To trill or not to trill? Territorial response to a heterospecific vocal trait in male collared doves, *Streptopelia decaocto*

Jean Secondi,[a,b] Paula M. den Hartog,[a] and Carel ten Cate[a]
[a]Behavioural Biology, Institute of Evolutionary and Ecological Sciences, PO Box 9516, 2300 RA Leiden, The Netherlands, and [b]Molecular Population Biology Group, Department of Animal Ecology, Lund University-Sölvegatan 37, S 223 62 Lund, Sweden

Responding of individuals outside the conspecific range has been largely explained by biases in sensory or cognitive systems toward particular traits or trait values. More recently, it has been shown that such responses might occur if individuals still respond to signal traits that have been lost over time. However, empirical evidence remains scarce. We report a case supporting the latter mechanism. Phylogenetic analysis suggests that the collared dove, *Streptopelia decaocto*, had lost the trilled vocalization present in most congeneric taxa. We tested whether males retained the ability to respond to these trills in the context of territory defense. We synthesized trilled songs by inserting trills from the sister species *S. roseogrisea* into *S. decaocto* songs. We show that trilled songs yielded higher responses than did natural conspecific songs, and that the intensity of the response depended on the number of trilled elements. We also show that trilled songs elicited as strong reactions as frequency modulated coos, which are stronger releasers of territorial response than are nonmodulated coos, but are not produced by every males. Additional tests suggest that the frequency pattern is the most important feature of the trill used by males. However, it is still unknown whether reactions to trilled and frequency modulated coos have the same perceptual basis. To our knowledge, this study is the first report of a strongly deviating signal that is still effective in vocal intrasexual communication in birds. *Key words:* Columbidae, signal evolution, song complexity, territorial interactions, trait loss, trill. *[Behav Ecol 14:694–701 (2003)]*

Behavioral studies on a wide array of taxonomic groups—including insects (Proctor, 1992), fishes (Basolo, 1990), lizards (Quinn and Hews, 2000), amphibians (Ryan and Rand, 1990), or birds (Jones and Hunter, 1998)—have repeatedly demonstrated that signal receivers may react to signals outside the conspecific range. Two major explanations have been proposed to account for such responses. First, a signal trait may have been lost during radiation without a parallel loss of the response to the trait. Individuals remain therefore able to respond to an ancestral trait completely absent from the current conspecific repertoire (Gray and Hagelin, 1996; Quinn and Hews, 2000; Ryan and Rand, 1998, 1999). Second, sensory systems may be biased toward particular values of some signal parameters such as size, frequency, or chroma (Collins, 1999; Endler and Basolo, 1998; Hunt et al., 1997; Ryan and Keddy-Hector, 1992). This can be due to a tuning for other biological functions (Proctor, 1992; Sakaluk, 2000) or can result from inherent properties of sensory or cognitive systems (Enquist and Arak, 1994; Neubauer, 2000; Ryan and Keddy-Hector, 1992).

Signals of increasing complexity are likely to evolve because more complex signals are expected to stimulate more sensory or cognitive systems than simpler ones (Collins, 1999; Neubauer, 2000; Ryan and Rand, 1990). This response to more stimulating signals may make individuals respond to signals traits absent from their species-specific repertoire. In the Túngara frog, e.g., males and females respond more intensely to artificially modified signals than to regular conspecific ones (Kime et al., 1998; Ryan and Rand, 1990). Surprisingly, few authors investigated such phenomenon for

birdsong, one of animal signals the most extensively studied. Nevertheless, female preference for larger repertoires, a dimension of song complexity, has been reported in the common grackle (Gray and Hagelin, 1996) and the zebra finch (Collins, 1999), both bird species without repertoire. Female preference for longer songs is also observed in the latter species (Neubauer, 2000) and in aquatic warblers, *Acrocephalus paludicola* (Catchpole and Leisler, 1996). A possible explanation for this apparent limited interest is that oscine song, the dominant model for avian acoustic studies, is learned. Cultural processes may therefore limit or override nonlearned preferences for particular traits.

Unlike in oscines, song learning has not been found in *Columbidae* (doves and pigeons, see Baptista, 1996; Lade and Thorpe, 1964), reducing the opportunity for cultural processes to blur the expression of nonlearned preferences. In this family, tonal songs, i.e., elements with one frequency component and a narrow bandwidth, are widespread. Other acoustic traits occur less frequently (del Hoyo et al., 1997; Goodwin, 1983). At a finer scale, the genus *Streptopelia* presents a moderate diversity of song structures. Besides tones, noises (e.g., complex acoustic structures with a large frequency bandwidth), or trills (e.g., rapid repetitions of an amplitude modulation [AM] are observed; de Kort SR and ten Cate C, in preparation; Slabbekoorn et al., 1999). Up to three different coo types are observed in *Streptopelia* species, according to the context of signaling (perch coo, bow coo, nest coo; Goodwin, 1983). Two species, *S. decaocto* and *S. senegalensis*, produce tonal coos only, whereas other taxa either lack tones or include other vocal traits in their repertoire (de Kort SR and ten Cate C, in preparation; Slabbekoorn et al., 1999). Phylogenetic analyses indicate that a repertoire with tones only is a derived state (Figure 1). It also strongly suggests that loss of trills has occurred at least once, in the collared dove, *S. decaocto*, resulting in the
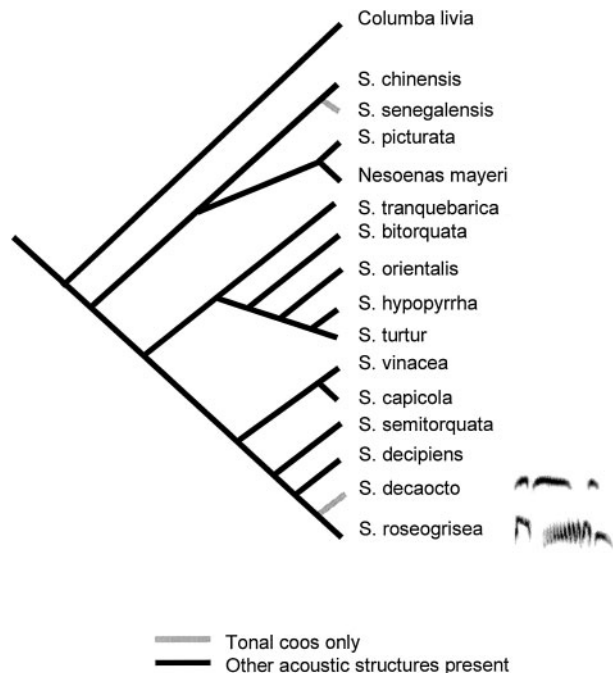

