Vocal communication in an avian hybrid zone

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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 two 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 two dove species, *Streptopelia vinacea* and *S. capicola,* compared to the vocalizations of the parental species. With playback experiments we assessed the response to hybrid and the two 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 three 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 to 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.

Introduction

Hybrid 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 three scenarios: introgression and merging of the two species, a stable hybrid zone, or reinforcement of characters that cause premating isolation (Liou & Price 1994; Servedio & Kirkpatrick 1997). In the first two 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 which 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 & Gray 2001), frogs (e.g., Littlejohn & Watson 1985) and birds (Catchpole & Slater 1995). In all these taxa hybridization may severely affect the structure of acoustic signals (crickets, e.g.: Mousseau & Howard 1998; frogs, e.g.: Bull 1978; Littlejohn 1976; birds, e.g.: Bensch *et al.* 2002; Ceugniet *et al.* 1999; Collins & Goldsmith 1998; de Kort *et al.* 2002; Delport *et al.* 2004; Dowsett-Lemaire 1999; Gee 2005; Gelter 1987) 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 & 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 & 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 two African doves: the Vinaceous dove, *Streptopelia* *vinacea*, and the Ring-necked dove, *S. 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, Figure 3.1). 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 & Thorpe 1964; Nottebohm & 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.

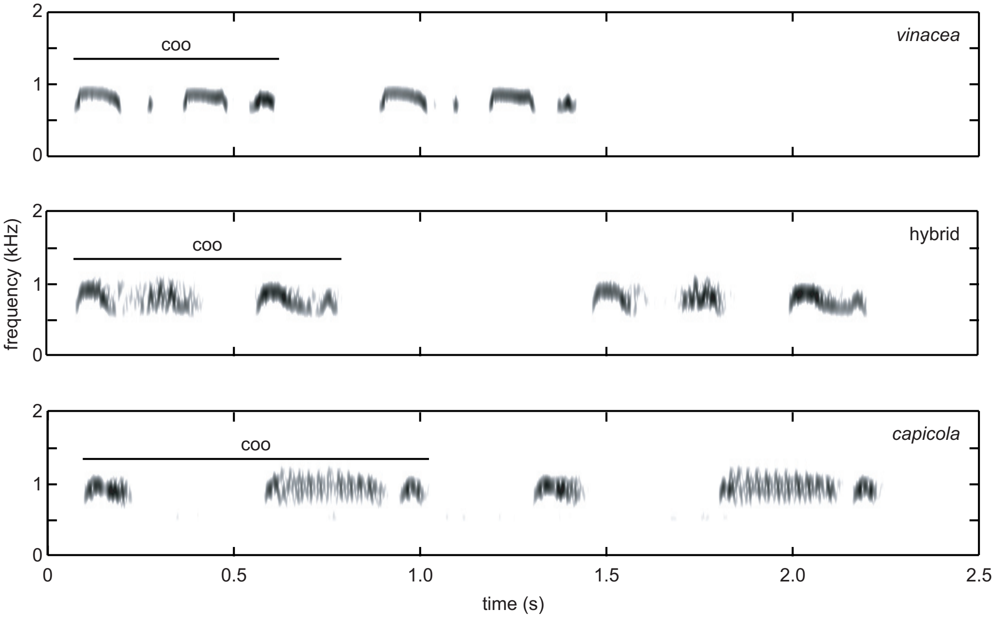

Figure 3.1 Spectrograms of two perch coos of a *vinacea*, a hybrid and a *capicola* individual. Recordings from de Kort *et al.* (2002a). The spectrograms were made using the following settings: Hanning window, sample frequency of 44,100 Hz; 2048 Fast Fourier Transform samples; window length of 512 samples; overlap 480 samples and 15dB dynamic range.

