed with unshared syllables.

placed on the ground (10 W, frequency response 400 Hz–10 kHz ± 3 dB) at the intensity of the songs normally produced by the wrens (90–93 dB measured at 1 m from the loudspeaker with a Brüel and Kjaer 2235, linear setting).

Signals were broadcast approximately 5 m inside the territory of the resident male from the site adjacent to the neighbour from which the signal was used, to mimic a territorial intrusion. The experimenter was 10 m away from the loudspeaker, outside the territory. The broadcasts started when the bird was at least 15 m from the loudspeaker, with its neighbours being quiet. For each individual, the two types of signals were broadcast once in a random order on the same day and were separated by at least 5 min or the time necessary for the tested bird to be quiet again and localized at 15–20 m from the loudspeaker. Only one bird per group was tested on any one day to prevent any habituation or escalation between neighbours of the group. We used different sets of stranger and neighbour songs for each male and for each period of the breeding season to avoid pseudoreplication and habituation (McGregor, 1992).

The recordings and playback experiments were done at three different periods of the breeding season: beginning (5 March–2 April) when birds establish their territories; middle (6 May–20 May) when birds are engaged in mating and mate guarding; end (22 June–8 July) when the reproductive activity decreases and young leave the nests.

Behavioural Measures

Male winter wrens display strong territorial defence behaviour by singing territorial songs, approaching the intruder/loudspeaker, and eventually physically attacking the intruder (Brémond, 1986; Mathevon & Aubin, 1997).

During the 60 s after the beginning of the broadcast, the target birds were tracked visually and we measured the following behavioural parameters: (1) Lat1song: latency of first song (onset of first song after the beginning of the broadcast song; when the male was not heard singing during the first 60 s, the maximal latency of 60 s was attributed); (2) Nsongs: number of songs; (3) Nposts: number of song posts; (4) $T < 10$ m: time spent at less than 10 m from the loudspeaker during the first 30 s after the beginning of the playback.

Statistical Analysis

To get a composite score of the territorial response which could be easily compared between the three periods of the breeding season, we used a principal component analysis (PCA) including the four behavioural parameters (McGregor, 1992). We used two-tailed Wilcoxon matched-pairs tests for comparisons of each behavioural parameter as well as PCA scores. All analyses were conducted using Statistica v6 (Statsoft, Tulsa, OK, U.S.A.).

RESULTS

At the beginning of the breeding season, wren males responded more strongly to the broadcast of a neighbour song than to a stranger song (Fig. 2). They replied significantly faster (Lat1song), moved (Nposts) and approached the loudspeaker more ($T < 10$ m; Wilcoxon matched-pairs test, $N = 23$; Lat1song: $Z = 1.996$, $P = 0.045$; $T < 10$ m: $Z = 3.059$, $P = 0.02$; Nposts: $Z = 2.301$, $P = 0.021$). They also had a tendency to sing more songs in response to the song of a neighbour but the difference was not significantly different (Wilcoxon matched-pairs test: $Z = 1.388$, $N = 23$, $P = 0.165$). At the middle and the end of the breeding season, wren males reacted strongly and similarly to both neighbour and stranger songs (Wilcoxon matched-pairs test: $N = 21$; middle: Lat1song: $Z = 0.037$, $P = 0.97$; $T < 10$ m: $Z = 0.266$, $P = 0.78$; Nposts: $Z = 0.296$, $P = 0.76$; Nsongs: $Z = 0.028$, $P = 0.97$; end: Lat1song: $Z = 0.965$, $P = 0.33$; $T < 10$ m: $Z = 1.480$, $P = 0.14$; Nposts: $Z = 0.331$, $P = 0.74$; Nsongs: $Z = 1.023$, $P = 0.31$).

The first principal component (PC1) of the PCA explained 64.7% of the total variance and all four behavioural variables correlated strongly with PC1 (Table 1). According to the loading coefficients, an individual high score on PC1 would correspond to a strong territorial response (more movements, more time spent near the loudspeaker, shorter latency to sing back and more songs).