Figure 1
Loss of acoustic complexity in the genus *Streptopelia*—*S. decaocto* and *S. senegalensis* are the only two species exhibiting tonal songs only in each of their perch, bow, and nest coo. Phylogenetic data from Johnson et al. (2001); song data provided by Selvino de Kort.

Figure 2
Waveforms and spectrograms of stimuli types used in the four playbacks experiments. Trills contain frequency and amplitude modulations. Frequency modulations are visible in spectrograms (upper panel), whereas amplitude modulations are better viewed in waveforms (lower panel). Numbers refer to the corresponding waveforms and spectrograms: (1) nonmodulated *Streptopelia decaocto* coo, (2) one-trill version of a *S. decaocto* coo, (3) two-trill version of a *S. decaocto* coo, (4) *S. roseogrisea* coo, (5) artificially modulated *S. decaocto* coo, and (6) naturally modulated *S. decaocto* coo. Amplitude modulation *S. decaocto* coos were made by combining spectrogram 1 and waveform 3 (see Methods).

reducing of the acoustic complexity of the species' repertoire. This situation provides an opportunity to test whether loss of trills was paralleled by a modification of receiver characteristics.

We focused on *S. decaocto* for three reasons. First, trills occur in its closest relatives and, in particular, in its sister species, *S. roseogrisea*, suggesting that sensitivity for this trait might be present in *S. decaocto*. Second, coos with a single frequency modulation (FM), occurring in one or several elements, are commonly observed in many individuals (Figure 2; ten Cate, 1992). These modulated coos elicit stronger territorial responses in males than do nonmodulated coos (Slabbekoorn and ten Cate, 1997; ten Cate et al., 2002). This allows us to compare the relative values of the heterospecific, trait with a highly efficient conspecific trait. Third, territorial response, typically expressed as an increase in flight and vocal activity, is easy to quantify in this species (Slabbekoorn and ten Cate, 1996).

We investigated the territorial response of male *S. decaocto* to trill, a trait absent in this species, in four playback experiments. (1) We assessed the relative response strength to trill by testing songs in which part a heterospecific trill has been inserted, against regular conspecific coos (hereafter referred to as nonmodulated). (2) We tested whether the strength of the response to trill depended on the number of trilled elements in a coo by measuring the relative responses to conspecific signals in which either one or two trills have been inserted. (3) We also compared the relative values of trilled coos against modulated coos. (4) We finally investigated the basis of the response to trill. FMs are present in both modulated coos and trilled coos. However, the latter ones also have an AM pattern that can carry information. Thus, we investigated whether AM has any functional value, which is currently unknown for this species.
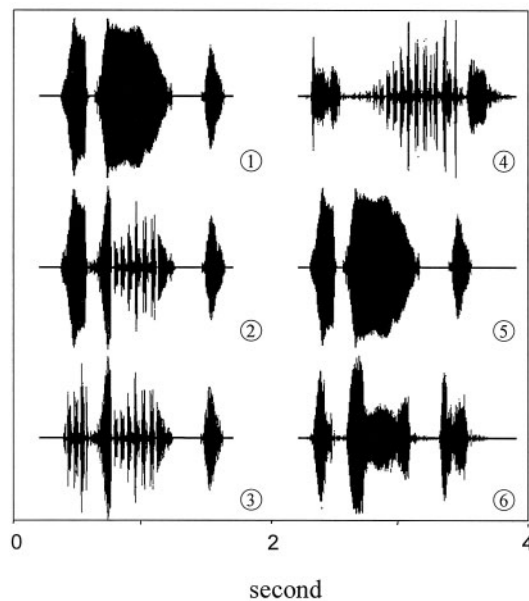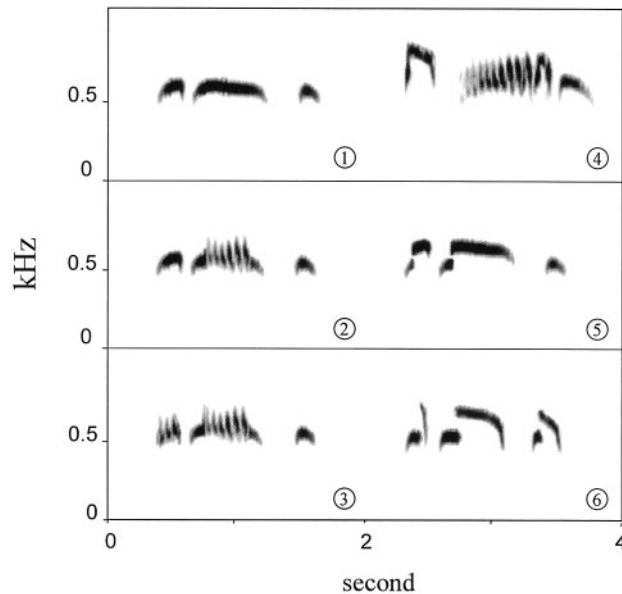
METHODS

The study population was located in Oegstgeest (52°11′ N, 4°28′ E), a residential village in the western part of The Netherlands. Site and population characteristics have been previously described elsewhere (Slabbekoorn and ten Cate, 1997). Tests were performed between 0530 and 1030 h from 14 March 2000–27 July 2000 for the first two experiments, and from 13 April 2002–21 July 2001 for the last two ones. A

sequential design similar to previous studies on *S. decaocto* was used (see Slabbekoorn and ten Cate, 1996, 1997). A 3-min pre-playback period provided the baseline activity and was followed by two 3-min periods consisting of 1 min of playback and 2 min of silence. A different stimulus was played during each playback period. Stimuli consisted of four bouts containing eight coos each. Ninety-five territories have been sampled the first year, and 48 the second year. Respectively, 31 and four birds have been used in two different experiments during the same breeding season, but no individual has been tested more than once in the same experimental set. The minimal interval between two tests exceeded 10 days for all but one bird, for which the interval was 4 days. We assume that the time lags between two tests and the short duration of playbacks (1 min per stimulus) ensured independent measurement of behavioral responses from the same individuals.