Methods

Study populations

The Vinaceous dove, *Streptopelia vinacea,* and the Ring-necked dove, *S. capicola*, are sister species of turtle doves which have a 2.5% mtDNA 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 (Figure 3.1). These two 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 (Chapter 2). 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 N01º 48' E31º 23' to N01º 45' E31º 23'). We studied adjacent allopatric populations of *capicola* in Queen Elizabeth National Park (N01º46' E31º23'), 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 (N02º14'

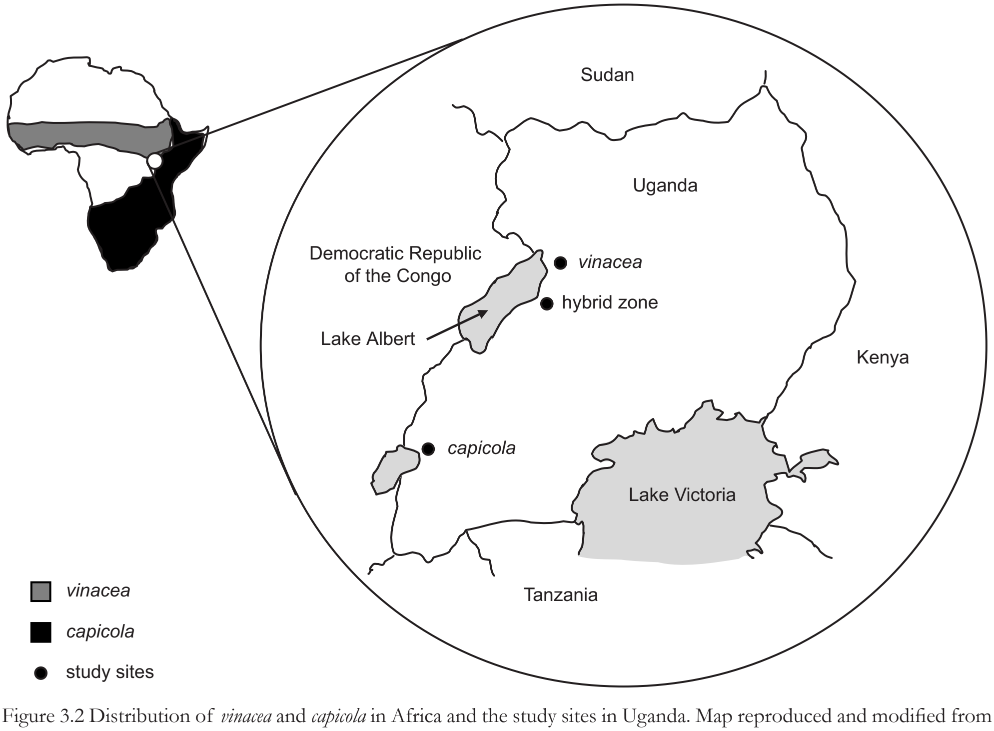

Figure 3.2 Distribution of *vinacea* and *capicola* in Africa and the study sites in Uganda. Map reproduced and modified from de Kort *et al.* (2002a).

E31°34') and approximately 50 km north of the hybrid population (Figure 3.2). The species are abundant in these three 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 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 three 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 twelve minutes and the setup was as follows: the pre-playback period consisted of 3 minutes silence (to measure baseline activities) and three playback periods each lasting 3 minutes: 1 minute stimulus and 2 minutes of silence (Figure 3.3). A similar design has been successfully used in previous playback studies with *Streptopelia* doves (Slabbekoorn & ten Cate 1997; de Kort *et al.* 2002b; Secondi *et al.* 2003b).

Experiments were carried out from sunrise to 11.00h and from 16.00h to sunset between September and December 2003. A speaker (Blaupunkt CB4500 100W, Kemo 40W #M034 built in amplifier) connected to a Creative Nomad Jukebox 3 was placed within the territory. Observers then positioned themselves at least 25 meters from the speaker. Observations were recorded with FIT-system software (Held & Manser 2005) on a Palm IIIx hand held 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

