# Hybrid vocalizations are effective within, but not outside, an avian hybrid zone

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Secondary contact between closely related species can lead to hybridization. The fitness of hybrid individuals within and outside the hybrid zone determines whether the hybrid zone expands into the ranges of the 2 parental species or remains a stable, geographically narrow area in between the allopatric ranges of the parental species. In birds, vocalizations play an important role in male–male competition and female mate choice and are often affected by hybridization. One of the factors that will influence male hybrid fitness is the ability to defend a territory against competitors by vocalizing. We tested the efficacy of territorial signals of hybrids of 2 dove species, *Streptopelia vinacea* and *Streptopelia capicola*, compared with the vocalizations of the parental species. With playback experiments, we assessed the response to hybrid and the 2 parental species vocalizations in the hybrid zone and adjacent allopatric populations of each species. In the hybrid zone, males did not respond differently to the 3 vocalization types. In both allopatric populations, however, males responded more to conspecific than to heterospecific signals and the response strength to hybrid signals was intermediate. Therefore, in the allopatric populations, hybrid males may have a reduced success in defending territories. In male–male interactions in the hybrid zone, hybrids may not have a disadvantage compared with males of the parental species. The ability to defend a territory against competitors may thus help maintain a stable hybrid zone in the area of overlap. *Key words:* acoustic signals, hybrid zone, playback, song, *Streptopelia* doves, territorial interactions. *[Behav Ecol 18:608–614 (2007)]*

H ybrid zones provide a window into understanding the evolutionary processes shaping species divergence. The emergence of premating barriers is often a crucial step in reproductive isolation (Dobzhansky 1940) and permeable barriers result in hybridization. Hybridization after secondary contact between closely related species leads to 3 scenarios: introgression and merging of the 2 species, a stable hybrid zone, or reinforcement of characters that cause premating isolation (Liou and Price 1994; Servedio and Kirkpatrick 1997). In the first 2 cases, hybrid fitness is not greatly reduced with respect to one or both parental species. In the case of reinforcement, the divergence in species recognition signals is a consequence of reduced hybrid fitness that selects against making incorrect species identifications (Butlin 1989; Otte 1989; Hoskin et al. 2005). The fitness of hybrids both within and outside the hybrid zone will determine whether species merge, a stable hybrid zone arises, or there is reinforcement and the species remain isolated. The study of hybrid characters allows us to take a closer look at which of these processes may be occurring.

Species-specific acoustic signals are often premating barriers. These signals function in male–male interactions and mate attraction in a wide range of taxa including crickets (e.g., Fitzpatrick and Gray 2001), frogs (e.g., Littlejohn and Watson 1985), and birds (Catchpole and Slater 1995). In all these taxa, hybridization may severely affect the structure of acoustic signals (crickets, e.g., Mousseau and Howard 1998; frogs, e.g., Littlejohn 1976; Bull 1978; birds, e.g., Gelter 1987; Collins and Goldsmith 1998; Ceugniet et al. 1999; Dowsett-Lemaire 1999; Bensch et al. 2002; de Kort et al. 2002a; Delport

et al. 2004; Gee 2005), and this may alter their effectiveness in male–male interactions and mate attraction.

Whereas several studies addressed the effects of hybrid acoustic signals on female choice, their effectiveness in male–male interactions has not received much attention (but see: Baker 1991; Scroggie and Littlejohn 2005). The efficacy of acoustic signals in male territorial interactions could affect mating success independent of female choice as it determines a male's access to resources of reproduction. It therefore discloses an important aspect of hybrid fitness (Scroggie and Littlejohn 2005), which in turn affects the maintenance and dynamics of hybrid zones.

In birds, the impact of sexual selection on male hybrid characters through male–male interactions and as a result on the stability of a hybrid zone has been shown for plumage characters (McDonald et al. 2001) and measures of male aggressiveness (Pearson 2000; Pearson and Rohwer 2000). Hybrid vocalizations that function in territorial interactions are expected to have an impact on the competitive abilities of male hybrids. Yet, not much is known about the effectiveness of hybrid vocalizations in wild populations of parental species and hybrids. We tested the response to avian male hybrid vocalizations in the field, addressing an important factor contributing to hybrid male fitness and the fate of the hybrid zone. As far as we know, this is the first study testing intermediate hybrid male signals in the context of male–male interactions in the field in both hybrid and adjacent allopatric parental populations.