Experiment 1: response to trilled specific songs

Two series of tests were performed. In the first one, trilled versions of conspecific coos were synthesized by inserting a part of a *S. roseogrisea* trill into a nonmodulated *S. decaocto* perch coo (Figure 2, spectrogram 1 and waveform 1). Nonmodulated coos were then played against their trilled version (Figure 2, spectrogram 2 and waveform 2). In the second series, we assessed the generality of the response to trill by testing whether the mere presence of a trill would override the absence of other song parameters known to be involved in specific recognition, by testing nonmodulated coos against *S. roseogrisea* coos (Figure 2, spectrogram 4 and waveform 4). A total of eight *S. roseogrisea* coos, eight nonmodulated *S. decaocto* coos, and eight trilled *S. decaocto* coos have been used in this experiment. In the first series, eight pairs of nonmodulated coos were matched with their trilled version, whereas in the second series, each nonmodulated coo was played against the *S. roseogrisea* coo from which the trill has been extracted for synthesizing the trilled version. In each series, all eight pairs of stimuli were tested in both presentation orders, thus requiring 16 tapes to be constructed. Each tape was played twice so that 32 individuals were tested in each series.

Trills were inserted in the second elements of nonmodulated coos. Only central parts were replaced so that onsets and offsets of elements were not altered (Figure 2). These parts may show slight increases and decreases in frequency, whereas central parts are characterized by a stable frequency level. Furthermore, the second element is the longest in *S. decaocto* coos. It was therefore possible to insert moderately long portions of trill in the signal. Only a part of *S. roseogrisea* trills could be inserted, because complete trills are often longer than any element of a *S. decaocto* coo. Furthermore, because the signals of both species differ slightly in frequency, the frequency of each trilled segment had to be adjusted to match the frequency of the coo in which it was inserted in. This operation was performed by using the spectral contour display command provided in Signal/RTS (Engineering Design, Belmont, Massachusetts). This method extracts from a spectrogram, for each time frame, the frequency with the maximal value of energy. The signal is therefore transformed into a function of frequency against time. The pitch of the signal is adjusted by adding a constant to the function. The signal is next reverted to a waveform. The operation is completed by applying the original amplitude envelope of the trill to the frequency shifted signal. A similar spectrogram extraction has been previously used for nonmodulated coos in order to remove all the background noise from selected outdoor recordings.

Experiment 2: influence of the number of trilled elements

To test whether the number of trills in a coo influenced the strength of the territorial response, a new set of eight stimuli was synthesized. A shorter trill was inserted in the first element of each trilled *S. decaocto* coo used in the first experiment, thus leading to a set of stimuli with trills in the first and the second element (Figure 2, spectrogram 3 and waveform 3). For each stimulus, both trills were extracted from the same *S. roseogrisea* coo. Two-trill coos were synthesized by using the same technique as in experiment 1.

To compare the relative response strength of males to nonmodulated, one-trill, and two-trill coos, we performed two series of playbacks using the same sequential design as in the first experiment. Each two-trill version was respectively tested against its nonmodulated coo and its one-trill version in the first and second series of playbacks. As in the first experiment, 16 tapes were constructed, and 32 individuals were tested in each series.

Experiment 3: relative efficiency of trilled and frequency-modulated coos

To assess the actual value of trilled coos, we compared two-trill versions to modulated coos, this latter type giving rise to stronger responses from territorial birds than did nonmodulated coos (Slabbekoorn and ten Cate, 1997). In this experiment, we synthesized modulated coos following instructions provided in Slabbekoorn and ten Cate (1997). According to their data, we chose an optimal frequency shift able to elicit the strongest territorial responses. The last two thirds of the first element and the last five sixth of the second element were shifted upward in frequency by an amount of 14% relative to the base frequency of the edited element (Figure 2, spectrogram 5 and waveform 5). The eight nonmodulated coos used in both previous experiments were modified and matched with their corresponding two-trill version. Sixteen tapes were made. Twenty-five tests were performed. Every tape was tested at least once.

Experiment 4: value of AM in trilled coos

A *S. roseogrisea* trill is made of a repeated AM and a repeated FM. Although structurally different, both modulation types could contribute to make a trill an efficient vocal trait. FMs are known to be meaningful for male collared doves (Slabbekoorn and ten Cate, 1997). FM in trills could therefore be perceptually similar. However, nothing is known about whether amplitude variations have any functional value in this species. To determine whether the amplitude pattern of the trill on its own is able to elicit stronger responses than does nonmodulated coo, we tested trilled signals keeping only their AM patterns. By using the same techniques as above, we extracted amplitude patterns of two-trill versions and used them to replace the natural amplitude pattern in nonmodulated coos. Thus, we obtained coos with a natural frequency pattern and two-trilled elements in amplitude only (Figure 2, spectrogram 1 and waveform 3). Consistently with previous experiments, eight pairs of matched stimuli were created, and 16 tapes were made. Twenty-seven males have been tested in this experiment. Every tape was tested at least once.

