

CHANGES IN THE STRUCTURE OF THE PEEP VOCALIZATIONS OF FEMALE DOMESTIC CHICKS (*GALLUS GALLUS DOMESTICUS*) WITH AGE

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ABSTRACT: Changes in the structure of the peep vocalization of female domestic chicks reared in pairs from day three post-hatching were investigated. Recording began on day five with each chick being recorded in isolation twice weekly over a ten week period post-hatching. Spectrographic analysis shows that the peep call develops an increasingly complex structure from the second week post-hatching with additional components introduced as the chicks age. Nine acoustic parameters (duration, maximum frequency, minimum frequency, difference between maximum and minimum frequency, peak frequency, peak frequency range, peak amplitude, energy and average power) of four different peep calls were analysed. Significant differences were found between the four types of peep call on seven of the nine acoustic parameters. Discriminant analysis showed that the different types of peep call could be accurately determined on the basis of these results. Correlations of the call parameters showed that the calls displayed lower levels of stability as call structure became more complex. Chicks also displayed high inter-individual variation and relatively low intra-individual variation over call parameters. Results are discussed in relation to hen-chick, chick-chick communication as the broody period declines.

The chick of the domestic fowl vocalizes before hatching (Guyomarc'h, 1974) and from as early as day 18 of incubation (Gottlieb and Vanderbergh, 1968). Tuculescu and Griswold (1983) classified these pre-natal calls as distress calls and pleasure calls. Greenlees (1993) showed spectrograms of these pre-hatching calls and concluded

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these calls were similar in structure to the post-hatching calls of the chick. Post-hatching the peep and twitter constitute the main call types (Kaufman and Hinde, 1961; Montevicchi, Gallup and Dunlap, 1973). Studies into causation show that the peep call is emitted in a variety of situations, such as a change in environmental temperature (Kaufman and Hinde, 1961), maternal isolation (Bermant, 1963) and removal of an imprinting object (Brown, 1979).

Spectrographic analysis has shown distinct structural differences between peeps and twitters (Collias, 1952; Collias and Joos, 1953; Guyomarc'h, 1962; Andrew, 1963, 1964; Collias, 1987). Peeps are characterised by descending frequencies while twitters tend to swing upwards in pitch (Collias, 1987). The 'distress call' (Collias and Joos, 1953), *ÔLe cri d'appel du Poussin isolé* (Guyomarc'h, 1962), and 'peeps' (Andrew, 1964) have all been classified by Wood-Gush (1971) as being the same call. Jennings and Kent (1996) demonstrated that three types of peep call can be produced by the same chick in the first week of life. These three types of peep had descending frequencies but with differing acoustic parameters.

Schjelderup-Ebbe (1913) described a number of vocalizations emitted by male and female fowl and described them in relation to social behaviour. According to Konishi (1963) the most complete verbal description of the vocal repertoire was conducted by Baeumer (1962). Spectrograms illustrate the range and complexity of fowl vocalizations (Collias, 1952; Collias and Joos, 1953; Konishi, 1963). Collias (1987) attempted the first spectrographic analysis and classification of the complete repertoire in a species of fowl (*Gallus gallus*). However, Collias (1987) restricted his analysis to only chick and adult calls. Brückner (1933) pointed out that the structural and vocal traits of chicks continually change with age.

Vocal development has been extensively studied in songbirds (e.g. Nelson et al., 1997). In contrast, call development in non-songbird species has received less attention (Ballintijn and ten Cate, 1997). However, recent research has shown that in another non-songbird species, the collared dove (*Streptopelia decaocto*; Ballintijn and ten Cate, 1997), vocal changes gradually occur with age. These studies indicate that whether through social interactions (for review see Baptista and Gaunt, 1994) or through some innate mechanism (Konishi, 1963; Nottebohm and Nottebohm, 1971), changes do occur in the acoustic and structural properties of juvenile vocalizations as they age. The syrinx is the main vocal organ in birds (Brackenbury, 1982) and as such, changes in vocalizations are likely to be related to changes in

syringeal anatomy (Ballintijn and ten Cate, 1997). In addition, Podos (1996) has indicated that motor constraints also play a role in vocal performance in swamp sparrows. It is proposed here to redress the current research bias in favour of songbird species by regular recording of a vocalization of domestic chicks as they age to discover if and how their calls develop. Accordingly, the purpose of this paper is to describe changes in structure of the peep call of female domestic chicks as they age from hatching to ten weeks post-hatching.