Consistent with the previous analysis, the wren males had a higher PC1 score in response to a neighbour song than to a stranger song at the beginning of the breeding season (Wilcoxon matched-pairs test: $Z = 2.311$, $N = 23$, $P = 0.02$; Fig. 3). However, at the middle and the end of the breeding season, males reacted strongly to both signals and no difference related to the nature of the broadcast song could be detected (Wilcoxon matched-pairs test: $N = 21$; middle: $Z = 0.08$, $P = 0.93$; end: $Z = 0.47$, $P = 0.64$).

DISCUSSION

The songs of winter wrens vary greatly with small geographical distances. In this study, we have shown that wrens can discriminate neighbour versus stranger songs.

The N/S vocal discrimination appears very early in the breeding season. Indeed, winter wrens show strong site fidelity from year to year and sporadically sing during the winter. Moreover, group dialects are stable over several years (S. Camacho-Schlenker & H. Courvoisier, personal communication). Thus, neighbouring birds are likely to know each other, as well as the group repertoire, by the beginning of the breeding season.

In our playback experiments, we used stranger songs that shared syllables with the neighbour songs. These shared syllables were systematically rearranged in a different order, leading to stranger song types that were not sung by either the tested individual or its neighbours. This suggests a key role of the syllable order (syntax) in song type construction and perception in this species as already suggested by Van Horne (1995). However, we cannot rule out that the global difference in syllable content was informative enough for the bird to discriminate between a neighbour and a stranger song as already suggested for macrodialects (Kreutzer, 1974b; Podos, 2007). We could not find shorter sequences of syllables that would be shared by all neighbours but not with strangers as a potential group signature. Contrary to what had been seen in other species (Briefer, Aubin, et al., 2008; Gentner & Hulse, 2000; Nelson & Poesel, 2007), the whole short song types shared among neighbouring winter wrens might thus encode the group signature. However, sharing of some signature is not always sufficient to explain N/S discrimination. For example, in other species, either a shared song type sung by a stranger bird or the bird's own song is still treated as a stranger song despite the sharing (Anderson, Searcy, & Nowicki, 2005; Searcy, Mc Arthur, Peters, & Marler, 1981; Wilson & Vehrencamp, 2001). Thus, more subtle variations in songs or individual voice characteristics could as well underlie N/S discrimination. In the winter wren, attempts to find any potential for individual coding in frequency and temporal parameters of songs have been unsuccessful so far (Camacho-Schlenker et al., 2011). Future studies in this species, for example by manipulating the syntax or the degree of sharing in broadcast songs, could be very interesting to address whether sharing is sufficient to trigger N/S discrimination, and to study which song parameters are involved.

Territorial behaviours have been envisioned as a trade-off between the cost of defence and the potential loss of, for example,