Statistical analyses

We recorded several variables reflecting the territorial response in *S. decaocto*: the number of coos; number of flights; the flight latency, i.e., the duration between the start of a period and the first flight; and the minimal distance to the

Table 1

Average changes in reponse between the pre-playback and the first playback period for each stimulus category tested in each experiment

	Difference	N	Z	p
Experiment 1				
S. roseogrisea				
Number of coos	−4.1	16	−0.026	.979
Number of flights	0.31	5	−0.948	.343
Flight latency (s)	−9.43	10	−0.510	.610
Minimal distance (m)	−1.19	4	−1.826	.068
Nonmodulated *S. decaocto*				
Number of coos	6.3	29	−2.023	.043*
Number of flights	1.5	29	−3.026	.002*
Flight latency (s)	−87.4	30	−4.309	<.0001*
Minimal distance (m)	−4.4	26	−3.891	<.0001*
One-trill *S. decaocto*				
Number of coos	11.1	14	−3.110	.002*
Number of flights	2.5	13	−2.925	.003*
Flight latency (s)	−79.9	13	−3.180	.001*
Minimal distance (m)	−1.4	8	−2.010	.035*
Experiment 2				
Nonmodulated *S. decaocto*				
Number of coos	11.75	15	−2.756	.006*
Number of flights	0.37	12	−0.632	.527
Flight latency (s)	−59.69	13	−2.447	.014*
Minimal distance (m)	−2.06	8	−1.825	.068
One-trill *S. decaocto*				
Number of coos	12.56	16	−2.327	.020
Number of flights	1.25	15	−1.719	.086
Flight latency (s)	−87.06	15	−2.728	.006*
Minimal distance (m)	−1.75	8	−0.980	.327
Two-trill *S. decaocto*				
Number of coos	10.22	31	−2.902	.004*
Number of flights	1.47	23	−3.825	.000*
Flight latency (s)	−93.44	28	−4.419	.000*
Minimal distance (m)	−2.87	14	−2.042	.041*
Experiment 3				
Two-trill *S. decaocto*				
Number of coos	10.08	8	−1.960	.050
Number of flights	0.58	5	−1.511	.131
Flight latency (s)	−18.08	6	−0.734	.463
Minimal distance (m)	−0.71	4	−0.730	.465
Modulated *S. decaocto*				
Number of coos	7.00	13	−1.259	.208
Number of flights	3.77	11	−2.719	.007*
Flight latency (s)	−77.23	12	−1.726	.084
Minimal distance (m)	−1.38	10	−0.867	.386
Experiment 4				
Two-trill *S. decaocto*				
Number of coos	8.30	10	−1.580	.114
Number of flights	1.77	10	−2.668	.008*
Flight latency (s)	−67.54	10	−2.244	.025
Minimal distance (m)	−2.92	6	−2.201	.028
Nonmodulated *S. decaocto*				
Number of coos	9.73	15	−22.019	.044
Number of flights	2.33	15	−22.768	.006*
Flight latency (s)	−275.47	15	−22.159	.031
Minimal distance (m)	−21.60	12	−21.418	.156

Differences were tested by using Wilcoxon signed-ranked tests.

* Significant difference after correction of the significance level for multiple comparisons using the Dunn-Šidák method.

loudspeaker. Scores were calculated considering each 3-min period, that is, a playback and its subsequent silent period, as a unit.

In all experiments, we tested whether each stimulus category elicited a behavioral response. For this purpose, we compared the scores obtained during the pre-playback and the first playback period by using Wilcoxon signed-ranked test. Nonmodulated coos in the first experiment and two-trill *S. decaocto* coos in the second experiment were used in the two series of playbacks. These data were pooled because individuals were different in both series. Sample sizes are therefore not equal for each stimulus category. Although this method tests whether birds reacted to a particular stimulus type at all, the relative potency of different stimulus types cannot be reliably assessed this way. To do so, we did a pair-wise comparison of the behavioral scores obtained during the two 3-min playback periods. To control for any carryover effect, we tested if responses depended on the presentation order. Differences of score between both playback periods were calculated for each individual. We then tested for an order effect by using Mann-Whitney *U* tests, with score differences as continuous variables and presentation order as the grouping variable. If no order effect was detected, data were pooled, and differences in response between stimuli were tested by using Wilcoxon signed-ranked tests. Four tests, one for each behavioral item, have been performed in each experimental group. As a consequence, significance thresholds were adjusted, according to the Dunn-Šidák method, to correct for type 1 error owing to multiple comparisons (Sokal and Rolf, 1995).

RESULTS

Experiment 1: response to trilled specific songs

No significant difference in responses was detected between pre-playback and first playback periods for *S. roseogrisea*. In contrast, the birds reacted strongly to both nonmodulated and one-trill *S. decaocto* coos (Table 1).

Next, we compared the scores obtained during nonmodulated and one-trill playback periods. No order effect was detected in any variable (Mann-Whitney *U*, all $p > .20$). Therefore, all individuals were pooled. Birds responded more strongly to one-trill versions than to non-modulated *S. decaocto* coos: the flight latency and the minimal distance were shorter. Differences for the minimal distance were still significant after correction for multiple comparisons (Figure 3).

For the second group, *S. roseogrisea* versus *S. decaocto*, no order effect was detected either (Mann-Whitney *U*, all $p > .067$), and data were pooled too. The number of coos was quite similar for both periods. However, the number of flights was higher and both flight latencies and minimal distances were shorter during *S. decaocto* playback. Difference in flight latency remained significant after correction (Figure 3).