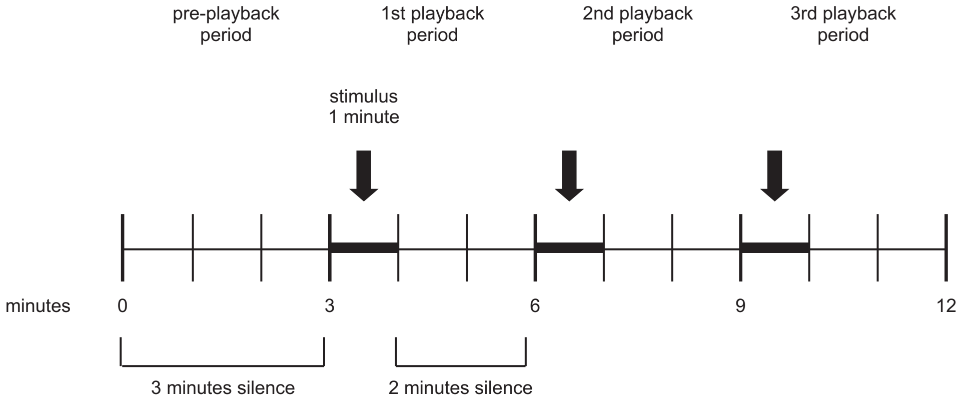

Figure 3.3 Playback design. Each experiment consists of a pre-playback period of 3 minutes. There are three playback periods consisting of one minute of stimulus followed by two minutes of silence. The stimuli are presented in all possible orders to test for order effects.

latency was defined as the time between the onset of the playback stimulus and the occurrence of one of the three 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 four responses. Each trial was conducted on a different subject and subsequent subjects were at least 200m 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 one minute. A natural bout (coos are usually produced in series called bouts) was chosen from these recordings and band pass filtered (500 - 1300Hz). The amplitude was normalized with Signal 3.12. To create one minute of sound, bouts were copied as many times as necessary to fill one minute 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 one minute. 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 75-80 dB at one meter from the speaker.

Statistics

A Principal Components Analysis (PCA) was conducted to create one response variable from the five 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 two 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 three 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

Table 3.1 Correlation matrix for the response variables included in the PCA. loadings for all variables for the first component are also shown.

response variable	flights	coos	calls	latency	fly time	loadings component 1
flights	1.000					.826
coos	0.013	1.000				.360
calls	0.774	0.075	1.000			.872
latency	-0.415	-0.592	-0.421	1.000		-.721
fly time	0.594	0.168	0.706	-0.438	1.000	.831

individual's territorial behaviour by contrasting the response to each stimulus to the pre-playback period for each population. Multiple comparisons 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 & 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 three stimuli (least means estimates) were compared in each population. Multiple pairwise comparisons were corrected with the Tukey method (Games & 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 (Table 3.1).

Response to playback periods compared to the pre-playback period

To test if there was a response to the playback stimuli, each stimulus played was compared to 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 to the pre-playback period (pairwise comparisons of the least-squares means estimates, Table 3.2). Neither species showed an increase in response to the hybrid and heterospecific coos compared to the pre-playback period. Hybrids showed a significant increase in response to all three stimuli, *vinacea*, *capicola* and hybrid coos, compared to the pre-playback period (Table 3.2).

In the Linear Mixed Model, the level of response of each population to the three stimuli and the pre-playback period was 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

Table 3.2 Effect of playback compared to the pre-playback period. Contrasts between least-squares means. *P* values were adjusted for multiple comparisons (see Methods) yielding an adjusted *P*. Bold values indicate significant *P* values.

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**

these two variables ($F_{6, 207}$=4.03, $P \leq 0.001$).

Response to the three 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 three stimuli was compared.

Capicola responded significantly more to *capicola* coos than to *vinacea* coos (Table 3.3 and Figure 3.4). The overall response to hybrid coos was intermediate between, and not significantly different from, the response to conspecific or heterospecific coos (Table 3.3 and Figure 3.4).

Vinacea responded significantly more to *vinacea* coos than *capicola* coos (Table 3.3 and Figure 3.4). The overall response to hybrid coos was intermediate between, and not significantly different from, the response to conspecific or heterospecific coos (Table 3.3 and Figure 3.4).

Hybrids did not show a significant difference in response to the coos of the three populations (Table 3.3 and Figure 3.4).

In the Linear Mixed Model, the response to the three 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, Figure 3.4). 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 two 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.

Table 3.3 Comparison of response to each of three stimuli played in each population, compared per population (pairwise comparisons of least-squares means estimates). *P* values were adjusted for multiple comparisons (see Methods) yielding an adjusted *P*. Bold values indicate significant *P* values.