We examined a hybrid system of 2 African doves: the Vinaceous dove, *Streptopelia vinacea*, and the Ring-necked dove, *Streptopelia capicola* (from now on referred to as *vinacea* and *capicola*). These sister species are morphologically similar but have very different species-specific territorial vocalizations (de Kort et al. 2002a, see Figure 1). Hybridization in doves is known to produce various forms of intermediate vocalizations as dove vocalizations develop without learning and most likely have a multilocus genetic basis (Lade and Thorpe 1964;
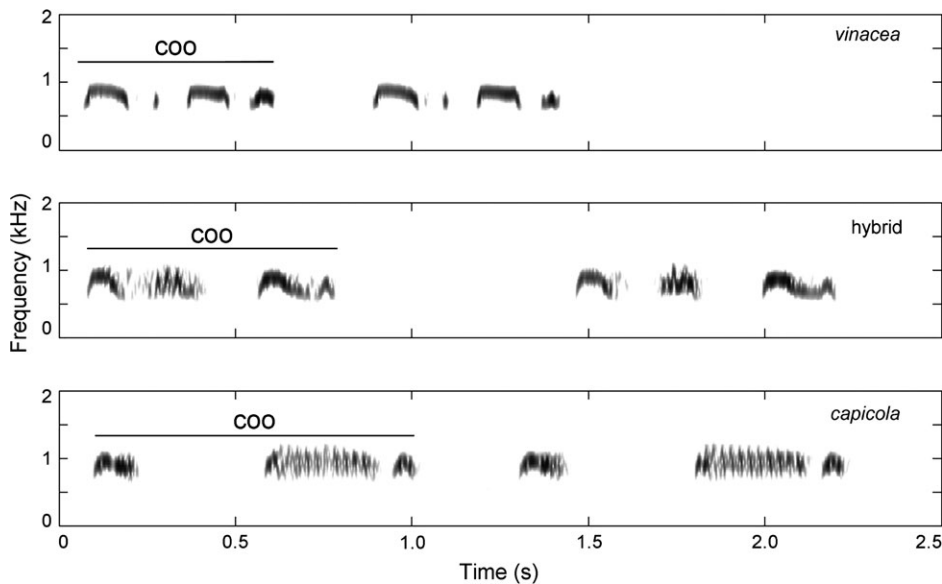
**Figure 1**
Spectrograms of 2 perch coos of a *vinacea*, a hybrid, and a *capicola* individual. Recordings from de Kort et al. (2002a). The spectrograms were made using the following settings: Hanning window; sample frequency of 44 100 Hz; 2048 fast Fourier transform samples; window length of 512 samples; overlap 480 samples; and 15 dB dynamic range.

Nottebohm and Nottebohm 1971; Baptista 1996; de Kort et al. 2002a). Previous studies have shown that both *vinacea* and *capicola* respond to each other's vocalizations but respond more to conspecific vocalizations (de Kort et al. 2002b). However, it is unknown how the parental species respond to hybrid vocalizations and whether they distinguish them from conspecific vocalizations. Individuals in a recently discovered hybrid zone responded on average with a similar intensity to vocalizations of both parental species (de Kort et al. 2002b), but whether hybrids themselves discriminate between hybrid and pure species vocalizations is also unknown. As it is the response to hybrid vocalizations that will determine how effective hybrids can be in competing with each other and with the parental species, it is crucial to test the effectiveness of these vocalizations in the field.

Our study focuses on these hybrid vocalizations and the response to them by both the hybrid and parental species populations. The response to hybrid vocalizations will give an indication of their competitive abilities in the hybrid zone and allopatric parental populations. This will help evaluate the stability of the hybrid zone, its potential expansion or contraction, and the symmetry of possible introgression from one parental species to the other.