Experiment 2: influence of the number of trilled elements

Table 1 shows that nonmodulated coos, one-trill and two-trill versions elicited a territorial response when compared with the pre-playback period activity. We then compared two-trill versions to nonmodulated coos. We detected no effect for the order of presentation of the stimuli (Mann-Whitney *U*, all $p > .110$) so we pooled all individuals together. Males responded more strongly to two-trill versions than to non-modulated coos as the minimal distance to the loudspeaker and the flight latency were shorter, whereas the number of flights was higher. No significant difference was observed for the number of coos (Figure 3).
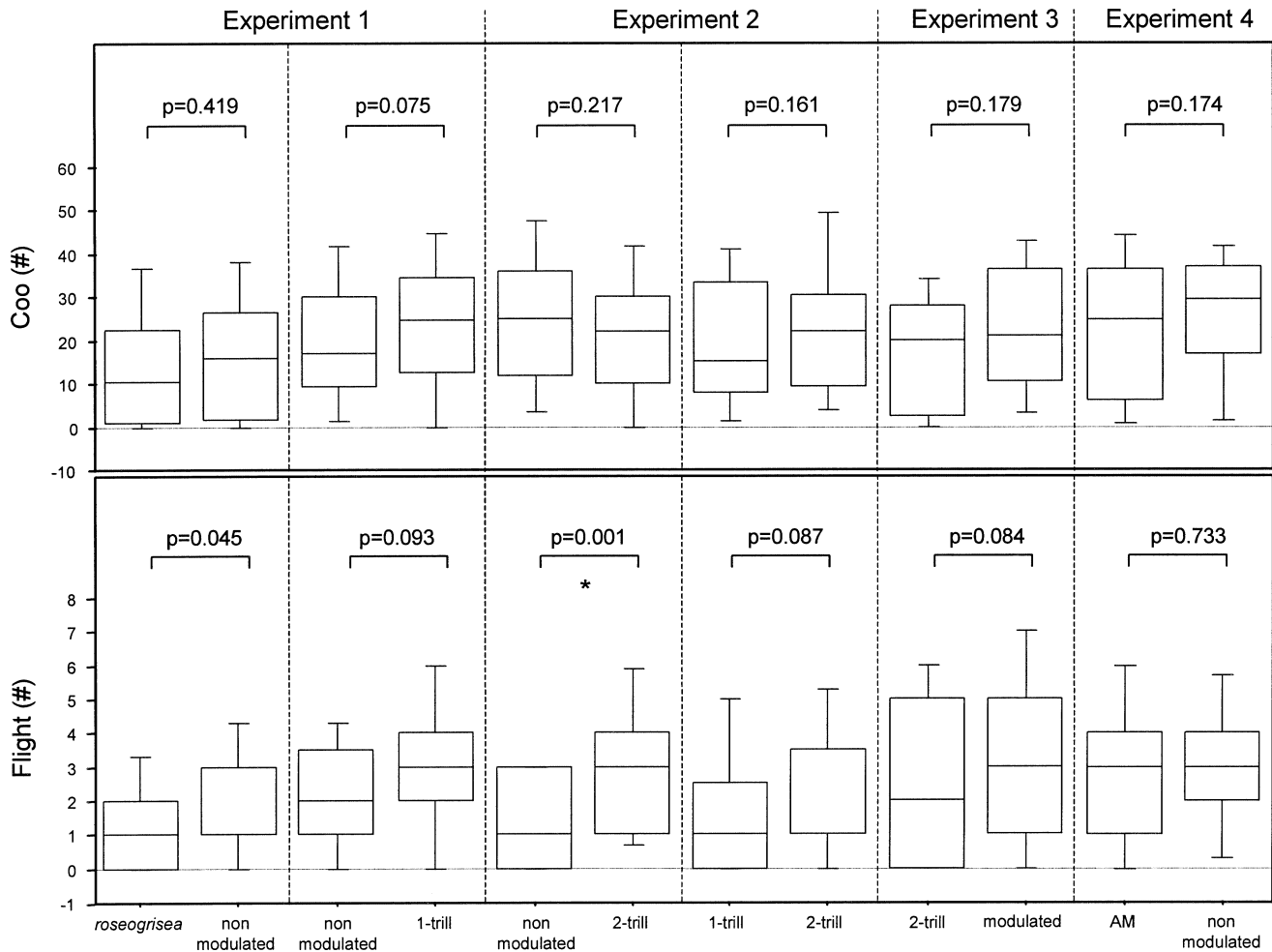
Figure 3
Responses of territorial males observed in each of four playback experiments performed in this study. Differences were testing by using Wilcoxon signed-ranked test. *Significant difference after correction of the significance level by using the Dunn-Šidák method.

Next, we compared the intensity of territorial responses to one-trill and to two-trill versions. No order effect was detected despite a marginally significant effect for the flight latency (Mann-Whitney U, $p = .021$, $\alpha' = 0.013$). Although there was still no difference in coo numbers, birds tended to give more flights with shorter flight latencies to two-trill playbacks. Moreover, they stayed significantly closer to the loudspeaker during the two-trill version playbacks (Figure 3). Thus, in general, responses were stronger to two-trill than to one-trill versions.

Experiment 3: relative efficiency of trilled and modulated coos

Two-trill versions and modulated coos elicited stronger reactions than those obtained during pre-playback period. Although, trends were similar to those observed in previous experiments, only a significant increase in flight number was detected for modulated coos (Table 1). The power of these tests is very low because of the small sample sizes. Significant differences for flight number and flight latency were actually observed for two-trill and FM *S. decaocto* when all individuals were included. Thus, we consider that birds actually reacted to both stimuli, but reactions were probably weaker than tests performed the previous year.

No order effect in stimulus presentation was detected (Mann-Whitney U, all $p > .45$), so data were pooled. Males

reacted equally strongly to both stimuli for all four parameters (Figure 3).

Experiment 4: value of AM in trilled coos

Both nonmodulated coos and AM coos triggered territorial responses. When compared with the pre-playback period, significant differences were observed in flight numbers for AM coos and for flight latency in nonmodulated coos (Table 1).