METHOD

Subjects

Sixteen brown leghorn chicks from two batches of eggs were randomly placed in pairs and reared together from day three post-hatching. Chicks were incubator hatched from eggs produced by the same flock of hens. The first batch (Batch A) contained four chicks, (1 male and 3 females) and Batch B contained twelve chicks, (3 males and 9 females). No pen contained more than one male. Male chicks were eliminated from the statistical analysis because of the small sample size, thus 12 female chicks were used.

Procedure

The procedures used in this paper are the same as those described in Jennings and Kent (1996). In addition, at four weeks the infrared heat lamps were removed as the chicks had enough plumage to enable them to stay warm, and the batch B testing procedure was used with all chicks. During recording an observer was situated behind a wooden screen with a 5 cm x 26 cm slot which allowed observation of the chicks with minimal interference. A tape recorder, located on a table behind the observation screen, was operated by the observer.

Measures

Twelve chicks emitted the long peep (week 1 post-hatching) and two component peep (weeks 2-4 post-hatching), eleven chicks emitted the three component peep (weeks 4-6 post-hatching) and component under peep (weeks 6-10 post-hatching). The chicks' vocalizations were analyzed using Canary 1.1 with a filter bandwidth set at 352.94 Hz on a

Macintosh II vx. Data were collected by selecting an entire call, pressing the command key and clicking the mouse button. This transferred the data to the Canary data log. The parameters chosen for analysis were:

1. Duration (ms)
2. Maximum Frequency (kHz)
3. Minimum Frequency (kHz)
4. Difference between Max. and Min. Frequency (kHz)
5. Peak Frequency (kHz)
6. Peak frequency range (kHz)
7. Average Power (watts)
8. Energy (joules)
9. Peak Amplitude (volts)

Duration refers to the length of the call. Maximum frequency and minimum frequency refer to the highest and lowest points respectively as assessed by the call spectrogram. Calls were enlarged to the size of the monitor to ensure accuracy. Peak frequency refers to the frequency with the highest amplitude. Peak frequency range was computed as the peak frequency minus the minimum frequency; this parameter gives the distance (in kHz) between peak frequency and minimum frequency. Parameters [7-8] give details of energy use. Analysis of the nine acoustic parameters was completed using the Statistical Package for the Social Sciences version 6.1 for Windows (SPSS 6.1; Nie *et al.*, 1975). Three examples of each call type were randomly selected and then analysed.

Statistical Procedures

The data for each call type for each chick were averaged and analysed using analysis of variance (ANOVA). Post hoc comparisons were conducted using Duncan's multiple range test, which allows a sequential comparison of the four groups of peep calls (Ferguson and Takane, 1989). Due to software constraints it was not possible to capture highest frequencies of some of the peep calls, therefore, a nominal maximum frequency of 11.1 kHz was assigned for peep calls when the maximum frequency was not available. In order to assess the level of variation across parameters, a discriminant function analysis was computed on variables that provided significant results in ANOVA. Pearson product moment correlations were computed between calls of the same type in order to assess the level of call stability that each vocalization type exhibited. The possibility that individual variation in

the peeps of chicks increased as they aged was examined using Levene's test for homogeneity of variances.

RESULTS

A description of the four peep calls

Variations in the peep call were studied over 10 weeks post-hatching. Calls were identified first by an aural inspection of the cassette tapes and then by a visual inspection of the spectrograms. Similar methods of call selection have been used by Seyfarth, Cheney and Marler (1980) and Jennings and Kent (1996). Four different types of peep call (Figure 1) were included in the analysis. These calls were all recorded at different ages. The long peep was recorded in the first week post-hatching (Figure 1 (a)) and described in detail previously (Jennings and Kent, 1996). The long peep has a complex structure with a wide frequency range. There is an upper inversion located at the top of the descending limb of the peep at 5 kHz. The two component peep, recorded from weeks 2 to week 4 post-hatching (Figure 1 (b)), has a wide frequency range similar to the long peep. This call also has an upper inversion at the top of the descending limb located at about 4 kHz. There is a second component located above the fundamental at 8 kHz which runs parallel to the limb at 4 kHz. The three component peep, recorded on weeks 4 to 6 post-hatching (Figure 1 (c)), is similar in structure to the long peep and two component peep. This peep call displays three components within its structure: the first at 3 kHz, the second located at 6 kHz and the third at 8 kHz. This call displays the typical structure of a peep call, with all three components descending in frequency over the duration of the call. The component under peep was recorded on weeks 6 to 10 post-hatching (Figure 1 (d)) and has several component bands located in the call. This call does not display any structure at the top of the descending limb. The distinguishing feature is the presence of component structure below the main descending limb at 1 kHz. Figure 1 shows that as the chicks age the structure of the peep calls becomes increasingly more complex.