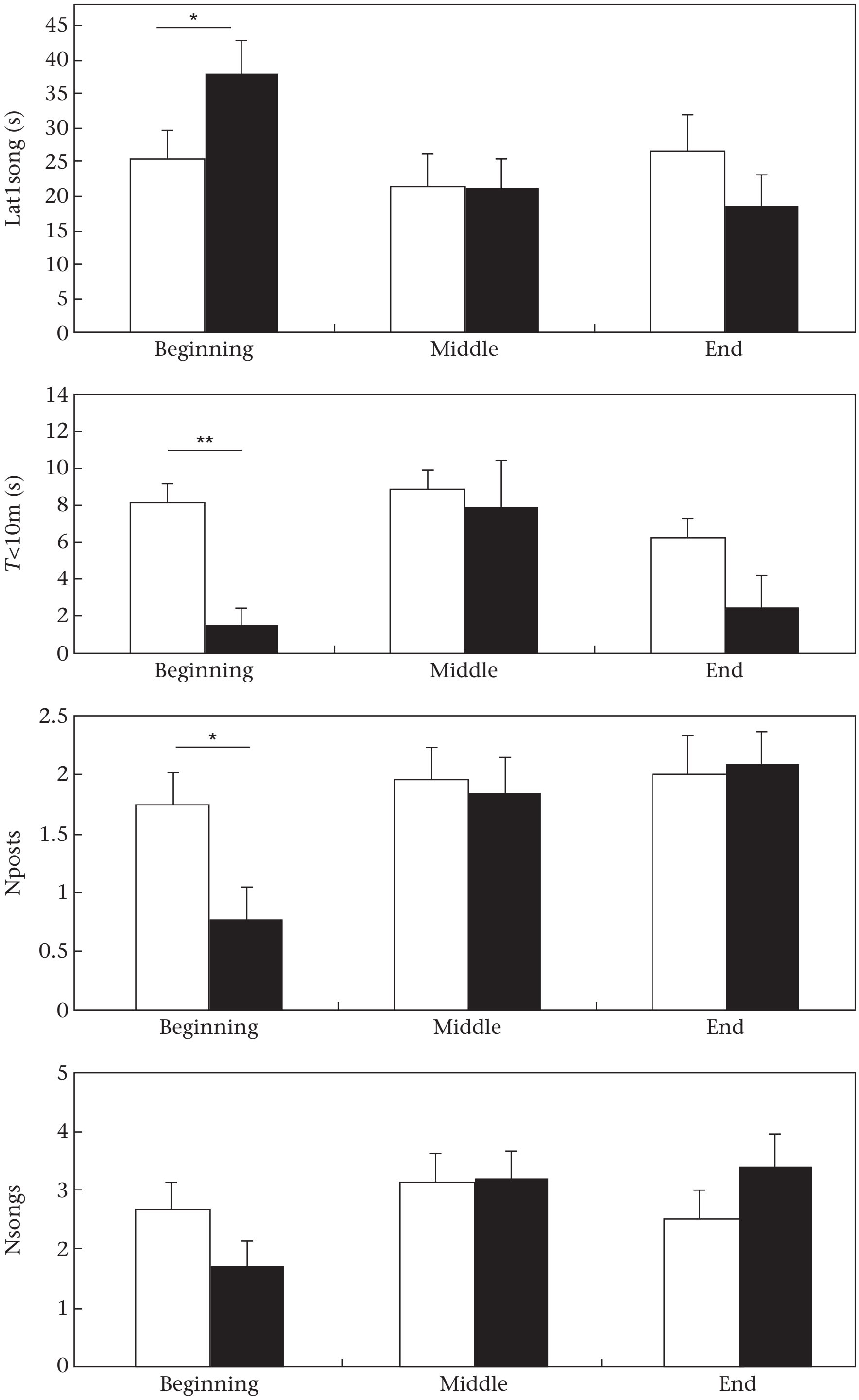

Figure 2. Behavioural responses to playback of neighbour (white) and stranger songs (black) at the beginning, the middle and the end of the breeding season. $^*P < 0.05$; $^{**}P < 0.01$; Wilcoxon matched-pairs test, see statistics in the text.

Table 1
Eigenvalues, explained variances and loadings of behavioural measures on the two first factors of the PCA

	PC1	PC2
Eigenvalue	2.59	0.75
% Variance	64.69	18.87
Lat1song	−0.835	0.461
Nsongs	0.880	−0.294
Nposts	0.792	0.266
T<10 m	0.698	0.621

food, mates or young (Switzer, Stamps, & Mangel, 2001; Temeles, 1994). As a consequence, one would expect a territory owner to adapt its level of aggressiveness to the identity and/or the behaviour of the intruder. In this regard, in many species, territory owners have been shown to respond more aggressively to strangers (potential territory seeker) than to known neighbours (settled individuals), a phenomenon known as the ‘dear enemy effect’ (Brooks & Falls, 1975; Fisher, 1954; Temeles, 1994). For example, in the skylark, a decrease in the territorial response to neighbour songs clearly occurs in the middle of the season when territories are well

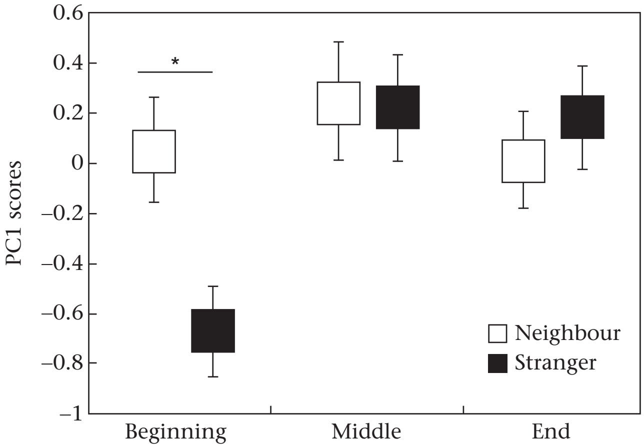

Figure 3. PC1 scores (mean ± SE) for neighbour and stranger playbacks performed during three periods of the breeding season. A high positive PC1 score corresponds to a strong territorial response. $^*P < 0.05$, Wilcoxon matched-pairs test.

