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Variation in Advertisement Call Properties of the Japanese Quail

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Abstract.- The aim of this study was to investigate the amount variation in four spectral and six temporal properties of advertisement calls between and within-male Japanese quail and to establish the effect of age of sexual maturation to these properties. The first, second, third syllables and damping parts were 68.2, 74.3, 501.1 and 95.9 ms long, on average, and had peak frequencies of 1719.9, 1989.9, 2203.2 and 2352.7 Hz, respectively. There was high between individual variations in all call traits. In relation to within-male variation, there were high medians and low ranges for spectral properties while low medians and high ranges for temporal properties. Moderate positive correlations between syllable lengths and age of sexual maturation, low negative correlations between interval lengths and age of sexual maturation were observed. Repeatability of the advertisement call characteristics were high, but estimates for spectral properties were slightly lower (0.66-0.82) than that for temporal properties (0.89-0.96). These results suggest that temporal call parameters have the potential to be used in individual identity and these traits might carry information used by females in mate choice. Spectral properties could be recognized as stable call properties that may be used in efficient transmission or species recognition.

Keywords: Quail, crow, individual identity, call parameters, repeatability.

INTRODUCTION

When visual communication is limited, birds mainly use the acoustic channel to communicate and a few features of the song that are resistant to degradation are generally used for species-specific recognition (Aubin *et al.*, 2004). This coding system allows the bird to transmit specific information at long ranges. Between-male variation in secondary sexual traits influences success in sexual competition to gain mating opportunities with choosy females (Andersson, 1994). Hence, examination of both between and within-individual variation is required to understand the evolution of sexual behaviours (Boake, 1994). One way of quantifying between-individual variation in a phenotypic trait while taking within-individual variation into account is to use the quantitative genetic concept of repeatability (Falconer and Mackay, 1981; Boake, 1989). Higher variation between individuals compared to that within individuals, *i.e.* high repeatability, suggests the possibility of high heritability values (Boake, 1989). Traits with important signalling functions in mate choice are expected to show higher repeatability than less-critical traits.

The Japanese quail was first domesticated in the 11th century as a songbird for advertisement calls of males and still lives in the wild in Asia (Cheng and Kimura, 1990). The Japanese quail was recognized as a food source at the beginning of the 20th century and farmed for commercial meat and egg production (Mills *et al.*, 1997). Besides its own merit in fancy and commercial breeding, Japanese quail is a valuable model system for a variety of scientific studies. Male Japanese quails produce territorial songs that consist of three syllables; two short trills followed by an extended syllable that fades away with a short damping component. Guyomarc'h *et al.* (1998) reported that the temporal patterns of these calls were highly stereotyped and could play a role in inter-individual recognition. The role of male mating calls in female mate choice and indication of male advertisement calls containing species-specific and individual information about the caller were also reported (Guyomarc'h *et al.*, 1998; Deregnaucourt *et al.*, 2001; Deregnaucourt and Guyomarc'h, 2003). On the other hand, age and reproductive status of the males are the factors affecting the syllable and interval lengths of the calls (Schleidt and Shalter, 1973; Deregnaucourt *et al.*, 2009). There is no influence of learning on

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Galliforms' call and it is believed that their call features are mainly determined by the genetic constitution of the individual (Deregnaucourt *et al.*, 2001).

The aims of this study were two fold. The first objective was to investigate the amount of variation in advertisement call properties between and within male Japanese quail to estimate the repeatability because both sources of trait variation can influence the course of sexual selection. The second aim was to test the age of sexual maturity effect on the call properties.

MATERIALS AND METHODS

The data for this study were obtained from the Japanese quail population (*Coturnix coturnix japonica*) at the Quail Breeding Unit of Gaziosmanpasa University, Tokat, Turkey. Birds used in this study were obtained from five consecutive hatchings by artificial incubation. Analyses were carried out with the records of 1514 advertisement calls obtained from randomly selected 393 male Japanese quails from the study population. We kept the birds in mixed gender groups of 15 to 20 individuals to allow the males in contact with females and have physical interactions with other individuals. Chicks were housed for the first three weeks under 24 hour light, with following weeks at 16:8 light:dark cycle. The temperature started at 36°C. Temperature was decreased by 3°C every week until it reached 24°C. Birds were allowed *ad libitum* access to food and water. They were fed with 240 g/kg crude protein (CP) and 13.39 MJ ME/kg starter diet for 21 days, 190 g/kg CP and 12.55 MJ ME/kg grower diet between 22 and 35 days of age and thereafter 170 g/kg CP and 11.50 MJ ME/kg breeder diet.