## METHODS

### Study populations

The Vinaceous dove, *S. vinacea*, and the Ring-necked dove, *S. capicola*, are sister species of turtle doves that have a 2.5% mitochondrial DNA divergence (populations sampled in Cameroon and South Africa [Johnson et al. 2001]). The species-specific territorial vocalizations, perch coos, are markedly different and the only discriminating character in the field (see Figure 1). These 2 species meet in a narrow contact zone in Uganda (de Kort et al. 2002a). The hybrid zone seems to be a recent contact zone that may have arisen due to the loss of the rainforest as a barrier to dispersal for these savannah species (de Kort et al. 2002a). Preliminary analyses revealed that individuals from the contact zone are genetically intermediate ranging from a genotype similar to *vinacea* to one similar to *capicola* suggesting a hybrid swarm (den Hartog et al., in preparation). Hybrids in this area have perch coos that range from

*vinacea* to *capicola* perch coos and show high variability within and between individuals (de Kort et al. 2002a).

The hybrid population is found along Lake Albert between the villages of Biiso and Butiaba and is approximately 6 km wide from North to South (from 01°48′N, 31°23′E to 01°45′N, 31°23′E). We studied adjacent allopatric populations of *capicola* in Queen Elizabeth National Park (01°46′N, 31°23′E), approximately 270 km south of the hybrid population, and *vinacea* in Murchison Falls National Park, south of the village of Paraa and the Victoria Nile (02°14′N, 31°34′E) and approximately 50 km north of the hybrid population (see Figure 2). The species are abundant in these 3 sites.

Male doves are territorial and advertise their presence by perch cooing at different conspicuous positions within their territory (Goodwin 1983; Baptista 1996). They also defend their territories against intruders by chasing them out of the territory and uttering calls while in flight. If they land in close proximity, the territory holder may display aggressively with an
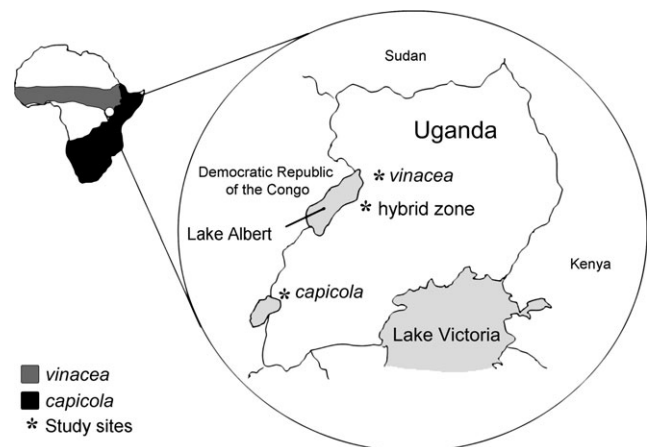


**Figure 2**
Distribution of *vinacea* and *capicola* in Africa and the study sites in Uganda. Map modified from de Kort SR, den Hartog PM, ten Cate C, 2002. Diverge or merge? The effects of sympatric occurrence on the territorial vocalizations of the vinaceous dove *Streptopelia vinacea* and the ring-necked dove *S. capicola*. J. Avian Biol. 33:150–158 with permission from Blackwell Publishing.
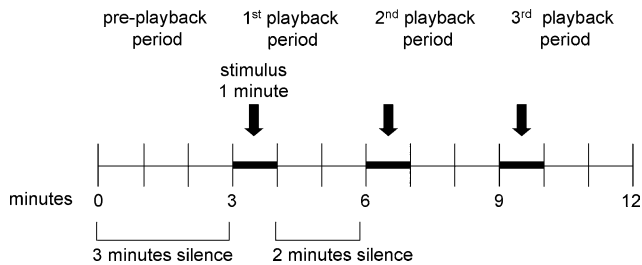
**Figure 3**
Playback design. Each experiment consists of a pre-playback period of 3 min. There are 3 playback periods consisting of 1 min of stimulus followed by 2 min of silence. The stimuli are presented in all possible orders to test for order effects.

accompanying vocalization (bow coo) to the intruder. Upon returning to his territory after having chased an intruder, the territory owner usually perch coos.