Changes in the structure of the peep call were associated with an increase in the age of the chicks. However, the parameters of maximum frequency, minimum frequency and difference between max. and min. frequencies showed little variation between the peep calls (Table 1). There is an increase in the range and standard deviation

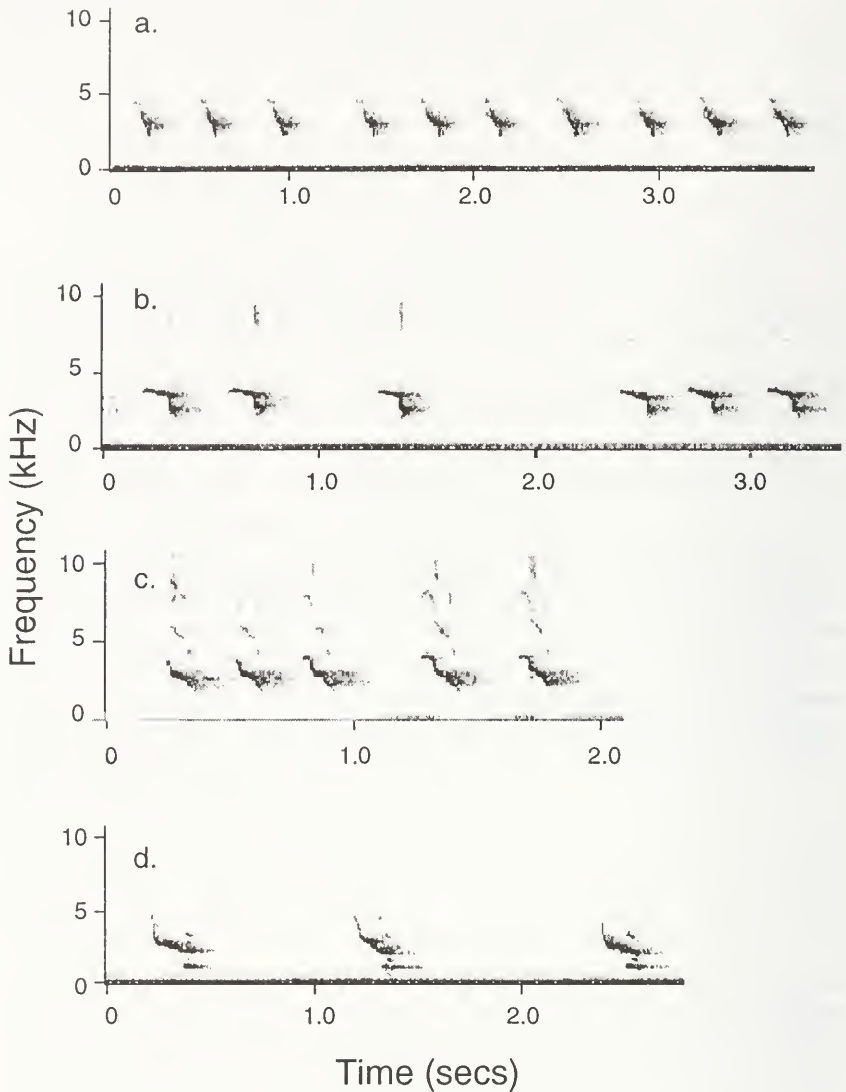


Figure 1. Spectrograms of the four call types analyzed: a, the long peep; b, two component peep; c, three component peep; and d, component under peep.

between the peep calls for these parameters. The mean of average power displays an increase from the long peep to the two component peep which then falls as the number of components increases. Standard deviation for the different parameters increases over call types, showing variation in calls as the chicks aged. The mean for energy and peak amplitude increases as the calls become structurally more complex;

there is also an increase in the standard deviations shown by calls over these two parameters. The mean for the parameter of peak frequency decreases as the chicks age and the standard deviation increases.

Table 1. Mean, range, standard deviation (S.D.) and coefficient of variation (C.V.) for the four calls at nine different parameters.