Recordings

The foam produced by the cloacal gland is an androgen dependent secondary sexual character in the male Japanese quail and could be used as an external index of sexual maturity (Mohan *et al.*, 2002; Marin and Satterlee, 2004). Males were inspected daily (after 25 days of age), to determine the day of cloacal gland foam production, and this day was recorded as the age of sexual maturity (ASM). Calls of males used in this study were recorded when the individuals were 8 week of age and they were completely sexually mature, as testified by the development of the proctodeal gland with foam production. Males were placed in a sound-proof chamber (1x1.5x0.5m) for a period of five minutes and their crows were recorded. When recording of a male call was unsuccessful, the procedure was repeated two days after the first attempt. All males were recorded within 2 weeks. Advertisement calls were recorded with a personal computer (sampling rate=32 kHz) equipped with a Sennheiser MD 41 dynamic microphone.

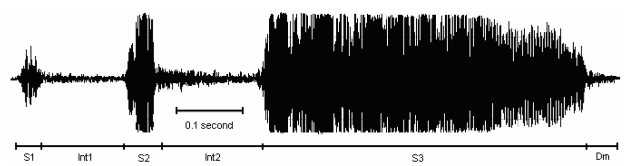

Fig. 1. Oscillogram of a male Japanese quail call. S1, Int1, S2, Int2, S3 and Dm are the lengths of the first syllable, interval one, the second syllable, interval two, the third syllable and damping, respectively.

Acoustic analyses

Japanese quail's calls are composed of three parts; two short syllables followed by an extended trill that ends with a short component that was called 'damping' (Fig. 1). The damping (Dm) is a measure of the fading of vibratory motion of the third syllable. Hence, each recorded song was analyzed to measure six temporal [durations of syllables (S1, S2 and S3), intervals (Int1, Int2) and damping (Dm)] and four spectral properties [peak frequencies of syllables (Fr1, Fr2, Fr3) and damping (FrD) component]. The peak frequency displays the frequency of the strongest spectral component in the selected entire syllable.

Statistical analyses

Variability in each call property between and within males was expressed as coefficients of variation. Coefficients of variation between males were based on average values for each male. The level of association between each pair of call variables and ASM was determined by correlation analyses. Only males for which we had at least three crows were included in ANOVA analyses to estimate the repeatability of male song properties. Corrected sample size (*n*0), that is a coefficient related to the sample size per group in the analysis of variance, and standard errors for the repeatability estimates were calculated following the procedures outlined by Lessells and Boag (1987) and Becker (1992).

RESULTS

The statistical description and variability of call properties is summarized in Table 1. Sample sizes for the examined traits vary because all parameters could not be measured for every call. For example, relatively small data size in Fr1 component mainly arose from the lack of first syllable of some males. The length of the first component (Int1) was over two times longer than the length of the second interval (Int2). The first and second syllable length was short and near to each other but the third syllable was remarkably long. Interestingly, component frequencies increased consistently throughout the call.

Variation expressed in terms of the coefficient of variation (Table I), was higher for the lengths of syllables and intervals than for spectral properties of the syllables (Mann-Whitney test: $U=0.0$, $Z = -2.558$, $P < 0.05$). The greatest variance existed in Int1 and Dm parts of the crow. Coefficients of variation within male's recording samples were also calculated and represented as medians and ranges (Table I). Unlike the medians, the ranges of the within-male CVs were higher for song properties related with the frequency domain than those related with the time domain. The lowest medians and ranges of the within-male CVs were estimated for the length of the third syllable.