established but neither at the beginning nor at the end of the breeding season when borders are less stable and when neighbours or young may intrude into territories (Briefer, Aubin, et al., 2008). However, few species either do not show any N/S discrimination (Bee, 2003; Lachish & Goldizen, 2004; Temeles, 1994) or show more aggressive responses to simulated intruding neighbours than to strangers in situations where neighbours could be more threatening than a stranger (Leader, Wright, & Yom-Tov, 2002; Olendorf, Getty, Scibner, & Robinson, 2004). For example, Temeles (1989, 1990) showed that territorial northern harriers, *Circus cyaneus*, are more aggressive to neighbours than to strangers because strangers are floaters intruding to steal food, whereas neighbours attempt to steal both food and portions of the resident's territory. In mammals, male meadow voles, *Microtus pennsylvanicus*, also respond less to strangers, which are transient males whereas neighbours compete for both females and portions of territories and can kill offspring (Ferkin, 1988). Winter wrens are sedentary and, in spring, live in small groups of adjacent territories which are relatively stable during a breeding season and even from one season to the next (Armstrong, 1955; S. Camacho-Schlenker & H. Courvoisier, personal communication). Consequently, one would expect to see a 'dear enemy effect', with a decrease in agonistic behaviours at least in the middle of the season, between those well-known and well-established neighbours. Thus, why would a male winter wren react more aggressively to a neighbour than a stranger song early in the breeding season and maintain such a strong response to the song of its neighbours throughout the breeding season?

Winter wrens have not been reported to destroy nests or offspring of conspecifics but they certainly exert a high pressure on territory borders and mates. Actually, apart from playback experiments, we could observe intense spontaneous vocal contests between neighbours from March to July, mainly at dawn but also throughout the day. Males sing from inside their territory but also quite often all along their borders, redefining them and maybe trying to push them a bit forwards. As in other species, territorial defence behaviour in the winter wren has been shown to depend on past territorial challenges, simulated intrusions leading to long-term increases in dawn singing, and to a potential escalation of vocal contests (Amrhein & Erne, 2006; Amrhein & Lerch, 2010; Erne & Amrhein, 2008; Schmidt, Ahmrein, Kunc, & Naguib, 2007). Thus, frequent intrusions or threatening behaviours such as singing at the border of the territory can contribute to maintaining a high level of vigilance and aggressiveness between neighbours. During the primary establishment of territory borders, the two copies of a stranger song (never heard before) as broadcast in our experiment would be less threatening than the two copies of a known song sung by a known neighbour with previous history of territorial contests.

A decrease in aggression among neighbours, as seen with the dear enemy effect, presupposes the neighbours not only to be well known and well established but also to be trustworthy, in the sense that they would respect the territory borders. In the red-winged blackbird, *Agelaius phoeniceus*, males increase vigilance and aggressiveness towards neighbours that have crossed the territory borders and cuckolded the resident (Olendorf et al., 2004). In the song sparrow, *Melospiza melodia*, males can discriminate between aggressive and nonaggressive neighbours (Hyman & Hughes, 2006) and would retaliate against aggressive neighbours either after a direct contest (Akçay et al., 2009) or by eavesdropping on other neighbours' contests (Akçay, Reed, Campbell, Templeton, & Beecher, 2010). During the playback experiments, we placed the loudspeaker a few metres inside the territory border. Although this procedure has been widely used in experiments showing a dear enemy effect, it could be sufficient to mimic the intrusion of an untrustworthy neighbour and drive strong retaliation behaviours towards the trespassing male (Olendorf et al., 2004).