Parameters	Call Types	n	Mean	Range	S.D.	C.V.
Duration	Long Peep	12	329.8	112.7	36.8	11.16
	Two Component	12	331.7	105.7	29.4	08.86
	Three Component	11	361.9	226	66.1	18.27
	Component under	11	402.3	191	49.3	12.26
Max. frequency	Long Peep	12	11.1	0.1	0.039	0.35
	Two Component	12	11.0	1.15	0.331	3.00
	Three Component	11	10.7	3.067	0.934	8.73
	Component under	11	10.5	2.967	1.018	9.70
Min. frequency	Long Peep	12	1.525	2.033	0.787	51.61
	Two Component	12	1.181	2.167	0.860	72.82
	Three Component	11	1.627	1.000	0.321	19.73
	Component under	11	0.944	0.433	0.129	13.67
Diff. between max. and min. frequency	Long Peep	12	9.5	2.133	0.794	08.36
	Two Component	12	9.9	2.200	0.821	08.29
	Three Component	11	9.1	3.967	1.079	11.86
	Component under	11	9.5	3.167	1.047	11.02
Peak frequency	Long Peep	12	3.564	0.967	0.258	07.24
	Two Component	12	3.323	1.433	0.461	13.87
	Three Component	11	2.779	1.267	0.42	15.11
	Component under	11	2.448	1.833	0.506	20.67
Peak frequency range	Long Peep	12	2.042	3.0	0.861	42.17
	Two Component	12	1.944	4.0	0.996	51.24
	Three Component	11	1.056	2.8	0.640	60.61
	Component under	11	1.281	2.2	0.757	59.10
Average power	Long Peep	12	209.6	177.4	51.508	24.57
	Two Component	12	291.0	221.7	67.907	23.34
	Three Component	11	263.3	214.4	74.847	28.43
	Component under	11	223.9	258.8	85.55	36.58
Energy	Long Peep	12	29.5	28.53	8.034	27.23
	Two Component	12	37.3	29.47	7.616	20.42
	Three Component	11	47.2	63.87	16.196	34.31
	Component under	11	47.2	47.87	17.259	36.57
Peak amplitude	Long Peep	12	77.7	7.733	2.144	2.76
	Two Component	12	77.4	3.267	1.025	1.32
	Three Component	11	77.9	5.167	1.658	2.13
	Component under	11	78.7	6.600	2.045	2.60

A one way analysis of variance (ANOVA) on the nine parameters investigated differences between the calls. Significant differences between the four peep types were found for seven of the nine parameters (duration, min. frequency, peak frequency, peak frequency range, average power, energy and peak amplitude; Table 2).

Table 2. ANOVA for the nine parameters on four types of peep vocalization. Total Number of calls was 45 and the degrees of freedom were 3,42.

Parameters	Calls	
	F	P
Duration (ms)	5.9334	0.0018
Max. Frequency (kHz)	1.5801	NS
Min. Frequency (kHz)	3.3580	0.0275
Diff. btw max. and min. freq. (kHz)	1.1606	NS
Peak Frequency (kHz)	15.8153	0.0001
Peak frequency range (kHz)	3.7429	0.0180
Average Power (joules)	3.2490	0.0311
Energy (watts)	4.9582	0.0049
Peak Amplitude (volts)	13.1084	0.0001

Multiple comparisons using Duncan's method revealed significant differences between the component under peep and the other three types of peep call for the parameters of duration (ms) and peak amplitude (volts). Significant differences were found between the component under peep and the long peep, three component peep for minimum frequency (kHz). Significant differences were found between the long peep and the three component peep, component under peep for energy (watts). For average power (joules) a significant difference was found between the two component peep and the long peep, component under peep. Significant differences were also found between the long peep, the three component peep, component under peep; the two component peep and the three component peep, component under peep for the parameter of peak frequency (kHz; Table 3). A significant difference was found for the peak frequency range (kHz) between the three component peep and the long peep, two component peep.

A stepwise discriminant function analysis was conducted using the seven parameters that showed significant results in the ANOVA and post hoc multiple comparison procedures. This analysis was employed in order to assess the degree to which each acoustic parameter could be

Table 3. Multiple comparisons using Duncan's multiple range test. Comp., component; *, denotes significant differences between Call Type A and Call Type B at the .05 level; **, denotes differences at the .01 level.

Parameter	Call Type A	Mean Difference	Call Type B	Mean From
Duration (ms)	Long Peep	329.92**	Comp. Under Peep	402.27
	Two Comp. Peep	331.67**		
	Three Comp. Peep	362.00*		
Min. Frequency (kHz)	Long Peep	1.083*	Comp. Under Peep	0.367
	Three Comp. Peep	1.091*		
Peak Frequency (kHz)	Three Comp. Peep	2.778**	Long Peep	3.563
	Comp. Under Peep	2.449**		
	Three Comp. Peep	2.778*	Two Comp. Peep	3.233
Peak Frequency Range (kHz)	Long Peep	2.042*	Three Comp. Peep	1.152
	Two Comp. Peep	2.056*		
Average Power (joules)	Long Peep	209.17*	Two Comp. Peep	290.42
	Comp. Under Peep	223.46*		
Energy (watts)	Three Comp. Peep	46.818**	Long Peep	29.583
	Comp. Under Peep	46.909**		
Peak Amplitude (volts)	Long Peep	77.167**	Comp. Under Peep	81.727
	Two Comp. Peep	76.833**		
	Three Comp. Peep	77.455**		

used to discriminate between the four call types. Results of the analysis produced three significant functions which distinguished between the four call types. Of the seven variables entered, peak frequency and duration provided the largest correlation in the first discriminant function. Energy and average power provided the largest correlation with the second function. The remaining three parameters were entered into the third function (Table 4). Results from Table 4 indicate that peak frequency and duration are the most important discriminating variables, although all seven variables that were entered contributed significantly to discrimination.