Age of sexual maturation of the examined males ranged from 25 to 42 days. Therefore, recorded individuals were divided into 6 group based on ASM with three day intervals (the range of age for each group in terms of ASM were 25-27, 28-30, 31-33, 34-36, 37-39 and 40-42, respectively). There were no differences among the ASM groups in their age of recording ($F_{246, 5} = 2.55$; $P>0.05$). This could be expected because regardless of the ASM all males were recorded within 8 to 10 weeks of age. Temporal properties of the song tabulated within sexual maturation groups were presented in Figures 2 and 3. Because, the effect of ASM on spectral

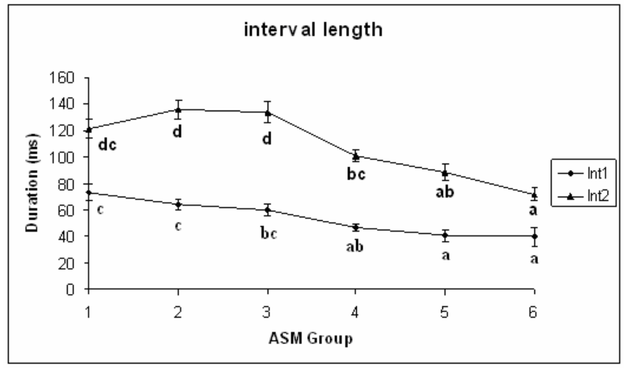

Fig. 2. Changes of the mean (error bars=SEM) interval lengths against the sexual maturity groups (means within interval lengths with different letters are significantly different (P<0.05) based on Duncan test).

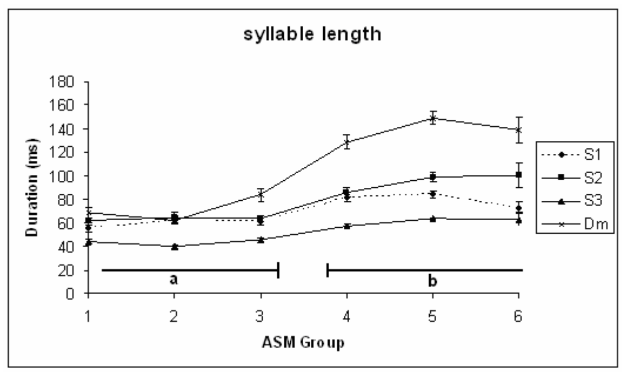

Fig. 3. Changes of the mean (error bars=SEM) syllable and damping lengths against the sexual maturity groups (S3 values represented in the graph were obtained dividing actual values of the S3 by 10; the letter below the means indicates that the means for the first three ASM group were different (Duncan test, P<0.05) from the means for the last three ASM group within each property).

characteristics of the call were insignificant (one-way ANOVA, $P>0.05$), spectral properties were not consider in this part of the study. Interval lengths decreased while syllable lengths increased significantly (one-way ANOVA, $P<0.01$ for all temporal parameters of call) with increasing ASM. The decrease in Int2 with the increasing ASM was higher than that in Int1. Among the temporal call properties, the highest response (over 100%) to the

Table I.- **Between and within-male variability in calling song properties.**

Property	Between male						CV (%) within male	
	N	Mean	SD	Min	Max	CV(%)	Median	Range
Int1	336	56.0	29.03	5.2	229.5	51.82	11.78	23.83
Int2	373	113.5	43.63	10.3	322.3	38.42	6.79	24.75
S1	336	68.2	20.17	29.2	150.0	29.56	7.93	24.01
S2	372	74.3	29.94	22.8	230.5	40.31	9.81	32.89
S3	393	501.1	143.13	211.3	1109.5	28.56	4.30	13.49
Dm	393	95.9	49.38	17.4	265.0	51.50	13.07	42.43
Fr1	311	1719.9	209.39	842.2	2712.9	12.17	4.66	24.34
Fr2	350	1989.9	324.59	1125.5	3103.3	16.31	6.72	32.31
Fr3	387	2203.2	382.12	1568.5	4164.0	17.34	4.72	35.78
FrD	365	2352.7	496.82	1175.8	3676.0	21.12	4.64	39.53

S1, S2 and S3 are the duration of the first, second and third syllable respectively; Int1 and Int2 are the durations of interval one and two; Dm is the damping duration. Fr1, Fr2, Fr3 and FrD are the peak frequencies of the first, second, third syllables and damping part, respectively. Scale for duration and frequency measurements are in “ms” and “Hz”, respectively.