## Experimental design and procedure

We carried out 72 playback experiments: 24 experiments in each of the 3 populations. In each playback experiment, 3 stimuli were presented: a *capicola, vinacea,* and hybrid perch coo. The 3 stimuli were given in all possible orders to allow controlling for order effects. This resulted in 6 sequences, and each sequence was used 4 times (making 24 experiments). Each experiment lasted 12 min and the setup was as follows: the pre-playback period consisted of 3 min silence (to measure baseline activities) and 3 playback periods each lasting 3 min: 1 min stimulus and 2 min of silence (see Figure 3). A similar design has been successfully used in previous playback studies with *Streptopelia* doves (Slabbekoorn and ten Cate 1997; de Kort et al. 2002b; Secondi et al. 2003).

Experiments were carried out from sunrise to 11 h and from 16 h to sunset between September and December 2003. A speaker (Blaupunkt CB4500 100 W, Kemo 40 W #M034 built in amplifier) connected to a Creative Nomad Jukebox 3 was placed within the territory. Observers then positioned themselves at least 25 m from the speaker. Observations were recorded with FIT system software (Held and Manser 2005) on a Palm IIIx handheld computer. Five response parameters were scored during an experiment: number of coos (coos), number of flights (flights), time spent flying (fly time), number of flight calls (calls), and response latency (latency). The latency was defined as the time between the onset of the playback stimulus and the occurrence of one of the 4 responses described above. In the pre-playback period, latency was defined as the time from the beginning of the experiment until the occurrence of one of the 4 responses. Each trial was conducted on a different subject, and subsequent subjects were at least 200 m apart. Experiments were stopped if the focal male could not be observed or when it interacted with a bird other than his female.

The experiments were carried out with permission from the Uganda Wildlife Authority and the Uganda National Council for Science and Technology.

## Playback stimuli

Perch coos used as stimuli were from 24 *vinacea,* 24 *capicola,* and 24 hybrid individuals recorded by Selvino de Kort in the same populations from October to December 2000 (de Kort et al. 2002a). Stimuli were derived from a different individual for each experiment to avoid pseudoreplication (Kroodsma

et al. 2001). Recordings from the hybrid zone that were indistinguishable from *vinacea* or *capicola* perch coos were not used as hybrid stimuli. This was done to ensure that hybrid stimuli are from hybrid individuals and not from parental species individuals in the hybrid population.

The recordings from which the stimuli were derived were made with a Sennheiser ME67 microphone and a Sony TCD-D8 DAT-corder with DT-90 tapes at a 48-kHz sample rate. Recordings with the best signal to noise ratio were selected to create playback stimuli of 1 min. A natural bout (coos are usually produced in series called bouts) was chosen from these recordings and band-pass filtered (500–1300 Hz). The amplitude was normalized with Signal 3.12. To create 1 min of sound, bouts were copied as many times as necessary to fill 1 min of playback. Bouts were separated by a pause between them lasting 10% of the bout length to have the quantity of silence proportionate to the quantity of sound in the playback stimulus of 1 min. If a bout was halfway at the end of a minute, care was taken that the minute ended with a full coo. The stimuli were played back at a sample rate of 44.1 kHz. The amplitude of the playback stimuli ranged from 75 to 80 dB at 1 m from the speaker.

## Statistics

A principal components analysis (PCA) was conducted to create one response variable from the 5 variables that were scored (coos, flights, fly time, calls, and latency); a method for analyzing playback response measures suggested by McGregor (1992).

The first factor of the PCA was used as the dependent response variable in a linear mixed model in SAS 9.1.3 (Proc Glimmix). Two linear mixed models were made in which the variables "stimulus" and "population" were entered as fixed parameters, and the interaction between these 2 parameters was also entered into the model. Repeated measures were taken into consideration by entering individuals as random effects. Each experiment (set of 3 stimuli) was also included as a random effect as it was used once in each of the 3 populations. In both models, the degrees of freedom were calculated with Satterthwaite's formula (Littell et al. 1996).

