丹顶鹤性活动的声行为研究

李淑玲[1,2]，包 军[2]，王文峰[3]，白晓杰[3]，崔卫国[2]

(1. 东北林业大学，哈尔滨 150080；2. 东北农业大学，哈尔滨 150030；3. 齐齐哈尔市龙沙公园，齐齐哈尔 16100)

摘要：丹顶鹤繁殖期的性活动可分为雄鹤求偶、雌鹤对雄性求偶的应答、两性交配和交配完结 4 个阶段，其相应的鸣声模式分别为雄性的求偶鸣声、雌性对雄性求偶的应答声和两性的对鸣声、两性对唱的交配声和两性的高声合唱。4 个阶段鸣声都是以基本音的主频率(PF)为主音的单音调声，前 3 个阶段都带数个近似 $f_n = nf_0(f_0 = FP)$ 关系的低幅值谐频成分，第 4 个阶段带数个近似 $f_n = nf_0(f_0 = FP)$ 关系的高幅值谐频成分；品质因数(Q_{3dB})多半为 4～6，声脉冲重复频率(RFP)一般为 150～180Hz，而第 2 阶段声的 RFP 一般为 180～260Hz。雄性鸣声的每个单次叫声中含有的音节数较少，一般不超过 4 个；而雌性鸣声比较复杂，每个单次叫声中含有的音节数较多，一般都在 7～8 个以上；但雌雄鸣声的每个音节都是由 3 个声脉冲组成。雄鹤鸣唱声频率变化范围较小，而雌鹤鸣唱声频率变化形式是由低到高达到高峰后又开始下降。4 个阶段的鸣声都具有较好共鸣。只有第 2 阶段发声运动较快。而且发现雄鹤鸣唱单次鸣叫声的音节数“增多”。各阶段鸣声特性均存在差异，不同配偶间均存在显著差异，研究结果表明丹顶鹤雌雄都具有不同的鸣声，且其性活动过程中不同的鸣声行为具有较高的个体识别信号潜能。另外，求偶鸣叫声和求偶应答与对鸣声在性活动鸣声中起着决定性的作用。

关键词：丹顶鹤；性活动；声行为

Researches on vocal behaviour of red-crowned crane in sexual activities

LI Shu-Ling[1,2], BAO Jun[2], WANG Wen-Feng[3], BAI Xiao-Jie[3], CHUI Wei-Guo[2] (1. *Northeast Forestry University*, *Harbin* 150080; 2. *Northeast Agricultural University*, *Harbin* 150030; 3. *Qiqihar Longsha Garden*, *Qiqihar* 16100). ***Acta Ecologica Sinica*, 2004, 24(3): 503～509.**

Abstract: In breeding season, sexual behavioral activities of red-crowned crane can be divided into four stages: male courtship, response to male by female, mating and post- mating. The corresponding vocal models by both sexes were the courtship song of male, responding song of female to its spouse with antiphonal song of both sexes, mating antiphonal songs of both sexes, and loud-antiphony songs of both sexes after mating. This experiment was conducted in Zalong Protect Zone, Qiqihar and continuous observation was adopted. There were 16 hours from early morning to evening on each observation everyday. Breeding behavior and songs were recorded for three pairs of red-crowned crane which had representational character, using the method of direct observation and video recording. The recording was processed by MATLB analytic software that was offered from biophysics research institute of China Academy of Science and the outcomes were given in sonogram, oscillogram and frequency spectrum of songs of four stages of the surveyed cranes and their frequency domain, time domain, and intensity properties. The data obtained were processed completely by SAS software. (Ver 6.12 for Windows, Statistical Analysis Institute, 1996), the mean process was used to compute the mean and standard difference. ANOVA course was taken for difference analysis and Multiple comparison was made for different levels of the acoustic properties. The songs of these four stages are single tonal ones, of which it principal tone was characterized as the principal frequency of basic sound. The first

基金项目：黑龙江省自然科学基金资助项目(C_{00-35})

收稿日期：2003-06-16；**修订日期**：2003-10-26

作者简介：李淑玲(1965～)，女，黑龙江省哈尔滨市人，博士，高级工程师，主要从事动物的营养饲料与行为生态。E-mail：hljshulingli@163.com