The degree of similarity between the four call types was assessed visually using a scatter plot (Figure 2) of the first two discriminant functions (peak frequency; duration/average power; energy). This

Table 4. Stepwise discriminant analysis showing the three significant functions computed and related statistics. * indicates largest absolute correlation between each variable and each discriminant function.

Parameter	Function 1	Function 2	Function 3
Duration (ms)	-0.12875 *	0.4227	-0.03281
Min. Frequency (kHz)	0.10453	-0.04222	0.18046 *
Peak Frequency (kHz)	0.20709 *	0.4227	-0.03281
Peak frequency range (kHz)	0.0719	0.08462	0.38014 *
Average Power (joules)	0.01339	-0.23472 *	0.15587
Energy (watts)	-0.10456	-0.1331 *	-0.12752
Peak Amplitude (volts)	-0.1743	0.19121	0.21327 *
Eigenvalue	25.1101	3.7936	0.7639
% Variance	84.64	12.79	2.57
Canonical Correlation	0.9807	0.8896	0.6581
Wilks' Lambda (λ)	0.00453	0.11827	0.566939
χ^2	215.884	85.391	22.7
df	18	10	4
Significance	0	0	0.0001

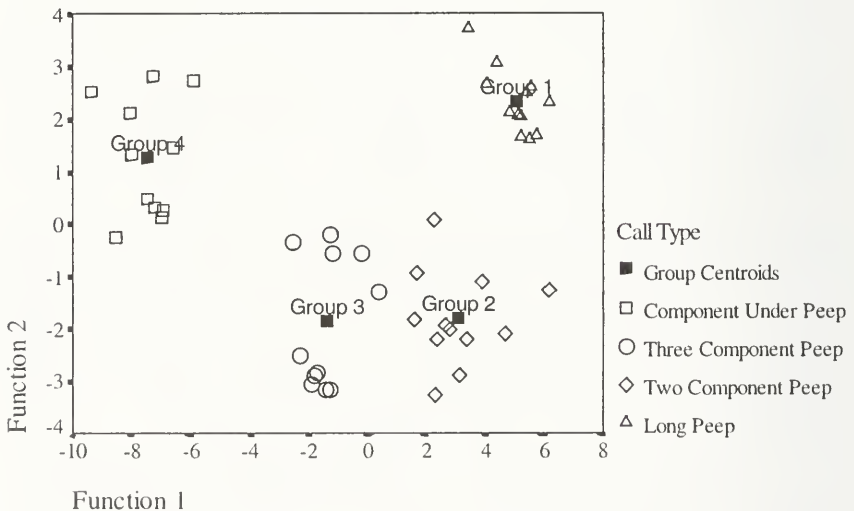


Figure 2. Scatterplot showing the separation of the four different types of peep call produced by the first two discriminant functions.

shows that each of the individual chicks clusters around each of the centroids for call type with no evidence of overlap among the four call types. In addition, the classification success of the three significant functions was 100%. This indicates that sufficient variation is exhibited by the call parameters included in the analysis to facilitate accurate prediction of call identity and to a lesser extent the individual identities of the chicks as they aged.

The stability of the Acoustic Parameters

The stability of the acoustic parameters was examined for the four call types using Pearson Product-moment correlations (r) (Table 5). For the long peep and two component peeps there are significant correlations between calls on all parameters at the .05 or .01 level. As the chicks aged calls became less stable as indicated by the lower correlations. The three component call shows significant correlations for eight of the nine parameters with one non-significant correlation for the parameter of energy. The component under peep shows two parameters with non-significant correlations (energy and low frequency). Furthermore, the correlations are increasingly showing .05 level significance.

Assessment of inter- and intra-individual variation in the four call types

The level of inter- and intra-individual variation exhibited by the calls was assessed over the nine acoustic parameters using Levene's test for homogeneity of variances. The results showed that there is considerable variation between the chicks for the four types of peep call (table 6). The call type that displays the highest variance between chicks (over parameters) is the component under peep followed by two component peep and the long peep. Intra-individual variance was also assessed using Levene's test. Results indicate that intra-individual variation in the call types is low with the exception of the component under peep which shows significant variance in five of the acoustic parameters (table 6).