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

In other words, hybrids do not distinguish between parental species and hybrid vocalizations, while 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 & ten Cate 1997). The intermediate response of both allopatric populations to hybrid coos may have two 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 & Rohwer 2000; Rosenfield & Kodric-Brown 2003). Hybrid competitive abilities, hence fitness, in the allopatric parental populations affects the width and movement of the zone (Pearson & Rohwer 2000). The reduced effectiveness of hybrid vocalizations compared to 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 & Goldsmith

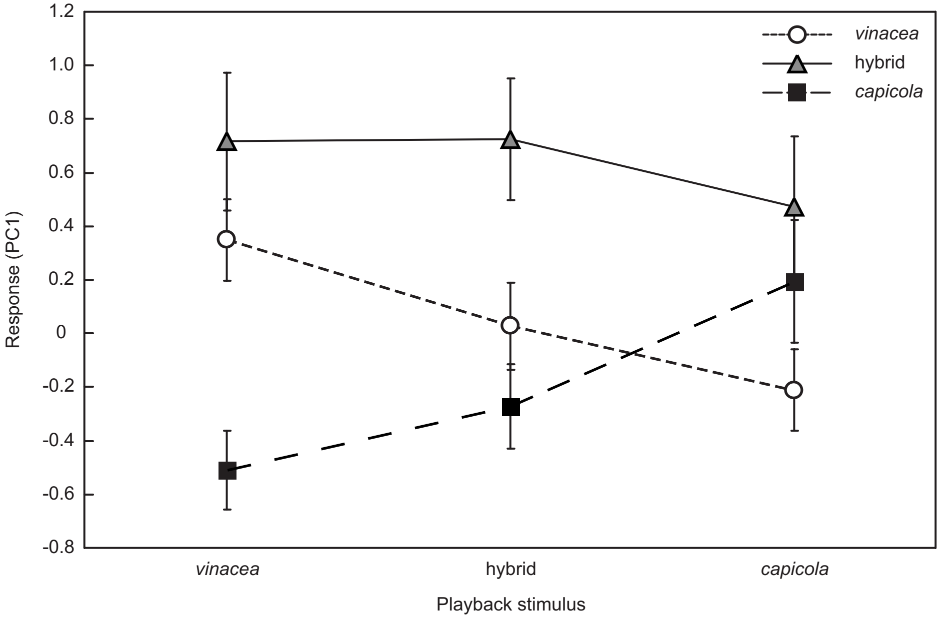

Figure 3.4 Response of each population to each of the three stimuli. *Vinacea* and *capicola* respond most to the conspecific stimulus and least to the heterospecific stimulus with an intermediate response to the hybrid stimulus. The hybrid population responds equally to all three playback stimuli. The response variable PC1, is the first factor of the Principal Components Analysis of the five 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 three stimuli for each population.

1998). However, male captive red-legged and rock partridges respond equally to conspecific and F1 hybrid calls (Ceugniet & 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 & Goldsmith 1998) the vocalizations of the two 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. 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 three different scenarios or combinations thereof: recent contact and low dispersal; hybrid superiority within an ecotone but not outside it; and, hybrid inferiority (Rohwer & Wood 1998). If hybrids within the hybrid zone are not selected against, the zone will be stable and possibly become broader (Moore & Buchanan 1985; Pearson 2000; Pearson & Rohwer 2000).

The response of males in the hybrid zone could be learned as males encounter a large variability in coos within the hybrid zone. Neighbouring males within the hybrid population often vary much more in their acoustic characters than neighbours 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 to 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 & Leisler 1986; Prescott 1987; Baker 1991), while in others the response was reduced in sympatry compared to allopatry (Gill & 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 & 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 three stimuli. However, there are many confounding variables such as season, weather and population density which 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 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 & ten Cate 1998a), while the hybrids do not show a shift in the response curve to the acoustic parameter area between the two species, but a broad curve encompassing the two 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 two 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 & 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 & 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 & Watson 1976b). In some cases hybrid females prefer hybrid signals while parental species females prefer conspecific signals rendering hybrid signals advantageous in certain contexts (frogs, *Hyla*: Doherty & 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 & Goldsmith 1998) with the strongest response to the conspecific vocalizations, intermediate response to hybrid vocalizations and the weakest to the heterospecific vocalizations (Deregnaucourt & 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 to 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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