Winter wrens reacted less strongly to a stranger than to neighbours at the beginning of the breeding season but, later on, reacted as strongly to both stranger and neighbour songs. Males may fail to extract sufficient information from the songs to discriminate between stranger and neighbour songs later in the season, and respond to both as if they were neighbour songs. This could result from an increase in environmental noise. However, it has been shown that, at the distance used in this study, winter wren songs propagate well with or without leaves (Holland, Dabelsteen, Pedersen, & Larsen, 1998; Mathevon & Aubin, 1997) and we always performed our broadcasts when the area was quiet to limit interference with other birds. Furthermore, birds could hear the full songs before approaching or replying (as they very rarely overlapped our broadcasts) and one or two renditions of songs are known to be sufficient to elicit a differential response to neighbour and stranger songs at different periods of the breeding season in other species (Briefer, Aubin, et al., 2008; Brooks & Falls, 1975). This late high response to any conspecific could be rather due either to an increase in general arousal under hormonal control (Pellerin, 1981) or to the fact that wrens are more reactive to any intruder during periods of mate/nest guarding than during the initial establishment of the territory borders.

As well as the defence of territory borders, territorial songs are also involved in competition between males for mate attraction and guarding, as well as in intersexual selection. Extrapair copulations in the winter wren have been described and extrapair paternity, EPP, has been found in 16.3% of offspring (Brommer, Korsten, Bouwman, Berg, & Komdeur, 2007) although it is not documented whether EPP could be attributed to neighbours or stranger males. The most frequently observed pattern in passerines is that neighbouring males are most likely to be extrapair fathers (Hill, Akçay, Campbell, & Beecher, 2011). This could be explained obviously by an easy and rapid access to the mates of the neighbours living close by, especially in very sedentary species, but also by the fact that females have been shown to prefer neighbour versus stranger songs (Baker, McGregor, & Krebs, 1987; O'Loghlen & Beecher, 1997; 1999). However, in most species, a dear enemy effect is observed too. For example, the song sparrow has a higher EPP (24%), attributed to neighbouring males but this species shows a dear enemy effect in its territorial responses (Hill et al., 2011; O'Loghlen & Beecher, 1997; 1999). Thus, EPP alone cannot explain why winter wrens would react strongly to neighbours throughout the breeding season.

In Western Europe, most male winter wrens are polygynous and multiple nest building by the males is a prerequisite for breeding. During the courtship display, the male leads the female around the different nests in his territory. After settling on a territory by choosing a nest, the female attempts to breed (Armstrong, 1955; Garson, 1980). In such conditions, getting a larger territory with more suitable nest sites (and associated resources to feed mates and nestlings) may be a key factor to increase male fitness. Conversely, losing part of its territory may have a direct impact on the reproductive success of a male. Indeed, winter wren males on territories with a large number of vacant nests are more likely to be chosen by a female and have a better mating success, suggesting that potential nest sites are a key resource of the territory and an indicator of male quality (Evans & Burn, 1995; Garson, 1980), as suggested in other territorial polygynous species displaying multiple nest building by males (Friedl & Klump, 1999; 2000; Johnson & Searcy, 1993; McGregor, Clayton, Kolb, Stockley, & Young, 1990; Szentirmai, Komdeur, & Szekely, 2005; Verner & Engelsen, 1970). Most species lacking a dear enemy territorial response as reported by Temeles (1994) also defend nesting areas. Furthermore, the rate of mate switching is high in the winter wren. During each breeding season, females generally make two breeding attempts each with a different male (Garson, 1980; Kluijver, Ligtvoet, van den Ouwelant, & Zegwaard, 1940). Predation on nests is common, and when it happens, the female may settle on a vacant nest on the same territory but may also move between territories and be courted by several males (Armstrong, 1955; Evans & Burn, 1995; Garson, 1980). Thus, competition with other males, and most probably neighbours as discussed before, for potential nest sites and mates is likely to occur throughout the breeding season. To our knowledge, this study is the first to investigate N/S discrimination in a species with polygynous nest-building males and future research may improve our understanding of the complex relationship between mating systems and territorial competition among neighbours.

In conclusion, we showed that winter wrens can discriminate neighbour versus stranger songs despite their similarity in syllable content, and that neighbour songs elicit a strong territorial response from the territory owner throughout the breeding season. This last unexpected result for sedentary birds living in stable groups of adjacent neighbours emphasizes the fact that the intensity of the response to territorial intruders may be modulated by ecological constraints, social context, past experiences and mating systems.

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