Unexpectedly, a strong order effect occurred for flight latency and minimal distance (Mann-Whitney U, latency flight: $n_1 = 15$, $n_2 = 13$, $U = 176$, $p < .001$; minimal distance: $n_1 = 15$, $n_2 = 13$, $U = 163$, $p < .002$) but not for coo and flight numbers (Mann-Whitney U, $p > .45$). We therefore conducted analyses on two separate subsamples, nonmodulated coos being played as the first stimulus in one and AM coos being played as the first stimulus in the other. No significant differences could be detected for coo and flight numbers. In contrast, males consistently responded more aggressively to the second stimulus played (AM latency flight: $n = 14$, $Z = -2.229$, $p = .026$, ns; AM minimal distance: $n = 8$, $Z = -2.319$, $p = .020$, ns; nonmodulated latency flight: $n = 13$, $Z = -2.975$, $p < .003$; nonmodulated minimal distance: $n = 6$, $Z = -2.201$, $p = .027$, ns). As a consequence of this order effect, no difference in response to AM *S. decaocto* and nonmodulated *S. decaocto* was detected for all four behavioral variables investigated (Figure 3).
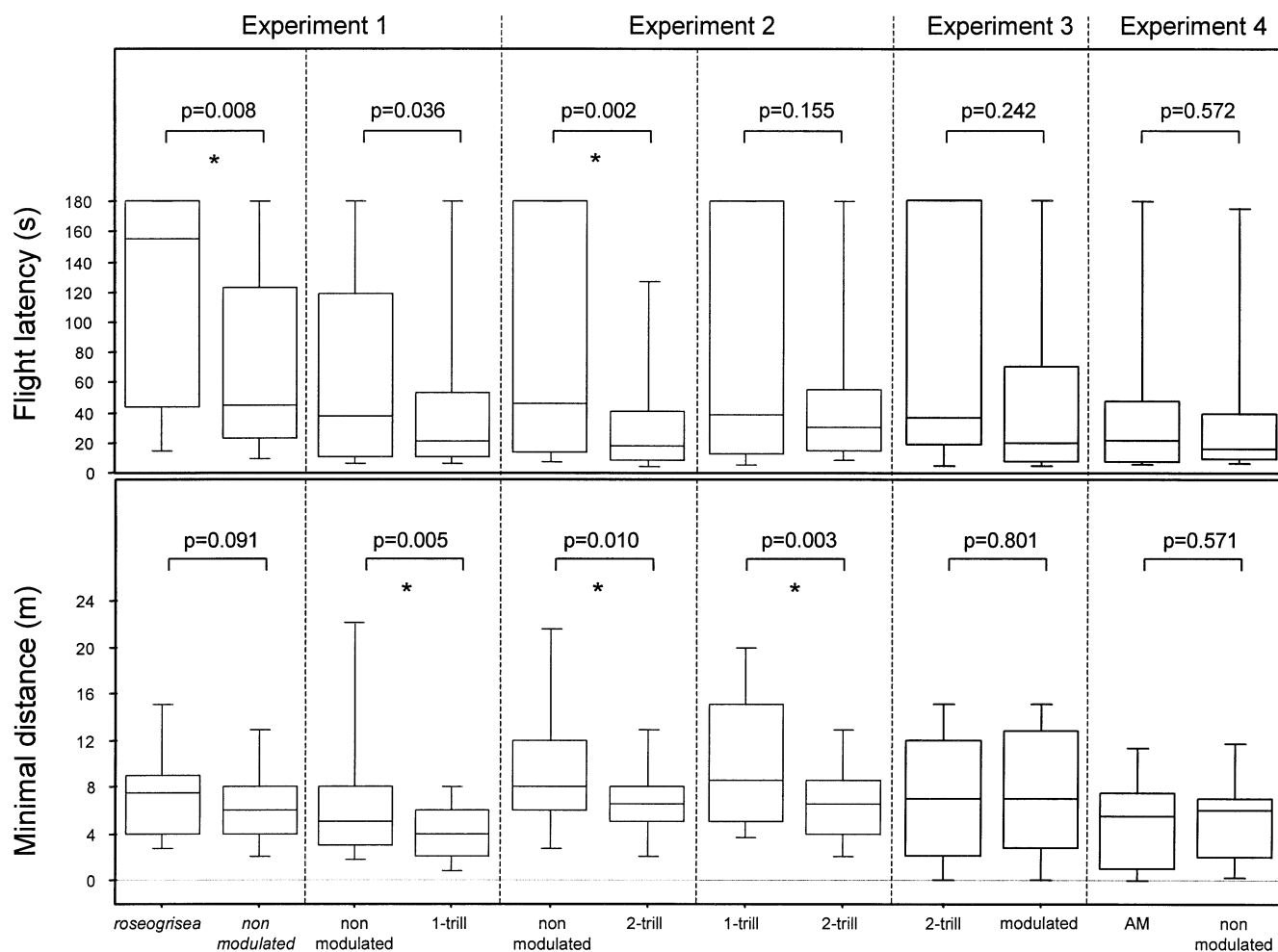
Figure 3, continued

A possible explanation for this result is that males do not discriminate between both stimuli. They might have considered the second playback as another attempt of intrusion from the same individual. This could have lead to an escalation of the territorial response, owners clearly trying to locate an intruder by flying more and coming closer to the loudspeaker. This experiment would suggest that the amplitude pattern of a trill does not increase the efficiency of a coo, in a territorial context. Strong responses observed for trills are therefore probably due to the presence of a repeated FM in the signal.