The first linear mixed model assessed whether the playbacks had an effect on an individual's territorial behavior by contrasting the response to each stimulus to the pre-playback period for each population. Multiple comparison adjustments were computed with the "simulate" method (SAS adjust = simulate, adjusting the $P$ values and confidence limits from the simulated distribution of the maximum or maximum absolute value of a multivariate $t$ random vector [Edwards and Berry 1987]).

In the second linear mixed model, to assess whether there were differences in response to each stimulus, the response to each of the 3 stimuli (least mean estimates) were compared in each population. Multiple pairwise comparisons were corrected with the Tukey method (Games and Howell 1976). Order effects and order–stimulus interactions were included in the models but removed when they did not have a significant effect.

## RESULTS

### Principal components analysis

The first factor of the PCA explained 55% of the variation in the data. The correlation table showed strong correlations between flights, fly time, and calls and less between these variables and coos and latency (see Table 1).

**Table 1**

**Correlation matrix for the response variables included in the PCA**

| Response variable | Flights | Coos | Calls | Latency | Fly time | Loadings component 1 |
|---|---|---|---|---|---|---|
| Flights | 1.000 | | | | | 0.826 |
| Coos | 0.013 | 1.000 | | | | 0.360 |
| Calls | 0.774 | 0.075 | 1.000 | | | 0.872 |
| Latency | −0.415 | −0.592 | −0.421 | 1.000 | | −0.721 |
| Fly time | 0.594 | 0.168 | 0.706 | −0.438 | 1.000 | 0.831 |

Loadings for all variables for the first component are also shown.

### Response to playback periods compared with the pre-playback period

To test if there was a response to the playback stimuli, each stimulus played was compared with the pre-playback period (baseline level of activities). In both the *capicola* and *vinacea* populations, the playback of the conspecific coos showed a significant increase in response compared with the pre-playback period (pairwise comparisons of the least-squares mean estimates, see Table 2). Neither species showed an increase in response to the hybrid and heterospecific coos compared with the pre-playback period. Hybrids showed a significant increase in response to all 3 stimuli, *vinacea*, *capicola*, and hybrid coos, compared with the pre-playback period (see Table 2).

In the linear mixed model, the level of response of each population to the 3 stimuli and the pre-playback period were determined by the population ($F_{2,46} = 9.06$, $P \leq 0.001$) in which the experiments were done, the playback period ($F_{3,207} = 13.05$, $P < 0.001$), and the interaction between these 2 variables ($F_{6,207} = 4.03$, $P \leq 0.001$).

### Response to the 3 stimuli compared within each population

To assess if there were differences in response to each stimulus, within each population, the response to each of the 3 stimuli was compared.

*Capicola* responded significantly more to *capicola* coos than to *vinacea* coos (see Table 3 and Figure 4). The overall response to hybrid coos was intermediate between, and not significantly different from, the response to conspecific or heterospecific coos (see Table 3 and Figure 4).

*Vinacea* responded significantly more to *vinacea* coos than *capicola* coos (see Table 3 and Figure 4). The overall response to hybrid coos was intermediate between, and not significantly different from, the response to conspecific or heterospecific coos (see Table 3 and Figure 4).

**Table 2**

**Effect of playback compared with the pre-playback period**

| Population | Stimulus | Estimate | Error | df | t | P | Adjusted P |
|---|---|---|---|---|---|---|---|
| *Capicola* | *Capicola* | 0.956 | 0.225 | 207 | 4.25 | <0.001 | **<0.001** |
| | Hybrid | 0.490 | 0.225 | 207 | 2.18 | 0.031 | 0.213 |
| | *Vinacea* | 0.252 | 0.225 | 207 | 1.12 | 0.264 | 0.900 |
| Hybrid | *Capicola* | 0.856 | 0.225 | 207 | 3.81 | <0.001 | **0.001** |
| | Hybrid | 1.110 | 0.225 | 207 | 4.94 | <0.001 | **<0.001** |
| | *Vinacea* | 1.100 | 0.225 | 207 | 4.9 | <0.001 | **<0.001** |
| *Vinacea* | *Capicola* | 0.132 | 0.225 | 207 | 0.59 | 0.556 | 0.998 |
| | Hybrid | 0.372 | 0.225 | 207 | 1.66 | 0.099 | 0.545 |
| | *Vinacea* | 0.694 | 0.225 | 207 | 3.09 | 0.002 | **0.019** |

Contrasts between least-squares means. P values were adjusted for multiple comparisons (see Methods) yielding an Adjusted P. df, degrees of freedom. Bold values indicate significant P values.