Table 5. Pearson product moment correlations (r), three calls from each of the four call types were used in an examination of nine parameters.

Parameters	Call Type	n	r	P	r	P
Duration (ms)	Long Peep	12	.8258	.01	.8263	.01
	Two component	12	.8277	.01	.4906	.05
	Three component	11	.8375	.01	.7721	.01
	Component under	11	.5913	.05	.8733	.01
Maximum Frequency (kHz)	Long Peep	12	.6742	.05	.9393	.01
	Two component	12	.9978	.01	1.000	.01
	Three component	11	.6856	.05	.6768	.01
	Component under	11	.7246	.05	.9645	.01
Minimum Frequency (kHz)	Long Peep	12	.9927	.01	.9958	.01
	Two component	12	.9746	.01	.9803	.01
	Three component	11	.9219	.01	.9127	.01
	Component under	11	.1339	NS	.3062	NS
Diff btw max. and min. Freq. (kHz)	Long Peep	12	.9954	.01	.9946	.01
	Two component	12	.9886	.01	.9684	.01
	Three component	11	.7618	.01	.7126	.05
	Component under	11	.7421	.01	.9570	.01
Peak Frequency (kHz)	Long Peep	12	.9031	.01	.8949	.01
	Two component	12	.9978	.01	1.000	.01
	Three component	11	.8560	.01	.9563	.01
	Component under	11	.7008	.05	.9486	.01
Peak frequency range (kHz)	Long Peep	12	.9867	.01	.9858	.01
	Two component	12	.8084	.01	.7513	.01
	Three component	11	.8581	.01	.9311	.01
	Component under	11	.5956	.05	.8295	.01
Average Power (joules)	Long Peep	12	.9045	.01	.9348	.01
	Two component	12	.6682	.05	.7492	.01
	Three component	11	.7727	.01	.6535	.05
	Component under	11	.8357	.01	.7070	.05
Energy (watts)	Long Peep	12	.9128	.01	.9595	.01
	Two component	12	.7629	.01	.7035	.01
	Three component	11	.7872	.01	.5640	NS
	Component under	11	.5486	NS	.7559	.05
Peak Amplitude (volts)	Long Peep	12	.923	.01	.9408	.01
	Two component	12	.7300	.01	.8429	.01
	Three component	11	.8115	.01	.8408	.01
	Component under	11	.6914	.05	.7407	.05

Table 6: Levene's test for homogeneity of variances showing inter- and intra-individual variances for each acoustic parameter for each call type.

Call Type	Parameters	Inter-individual variances	Intra-individual variances
Long Peep	Duration	NS	NS
	Max. frequency	.0020	NS
	Min. frequency	.0350	NS
	Max. - Min. frequency	.0001	NS
	Peak frequency	.0001	NS
	Peak frequency range	.0030	NS
	Average Power	.0280	NS
	Energy	.0001	NS
	Peak Amplitude	.0030	NS
Two Component Peep	Duration	NS	NS
	Max. frequency	.0001	.016
	Min. frequency	.0001	NS
	Max. - Min. frequency	.0001	.021
	Peak frequency	.0001	NS
	Peak frequency range	.0001	NS
	Average Power	.0001	NS
	Energy	.0001	.019
Peak Amplitude	.0001	NS	
Three Component Peep	Duration	.0030	NS
	Max. frequency	.0001	NS
	Min. frequency	NS	NS
	Max. - Min. frequency	.0001	NS
	Peak frequency	.0001	NS
	Peak frequency range	.0001	NS
	Average Power	NS	NS
	Energy	NS	NS
Peak Amplitude	NS	NS	
Component Under Peep	Duration	.0001	.041
	Max. frequency	.0001	.041
	Min. frequency	.0001	.044
	Max. - Min. frequency	.0001	.041
	Peak frequency	.0001	NS
	Peak frequency range	.0001	NS
	Average Power	.0001	NS
	Energy	.0001	.04
Peak Amplitude	.0001	NS	

DISCUSSION

The stated purpose of this study was to investigate changes in the structure of the peep call as female domestic chicks aged. Our results confirm Brückner's (1933) claim that structural changes occur with the vocalizations of the chick over time. Furthermore, we have shown at what ages these variations in structure occur. The chick produces the long peep during week one post-hatching and the two component peep during weeks two to four post-hatching. The three component peep is emitted during weeks four to six post-hatching and the component under peep is emitted from weeks six to ten. After ten weeks the female chick ceases to emit the peep call (Jennings, 1996).