DISCUSSION

Response to a heterospecific trait in territorial signaling

We demonstrated the presence of a male response to a vocal trait, the trill, which is completely absent from the conspecific repertoire of the collared dove, S. decaocto. This response to trilled signals is stronger than that to one class of normal conspecific signals, the nonmodulated coos. In the first playback experiment, males produced stronger territorial responses to coos in which heterospecific trills were inserted than to natural nonmodulated coos. Moreover, the second experiment revealed that the intensity of the response to trilled signals was gradual and depended on the number of trilled elements. However, differences between one- and two-

trilled versions remained limited, possibly because of ceiling effects on the recorded variables. Interestingly, the trilled vocalizations of S. roseogrisea did not give rise to a response. S. decaocto and S. roseogrisea perch coos differ by the number of elements in a coo, coo duration, and coo frequency (Slabbekoorn et al., 1999). Clearly, the presence of a trill does not override the absence of other acoustic cues, known to be important for inducing responses in male S. decaocto, like for instance the rhythm of the perch coo (Slabbekoorn and ten Cate, 1999). Previous studies suggested that male Collared doves were rather conservative regarding species-specific acoustic cues (Slabbekoorn and ten Cate 1998, 1999). It is therefore all the more striking to observe such strong reactions to largely modified signals. Indeed, the third experiment detected no difference in reaction to trilled versions and to coos containing a FM, which demonstrates that a trill coo is as effective as the most potent current signal used in territorial signaling in male S. decaocto.

The perceptual basis of the reaction to trill is currently unknown. It may be based on the same mechanism that makes S. decaocto very sensitive to presence or absence of FMs (Slabbekoorn and ten Cate, 1998; ten Cate, 1992). If so, the noticeable effect of inserting a trill may be that the trill "exploits" the perceptual mechanism used to detect FMs. In line with this, our last experiment suggests that the amplitude pattern, giving rise to the trill-like nature of trilled coos, is not used by males, because we could not detect differences in

reactions to nonmodulated coos and to trilled coos from which the trill frequency pattern has been removed. This outcome was unexpected because the amplitude is by far the most obvious characteristics of trill to human ear. Thus, reactions to trill could actually result from a sensitivity to rapid frequency variations. However, the order effect detected in this experiment precludes any firm conclusion.

Causes of trait loss

The phylogeny suggests that the lack of structures such as trills or noises in *S. decaocto* very probably results from vocal trait losses. A recent review suggests that losses might actually be more common than previously recognized and are probably widespread among most taxonomic groups (Wiens, 2001). In several cases, they lead to receivers responding to signal outside of their specific range. For instance, in a lizard species, *Sceloporus virgatus*, Quinn and Hews (2000) could show that body color patches remained an efficient aggressive signal, although this trait was no longer present in this taxon. In birds, most authors investigated transitions in plumage coloration (Wiens, 2001), but one study reported a vocal trait loss. In the common grackle, *Quiscalus quiscula*, males only sing one song type, whereas females prefer repertoires with several song types, which seems the ancestral state (Gray and Hagelin, 1996). In the present study, we could show that males retained the ability to respond to vocal traits not currently expressed in their repertoire. This ability is expressed in territorial interactions, whereas most previous studies focused on signals involved in sexual preferences (Collins, 1999; Neubauer, 2000; Witte and Curio, 1999). Actually, only a few authors conducted studies in the context of intra-sexual selection (Jones and Hunter, 1998; Morris and Ryan, 1996).

Trilled songs are structurally more complex than are songs with tones only and are therefore expected to provide greater stimulation to the auditory sensory system. Such a preference for more complex signals is observed in the Túngara frog (Ryan and Rand, 1990). A similar mechanism is plausible in *S. decaocto* as males produced a response graded in intensity from nontrilled to two-trill signals. This result is congruent with the view of an increase of reaction strength with an increase of signal complexity. Although more experimental data on related species are required, sensory sensitivity to acoustic complexity might be an important component driving song evolution in the genus *Streptopelia*. One can wonder then why a reduction of vocalization complexity occurred in the collared dove. The close relatedness of *S. roseogrisea* and *S. decaocto* makes it likely that their common ancestor showed a trill. Theoretically, individuals might have lost the ability to produce other vocal traits than tones. Drift in isolated populations can potentially produce such phenomenon. However, this would be surprising for the collared dove, an abundant and widely distributed continental taxon. Constraints on signal transmission across the habitat also do not seem a likely explanation, although it cannot be definitely discarded without further testing. However, both species inhabit an array of open or semi-open habitats in which transmission constraints are usually less stringent than for forested habitats. This is particularly true for signals with rapid temporal variations like trills (Wiley and Richards, 1982).

Several other mechanisms are more likely to have contributed to the loss of vocal complexity. For instance, high predation risks are suspected to have lead to recurrent losses of colour displays in lizards (Wiens, 1999) and plumage coloration (Martin and Badyaev, 1996; Shutler and Weatherhead, 1990) and courtship displays (Johnson, 2000) in birds. Likewise, interspecific competition, through interspecific aggression, could favor trait loss (Doutrelant et al., 2000).

This factor may have been important, as a recent study (de Kort SR and ten Cate C, in preparation) shows that the diversity of coo structures is affected by the occurrence of sympatric congeneric species in *Streptopelia* doves. Finally, another plausible explanation may come from female preferences for tonal songs. A sex difference in response would result in a trade-off between song functions that could explain the existence of a gap between male responses and the actual signal design. Testing this hypothesis requires the determination of the relative sexual preferences of females to various acoustic traits. For collared doves, this factor does not seem very prominent (Secondi et al., 2003).

Although the reasons for the evolutionary loss of a trill remain unclear, the results emphasize the importance of extending, to a wider array of signaling contexts than intersexual communication, studies on the perception of signals outside specific ranges (Götmark and Ahlström, 1997). By doing so, new insights about the processes driving signal evolution, particularly in the case of signals involved in several biological functions, as it occurs in birdsong, can be expected.

REFERENCES

Baptista LF, 1996. Nature and its nuturing in avian vocal development. In: Ecology and evolution of acoustic communication in birds (Kroodsma DE, Miller EH, eds). Ithaca: Cornell University Press; 39–60.

Basolo AL, 1990. Female preferences predate the evolution of the sword in swordtail fish. Science 250:808–810.

Catchpole CK, Leisler B, 1996. Female aquatic warblers (*Acrocephalus paludicola*) are attracted by playback of longer and more complicated songs. Behaviour 133:1153–1164.