Hybrids did not show a significant difference in response to the coos of the 3 populations (see Table 3 and Figure 4).

In the linear mixed model, the response to the 3 stimuli was determined by the population ($F_{2,69} = 8.03$, $P \leq 0.001$) in which the stimuli were played and the population stimulus interaction ($F_{4,138} = 4.45$, $P = 0.002$; see Figure 4). Order and the stimulus–order interaction were not significant and were therefore removed from the model; this did not qualitatively change the results.

## DISCUSSION

There are 2 main findings in this study. First, there was no evidence of a difference in hybrid response to both parental species and hybrid vocalizations. Second, the parental species respond differentially to the vocalizations of conspecifics and heterospecifics and intermediate to hybrids. In other words, hybrids do not distinguish between parental species and hybrid vocalizations, whereas both parental species do.

### Differential response in allopatric populations

In *Streptopelia* species, a greater response to playback indicates the intruder is rated as a stronger competitor and thus as a more serious threat (Slabbekoorn and ten Cate 1997). The intermediate response of both allopatric populations to hybrid coos may have 2 different consequences when hybrids disperse into parental populations. The first one is that a hybrid individual may have some advantage as an intruder as they may not be chased away as intensely as a conspecific. On the other hand, once established, hybrids will need to engage physically in territorial disputes more because their signal is less effective. Therefore, overall, hybrid males may be at a disadvantage in male–male competition for territories with the parental species in the allopatric populations.

Spreading into one allopatric parental population or the other will be equally (dis)advantageous for hybrid males because the response of both allopatric populations to hybrid vocalizations is comparable. Consequently, potential introgression is likely to be symmetrical unlike the asymmetric introgression found in other studies (Pearson and Rohwer 2000; Rosenfield and Kodric-Brown 2003). Hybrid competitive abilities, hence fitness, in the allopatric parental populations affect the width and movement of the zone (Pearson and Rohwer 2000). The reduced effectiveness of hybrid vocalizations compared with parental species vocalizations may keep hybridization confined to the narrow zone we see today, although it is premature to conclude this from these data.

In captive Japanese and European male quails, parental species also responded most to their conspecific vocalizations and intermediate to hybrid (F1) vocalizations (Collins and Goldsmith 1998). However, male captive red-legged and rock partridges respond equally to conspecific and F1 hybrid calls (Ceugniet and Aubin 2001). This could indicate different selection pressures on the species recognition signal in each species or differences in the degree of (dis)similarity between hybrid and parental species calls in these species. In *vinacea* and *capicola* doves (de Kort et al. 2002a) and in European and Japanese quail (Collins and Goldsmith 1998), the vocalizations of the 2 species and hybrids can be discriminated based on their acoustic parameters alone. In the red-legged and rock partridges, the differences seem to be less clear between the hybrids and the parental species (Ceugniet et al. 1999). Furthermore, we played back hybrid calls of all types found in the hybrid population, ranging from one species to the other including F1 calls, whereas Collins and Goldsmith (1998) and Ceugniet and Aubin (2001) only played back F1 calls. This could result in a different response at the population level.

**Table 3**

**Comparison of response to each of 3 stimuli played in each population, compared per population (pairwise comparisons of least-squares mean estimates)**