In addition to a verbal description and spectrographic presentation of the different forms of peep call, a parameter analysis was conducted. The calls presented above (Figure 1) all displayed descending frequencies yet have different structural qualities. Collias (1987) stated that there are certain basic acoustic parameters or elements in fowl vocalizations that can be combined to produce vocal signals. The descending limb of the peep is the basic element of this call. Acoustic variation can be accounted for by additional components and their interaction with the descending limb. These changes might be accounted for by changes in syringeal anatomy as the chick ages. We investigated four different types of peep call and compared them over nine different acoustic parameters.

Results show that as the chick ages the calls display lower frequencies (max. frequency, min. frequency and peak frequency; Figure 1 and Table 1). In addition, peak frequency also decreases with age. Coupled with a decrease in the frequencies employed in the peep calls, parameter analysis also showed an increase in energy and peak amplitude (Tables 1 and 3). This would enhance call propagation (Chappuis, 1971; Morton, 1975) by concentrating the amplitude of the signal in lower frequencies. Analysis of variance showed a significant difference between the four call types over seven of the parameters analysed (duration, minimum frequency, peak frequency, peak frequency range, average power, energy, peak amplitude). The parameters of maximum frequency and difference between maximum and minimum frequency show that the call types occupy similar frequency ranges.

Jennings and Kent (1996) presented three different types of peep call that were found to be highly stable forms of vocalizing. Figure 2 shows that individual calls scatter closely around the group centroid for

the long peep. From the second week post-hatching chicks scatter further from the group centroids for the respective call types (two component peep, three component peep and component under peep). Correlations of the calls presented in this study show that as the chicks aged the calls became less stable. Therefore, a decrease in call stability is associated with an increase in the age of the chicks. Inter- and intra-individual variation in the calls of adult fowl are widely recognised (Konishi, 1963; Collias, 1987, Kent, 1987, 1989). This study demonstrates that inter-individual variation is high over different types of peep call and that intra-individual variation is relatively low with the exception of the component under peep (table 6). Despite the increase in individual variation, different types of peep calls could be accurately assigned to the correct type of call based on the discriminant analysis of the parameters examined in this study (Figure 2).

By maintaining a wide frequency range and sharp intensity changes as a component of the calls, the hen and brood mates may be capable of making binaural comparisons of the frequencies (Gulick, 1971; Konishi, 1973). This could facilitate location of the chick by the hen or conspecifics as the broody period declines and independent behaviour becomes established (Workman and Andrew, 1989). As the female chicks aged the structure of the peep call became more complex with increased complexity of call structures. In addition, the acoustic parameters of the peep calls changed and calls could be statistically discriminated upon on the basis of these changes. There was an increase in energy and peak amplitude, a decrease in minimum and peak frequency and the maintenance of wide frequency ranges.

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REFERENCES

- Andrew, R.J. (1963). Effects of testosterone on the behavior of the domestic chick. *Journal of Comparative and Physiological Psychology*, 56, 933-940.
- Andrew, R.J. (1964). Vocalization in chicks, and the concept of "stimulus contrast".

Animal Behaviour, 12, 64-76.