Collins SA, 1999. Is female preference for male repertoires due to sensory bias? Proc R Soc Lond B 266:2309–2314.

del Hoyo J, Elliott A, Sargatal J (eds), 1997. Handbook of the birds of the world: sandgrouses to cuckoos, vol. 4. Barcelona, Lynx edición.

Doutrelant C, Leitao A, Otter K, Lambrechts MM, 2000. Effect of blue tit song syntax on great tit territorial responsiveness: an experimental test of the character shift hypothesis. Behav Ecol Sociobiol 48:119–124.

Endler JA, Basolo AL, 1998. Sensory ecology, receiver biases and sexual selection. Trends Ecol Evol 13:415–420.

Enquist M, Arak A, 1994. Symmetry, beauty and evolution. Nature 372:169–172.

Goodwin D, 1983. Pigeons and doves of the world. London: British Museum of Natural History.

Götmark F, Ahlström M, 1997. Parental preference for red mouth of chicks in a songbird. Proc R Soc Lond B 264:959–962.

Gray DA, Hagelin JC, 1996. Song repertoire and sensory exploitation: reconsidering the case of the common grackle. Anim Behav 52:795–800.

Hunt S, Cuthill IC, Swaddle JP, Bennet ATD, 1997. Ultraviolet vision and band-colour preferences in female zebra finches, *Taenopygia guttata*. Anim Behav 54:1383–1392.

Johnson KP, 2000. The evolution of courtship display repertoire size in the dabbling ducks (*Anatini*). J Evol Biol 13:634–644.

Johnson KP, de Kort SR, Dinwoodey K, Mateman CA, ten Cate C, Lessells CM, Clayton DH, 2001. A molecular phylogeny of the dove genus *Streptopelia*. Auk 118:878–884.

Jones IL, Hunter FM, 1998. Heterospecific mating preferences for a feather ornament in least auklets. Behav Ecol 9:187–192.

Kime NM, Rand AS, Kapfer M, Rand MJ, 1998. Consistency of female choice in the Túngara frog: a permissive preference for complex characters. Anim Behav 55:641–659.

Lade BI, Thorpe WH, 1964. Dove songs are innately coded patterns of specific behaviour. Nature 202:366–368.

Martin TE, Badyaev AV, 1996. Sexual dichromatism in birds: importance of nest predation and nest location for females versus males. Evolution 50:2454–2460.

Morris MR, Ryan MJ, 1996. Sexual differences in signal receiver-coevolution. Anim Behav 52:1017–1024.

Neubauer RL, 2000. Super-normal lenght song preferences of female zebra finches (*Taenopygia guttata*) and a theory of the evolution of bird song. Evol Biol 13:365–380.

Proctor HC, 1992. Sensory exploitation and the evolution of male mating behaviour: a cladistic test using water mites (*Acari: Parasitengona*). Anim Behav 44:745–752.

Quinn VS, Hews DK, 2000. Signals and behavioural responses are not coupled in males: aggression affected by replacement of an evolutionary lost colour signal. Proc R Soc Lond B 267:755–758.

Ryan MJ, Keddy-Hector A, 1992. Directional patterns of female choices and the role of sensory biases. Am Nat 139:S4–S35.

Ryan MJ, Rand AS, 1990. The sensory basis of sexual selection for complex calls in the túngara grog, *Physalaemus pustulosus* (sexual selection for sensory exploitation). Evolution 44:305–314.

Ryan MJ, Rand AS, 1998. Evoked vocal response in male túngara frog. Anim Behav 56:1509–1516.

Ryan MJ, Rand AS, 1999. Phylogenetic influences on mating call preferences in female tungara frogs, *Physaelemus pustulosus*. Anim Behav 57:945–956.

Sakaluk SK, 2000. Sensory exploitation as an evolutionary origin to nuptial food gifts in insects. Proc R Soc Lond B 267:339–343.

Secondi J, de Bakker M, ten Cate C, 2003. Female response to male coos in the collared dove *Streptopelia decaocto*. Behaviour 139:1287–1302.

Shutler D, Weatherhead PJ, 1990. Targets of sexual selection: song and plumage of wood warblers. Evolution 44:1967–1977.

Slabbekoorn H, De Kort S, ten Cate C, 1999. Comparative analysis of perch-coo vocalizations in *Streptopelia* doves. Auk 116:737–748.

Slabbekoorn H, ten Cate C, 1996. Responses of collared doves to playback of coos. Behav Process 38:169–174.

Slabbekoorn H, ten Cate C, 1997. Stronger responses to modulated coos in collared doves. Anim Behav 54:955–965.

Slabbekoorn H, ten Cate C, 1998. Perceptual tuning to frequency characteristics of territorial signals in collared doves. Anim Behav 56:847–857.

Slabbekoorn H, ten Cate C, 1999. Collared dove responses to playback: slaves to the rhythm. Ethology 105:377–391.

Sokal RR, Rolf FJ, 1995. Biometry. New York: Freeman.

ten Cate C, 1992. Coo types in the collared dove *Streptopelia decaocto*: one theme, distinct variations. Bioacoustics 4:161–183.

ten Cate C, Slabbekoorn H, Ballintijn MR, 2002. Birdsong and male-male competition: causes and consequences of vocal variability in the collared dove (*Streptopelia decaocto*). Adv Stud Behav 31:31–75.

Wiens JJ, 1999. Phylogenetic evidence for multiple losses of a sexually selected character in phrynosomatid lizards. Proc R Soc Lond B 266:1529–1535.

Wiens JJ, 2001. Widespread loss of sexually selected traits: how the peacock lost its spots. Trends Ecol Evol 16:517–523.

Wiley RH, Richards DG, 1982. Adaptations for acoustic communication in birds: sound transmission and signal detection. In: Acoustic communication in birds, vol. 1 (Kroodsma DE, Miller EH, eds). New York: Academic Press; 131–181.

Witte K, Curio E, 1999. Sexes of a monomorphic species differ in preferences for mates with a novel trait. Behav Ecol 10:15–21.