| Population | Stimuli compared | Estimate | Error | df | $t$ | $P$ | Adjusted $P$ |
|---|---|---|---|---|---|---|---|
| *Capicola* | *Capicola*–hybrid | 0.467 | 0.226 | 138 | 2.06 | 0.041 | 0.101 |
| | *Capicola*–*vinacea* | 0.704 | 0.226 | 138 | 3.12 | 0.002 | **0.006** |
| | Hybrid–*vinacea* | 0.238 | 0.226 | 138 | 1.05 | 0.294 | 0.545 |
| Hybrid | *Capicola*–hybrid | −0.254 | 0.226 | 138 | −1.12 | 0.264 | 0.502 |
| | *Capicola*–*vinacea* | −0.244 | 0.226 | 138 | −1.08 | 0.282 | 0.528 |
| | Hybrid–*vinacea* | 0.009 | 0.226 | 138 | 0.04 | 0.968 | 0.999 |
| *Vinacea* | *Capicola*–hybrid | −0.240 | 0.226 | 138 | −1.06 | 0.291 | 0.540 |
| | *Capicola*–*vinacea* | −0.561 | 0.226 | 138 | −2.48 | 0.014 | **0.038** |
| | Hybrid–*vinacea* | −0.321 | 0.226 | 138 | −1.42 | 0.158 | 0.333 |

$P$ values were adjusted for multiple comparisons (see Methods) yielding an Adjusted $P$. df, degrees of freedom. Bold values indicate significant $P$ values.

Another factor that may explain the differences in findings is that our experiments were conducted in the field, in which the vocalizations are played back, and responded to, in a natural territorial context.

### Indiscriminate response in the hybrid population

The indiscriminate response of the hybrid population suggests hybrid coos are as effective as parental species coos in male–male competition within the hybrid zone. Consequently, pure males do not have a selective advantage over hybrid males in the hybrid zone with respect to their vocalizations. Narrow hybrid zones are the result of 3 different scenarios or combinations thereof: recent contact and low dispersal; hybrid superiority within an ecotone but not outside it; and hybrid inferiority (Rohwer and Wood 1998). If hybrids within the hybrid zone are not selected against, the zone will be stable and possibly become broader (Moore and Buchanan 1985; Pearson 2000; Pearson and Rohwer 2000).



Response of *vinacea*, *capicola* and hybrid populations

**Figure 4**
Response of each population to each of the 3 stimuli. *Vinacea* and *capicola* respond most to the conspecific stimulus and least to the heterospecific stimulus with an intermediate response to the hybrid stimulus. The hybrid population responds equally to all 3 playback stimuli. The response variable PC1, is the first factor of the PCA of the 5 scored response variables. This is an interaction plot. The average response per population per stimulus is shown with standard error bars. Lines connect the response values for each stimulus and should not be interpreted as a linear relationship between the 3 stimuli for each population.

The response of males in the hybrid zone could be learned as males encounter a large variability in coos within the hybrid zone. Neighboring males within the hybrid population often vary much more in their acoustic characters than neighbors in the parental populations. Hybrid males therefore experience all types of variations in coos during territorial encounters, including parental species-like coos, and may have learned to respond to all the types of vocalizations they have been exposed to (Catchpole 1978). Various studies have shown, as reviewed by Irwin and Price (1999), that learning about vocal signals plays an important role in territorial responses to conspecifics and sympatric heterospecifics. For example, birds may respond differently to congeneric species vocalizations if they are in sympatry with them compared with when in allopatry even though the vocalizations themselves do not differ greatly between sympatry and allopatry. In some cases, the territorial response may be greater in sympatry (Catchpole and Leisler 1986; Prescott 1987; Baker 1991), whereas in others the response was reduced in sympatry compared with allopatry (Gill and Murray 1972; Morrison 1982). The most likely explanation for these results is learning about with whom to engage in the competition for resources as for interspecifically territorial species the response was stronger in sympatry than allopatry and vice versa with species that were not interspecifically territorial (Irwin and Price 1999). Although doves can learn to distinguish the vocalizations of different species (Beckers et al. 2003), the role of signal learning in the current situation calls for further study.