Table II.- **Variation and repeatability (r) of male call properties.**

Properties	Mean Square		F^a	N	n0	r	SE
	Between	Within					
In1	50.54	3097.56	61.29	336	3.85	0.94	0.025
In2	83.17	7048.86	84.75	373	3.83	0.96	0.019
S1	45.48	1515.30	33.31	336	3.85	0.89	0.043
S2	77.76	3376.47	43.42	372	3.83	0.92	0.034
S3	833.38	77826.62	93.39	393	3.83	0.96	0.017
Dm	233.77	9301.89	39.79	393	3.83	0.91	0.037
Fr1	14063.37	164906.36	11.73	311	3.84	0.74	0.093
Fr2	45550.95	388285.20	8.52	350	3.81	0.66	0.111
Fr3	36322.56	549623.69	15.13	387	3.75	0.79	0.078
FrD	51584.71	938364.50	18.19	365	3.81	0.82	0.069

[a] for all properties $P<0.001$

delayed ASM was observed in damping duration (Figs. 2, 3).

All of the repeatability estimates for the advertisement call characteristics were high (Table II), but estimates for spectral properties (frequencies of the components) were slightly lower (Mann-Whitney test: $U=0.0$, $Z = -2.566$, $P < 0.05$) than that for temporal properties (intervals and syllables lengths).

DISCUSSION

Our results indicate that temporal call parameters have the potential to be used in individual identity. On the other hand, spectral properties had low between individuals variation hence they could be recognized as more stable properties of the call. This could reflect a history of stabilising selection on advertisement calls for efficient transmission or species recognition.

In our study, all mean values of the temporal call properties were lower than reported by Collins and Goldsmith (1998). These differences could be the result of genetic differences between the populations. We examined the third syllable of the call excluding the damping component. When the damping duration was added to the duration of the third syllable, it was still 20% lower than their report. On the other hand, the values for peak frequencies of the syllables were higher than those reported by Collins and Goldsmith (1998).

Variation in the advertisement calls of animals and the potential of vocal parameters to be used in individual recognition has been proposed by many authors (Forrest and Green, 1991; Mathevon, 1996; Collins and Goldsmith, 1998; Mathevon *et al.*, 2003; Sharp and Hatchwell, 2005). In this study, the pattern of between-male CVs indicated different repeatability patterns for the spectral and temporal properties of the call. The high repeatability of song properties of male Japanese quail was due to increased variation between males rather than to decreased variation within individuals. Hence, estimated high repeatability for call properties may not indicate a correlated high heritability, but moderate heritability estimates might be expected.

The call properties that are more variable between-individuals than within-individuals can potentially be used in sexual selection as individual markers (Boake, 1994; Johnsen and Zuk, 1996; Hack, 1998; Aubin *el al*., 2004). It has also been reported that female Japanese quail express a preference among males (Deregnaucourt and Guyomarc'h, 2003; Ophir and Galef, 2003). Calls of male Japanese quail may be used by females to select among males, especially if they reflect aspects of male quality. Although repeatability of the frequency of the third syllable (0.19) and the duration of the first syllable (0.04) were unexpectedly low, Collins and Goldsmith (1998) reported high repeatability estimates for the vocal parameters of the Japanese quails.

Age and reproductive status of the males have been reported as factors affecting the temporal properties of the quail calls (Schleidt and Shalter, 1973; Deregnaucourt *et al.*, 2009). It is also known that males with genetically high growth potential reach the sexual maturity faster than the ones with low growth potential (Sezer *et al.*, 2006). Hence, this preliminary estimate of repeatability indicated that upcoming genetic analysis of the Japanese quail song properties would be feasible when they are based on recordings which take into account the age of sexual maturation of the examined males. Males used in this study were recorded within a five-minute at the very beginning of their sexual maturation. It would be interesting to measure repeatability over long time scales to test the consistency of a male's calls across years or seasons in future studies. Additional studies exploiting call properties that are important for individual recognition and their genetic basis are also required to understand the selection pressure on quail calls.

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