- Baeumer, E. (1962). Lebensart des Haushuhns, dritter teil-über seine Laute und allgemeine Ergänzungen. *Zeitschrift für Tierpsychologie*, 19, 194-416.
- Ballintijn, M.R. & ten Cate, C. (1997). Vocal development and its differentiation in non-songbird: The collared dove (*Streptopelia decaocto*). *Behaviour*, 134, 595-621.
- Baptista, L.F. & Gaunt, S.L.L. (1994). Advances in the studies of avian sound communication. *The Condor*, 96, 817-830.
- Bermant, G. (1963). Intensity and rate of calling in chicks as a function of social contact. *Animal Behaviour*, 11, 514-517.
- Brackenbury, J.H. (1982). The structural basis of voice production. In D.E. Kroodsmas & E.H. Miller (Eds.), *Acoustic Communication in Birds. Vol. 1. Production, Perception and Design Features of Sounds* (pp. 53-73). New York: Academic Press.
- Brown, C.P. (1979). Peeping and attachment to visual and auditory stimuli in day old chicks. *Behavioral Processes*, 4, 15-21.
- Brückner, G.H. (1933). Untersuchungen zur Tiersoziologie, insbesondere zur Auflösung der Familie. *Zeitschrift für Psychologie*, 128, 1-105.
- Chappuis, C. (1971). Un exemple de l'influence du milieu sur les émissions vocales des oiseaux: L'évolution des chants en forêt équatoriale. *Terre et Vie*, 118, 183-202.
- Collias, N.E. & Joos, M. (1953). The spectrographic analysis of sound signals of the domestic fowl. *Behaviour*, 5, 175-188.
- Collias, N.E. (1952). The development of social behavior in birds. *Auk*, 69, 127-159.
- Collias, N.E. (1987). The vocal repertoire of the red junglefowl: A spectrographic classification and the code of communication. *The Condor*, 89, 510-524.
- Ferguson, G.A. & Takane, Y. (1989). *Statistical Analysis in Psychology and Education* (6th Ed.). New York: McGraw-Hill.
- Gottlieb, G. & Vanderbergh, J.G. (1968). Ontogeny of vocalisation in duck and chick embryos. *Journal of Experimental Zoology*, 168, 307-326.
- Greenlees, B. (1993). *Effects of enriching the acoustic environment during incubation on hatching and post-hatch chick responses*. Unpublished M.Sc. Thesis. University of Guelph.
- Gulick, W.L. (1971). *Hearing: Physiology and Psychophysics*. New York: John Wiley & Sons.
- Guyomarc'h, J.-C. (1962). Contribution à l'étude du comportement vocal du poussin de "Gallus domesticus". *Journal de Psychologie Normale de Pathologique*, 3, 283-306.
- Guyomarc'h, J.-C. (1974). L'empreinte auditive prenatale chez le poussin domestique. *Revue de Comportement Animal*, 8, 3-6.
- Jennings, D.J. & Kent, J.P. (1996). Variations in the structure of the peep vocalization of female domestic chicks (*Gallus gallus domesticus*) on days five and six post-hatching. *International Journal of Comparative Psychology*, 9, 11-25.
- Jennings, D.J. (1996). *On the development of the vocal repertoire of the domestic fowl (Gallus gallus domesticus): From hatching to week 18 of life*. Unpublished M.A. Thesis. National University of Ireland.
- Kaufman, I.C. & Hinde, R.A. (1961). Factors influencing distress calling in chicks, with special reference to temperature changes during social isolation. *Animal Behaviour*, 9, 197-204.
- Kent, J.P. (1987). Experiments on the relationship between the hen and chick (*Gallus*

- gallus*): The role of the auditory mode in recognition and the effects of maternal separation. *Behaviour*, 102, 1-14.
- Kent, J.P. (1989). On the acoustic basis of recognition of the mother hen by the domestic fowl (*Gallus gallus*). *Behaviour*, 108, 1-9.
- Konishi, M. (1963). The role of auditory feed-back in the vocal behaviour of the domestic fowl. *Zeitschrift für Tierpsychologie*, 20, 349-367.
- Konishi, M. (1973). Locatable and nonlocatable acoustic signals for barn owls. *American Naturalist*, 107, 775-785.
- Montevicchi, W.A., Gallup, G.G. & Dunlap, W.P. (1973). The peep vocalization in group reared chicks (*Gallus domesticus*): its relation to fear. *Animal Behaviour*, 21, 116-123.
- Morton, E.S. (1975). Ecological sources of selection on avian sounds. *American Naturalist*, 109, 17-34.
- Nelson, D.A., Marler, P., Soha, J.A. & Fullerton, A.L. (1997). The timing of song memorization differs in males and females: A new assay for avian vocal learning. *Animal Behaviour*, 54, 587-597.
- Nie, N.H., Hull, C. H., Jenkins, J.G., Steinbrenner, K. & Bent, D.H. (1975). *SPSS: Statistical Package for the Social Sciences* (2nd Ed.). New York: McGraw Hill.
- Nottebohm, F. & Nottebohm, M.E. (1971). Vocalizations and breeding behaviour of surgically deafened ring doves (*Streptopelia risoria*). *Animal Behaviour*, 19, 313-327.
- Podos, J. (1996). Motor constraints on vocal development in a songbird. *Animal Behaviour*, 51, 1061-1070.
- Schjelderup-Ebbe, T. (1913). Honsenes stemme. Bidrag til honsenes psykologi. *Naturen*, 37, 262-276.
- Seyfarth, R.M., Cheney, D.L. & Marler, P. (1980). Vervet monkey alarm calls: Semantic communication in a free-ranging primate. *Animal Behaviour*, 28, 1070-1094.
- Tuculescu, R.A. & Griswold, J.G. (1983). Prehatching interactions in domestic chicks. *Animal Behaviour*, 31, 1-10.
- Wood-Gush, D.G.M. (1971). *The Behaviour of the Domestic Fowl*. London: Heinemann.
- Workman, L. & Andrew, R.J. (1989). Simultaneous changes in behaviour and in lateralization during the development of male and female domestic chicks. *Animal Behaviour*, 38, 596-605.