It looks like the hybrid population responded the most overall to all 3 stimuli. However, there are many confounding variables such as season, weather, and population density that may affect the response of individuals within a population. Therefore, comparisons across populations were not made as the experimental setup does not allow for control of these factors across populations.
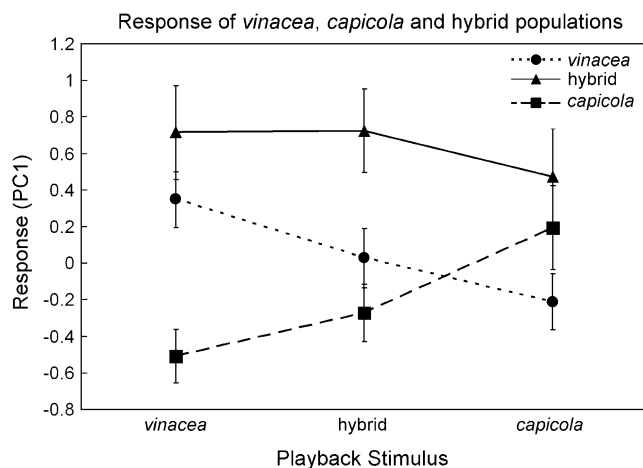
### Characteristics of the response data

The selective response of the parental population to their conspecific vocalization, as also found by de Kort et al. (2002b), and the unselective response of the hybrid population indicates that the hybrid population has a broader response curve than each of the parental populations. The parental species seem to be tuned to the range of parameter combinations that delineates their species-specific vocalization (Slabbekoorn and ten Cate 1998), whereas the hybrids do not show a shift in the response curve to the acoustic parameter area between the 2 species but a broad curve encompassing the 2 species and everything in between.

However, the response of the hybrid population as a whole does not rule out that each hybrid individual may have a narrow(er) response curve in one end of the spectrum (*vinacea*) or the other (*capicola*) or in-between (hybrid). Together, this would yield a broad response curve for the whole population. Ceugniet and Aubin (2001) found that captive F1 male hybrids between red-legged and rock partridges respond more to F1 hybrid calls than to the 2 parental species calls. In a natural hybrid zone with multiple hybrids and backcrosses, the broad population response curve could be built up of F1 individuals responding most to hybrid vocalizations and individuals with a genetic makeup closer to the parental species responding more to vocal variants resembling the parental species. Further experiments are needed to clarify this issue.

### Hybridization and mate choice

Studies into the effectiveness of hybrid signals in male–male interactions are rare (but see Baker 1991; Scroggie and Littlejohn 2005), and most studies have focused on female response to these signals. Hybrid signals do not seem to confer their bearers a selective advantage because parental species females (frogs, *Hyla*: Hobel and Gerhardt 2003) or both hybrid and parental species females have a reduced preference for them (crickets, *Chorthippus*: Bridle et al. 2006). Females may also not have a preference at all (frogs, *Geocrinia*: Littlejohn and Watson 1976). In some cases, hybrid females prefer hybrid signals, whereas parental species females prefer conspecific signals rendering hybrid signals advantageous in certain contexts (frogs, *Hyla*: Doherty and Gerhardt 1984; crickets, *Laupala*: Shaw 2000). In birds, a laboratory experiment with European and Japanese quail showed that European quail females' response mirrored that of the males (Collins and Goldsmith 1998) with the strongest response to the conspecific vocalizations, intermediate response to hybrid vocalizations, and the weakest to the heterospecific vocalizations (Deregnaucourt and Guyomarc'h 2003). The Japanese quail (*Coturnix c. japonica*) females showed no discrimination, but the authors argue this could be due to domestication. Even though these studies were carried out in the context of female choice, the results seem comparable with our study in which in the parental populations hybrid signals are not as effective as parental species signals, but in the hybrid zone they are. If hybrid females have the same response as hybrid males seem to have, then hybrid coos may be just as effective in attracting females as in territorial interactions between males.

### CONCLUSION

In conclusion, intermediate hybrid characters, such as territorial signals, need not bring about a loss of function of these characters. This is the first study testing intermediate hybrid signals in the field in a hybrid population and adjacent allopatric parental populations. The equal response to these hybrid signals in the hybrid population and the lower response to them in the parental populations suggest that hybrid territorial vocalizations are functionally on a par with parental species vocalizations within, but not outside, the hybrid zone. In so far as vocalizations are the main determinant of hybrid fitness, the likely evolutionary consequence at a population level is that the hybrid zone will remain a stable zone of contact. More studies are needed to be able to assess the importance of learning a response and to gain insight into the fitness of hybrids to understand the stability of the hybrid zone and fate of the species involved.

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