* **通讯作者** Author for correspondence, E-mail：jbao@mail.neau.edu.cn

致谢：本文得到中国科学院生物物理研究所蒋锦昌研究员的指导和帮助，在此给以最诚挚的谢意。

Foundation item: Heilongjiang Provincial Natural Sciences Foundation(No. C_{00-35})

Received date: 2003-06-16; **Accepted date**: 2003-10-26

Biography: LI Shu-Ling, Ph. D., Senior engineer, mainly engaged in the nutritional forage science and behavioral ecology of animals. E-mail: hljshulingli@163.com

three stages contained many harmonic frequencies with lower amplitude having approximate relation of $f_n=nf_0$, the fourth one contained many harmonic frequencies with higher amplitude having approximate relation of $f_n=nf_0$. Most quality factors were 4～6, repetition frequency of pulses was generally 150～180Hz, but it was 180～260Hz in the second stage. Acoustic properties of male songs were that there were less syllables in every single call and normally no more than four syllables. However, the songs of female were relatively complicated, acoustic properties of which were that there were many syllables in each single call and usually had 7～8 syllables, where each syllable was consisted of three pulses. The sound frequency of male singing had smaller extent variation, and that of female singing was changed from low to high and then to decrease. Songs of the four stages had better resonance. Only in second stag, the vocal frequency was faster, the others were slower. And it was discovered that the syllables of every single call in male singing were increased, it may be because of that the song was mixed with female's, on the other hand, it may be because of the song extending, this needs further research. The acoustic properties at different stages were the different and the marked difference was also found between the different spouses. The results of this study indicated that there were different vocal songs between males and females of red-crowned cranes and different vocal behaviors have specific latent energy in individual discrimination. In addition, the courtship song of male and responding song of female to its spouse with antiphonal song of both sexes play a decisive function in the sexual activities of red-crowned cranes.

Key words: red-crowned crane; sexual activities; vocal behavior

文章编号:1000-0933(2004)03-0503-07 **中图分类号**:Q958 **文献标识码**:A

鸟类的鸣声是种群内个体之间相互沟通信息的"语言",是与鸟类的集群、取食、领域、求偶、育雏、报警等活动有关的声通讯行为[1,2]。通过对鸟鸣声的研究,可以了解鸣声与行为的关系及不同鸣声的生物学意义。鸟类性活动又是鸟类繁殖的重要内容,它是指达到性成熟年龄的鸟类个体之间在繁殖季节为达到交配而繁衍后代的目的所进行的一系列活动。它所研究的内容主要包括性选择(sexual selection 即雄性的求偶与雌性的择偶)与婚配制度或交配体制(mating system)。国外在鸟类性活动与鸣声通讯方面已有较多的研究,如 Eens M 等人[3]与 Mountjoy D J[4]对欧洲椋鸟雄性鸣声和性选择与交配选择的研究,Searey W A[5]对鸟类鸣声曲目和交配选择的研究,Thierry L 等人[6]利用帝王企鹅声通讯研究了繁殖期企鹅在群体中的位置和接听鸟的体况的重要性,Concha M 等[7]对环颈雉雄性统治地位和求偶炫耀对雌性选择的影响研究,以及 Darid J W 等人[8]对未成熟雄性燕八哥(*Molothrus ater*)的求偶和通讯机能演变的研究。国内该领域的研究有李佩 等[9]对繁殖期黄喉 领域鸣声及其种内个体识别,蒋锦昌等[10]对虎皮鹦鹉声行为的研究以及姜仕仁等[11,12]分别对白头鹎繁殖期的声行为和短翅树莺鸣声进行了计算机声谱分析等大量工作,但目前这些对鸟声的研究大多还仅限于小型鸟类,而丹顶鹤(*Grus japonensis*)鸣声特征方面的研究仅见于张玲[13]对人工饲养条件下的丹顶鹤鸣声进行了初步分析。本文针对繁殖期内的丹顶鹤与性活动有关的鸣声行为进行了多参数定量分析,来探索丹顶鹤性活动鸣声行为特征及其生物学意义,为丹顶鹤鸣声的系统研究提供了基础数据。同时为我国鸟类声学的研究增添了新资料。

1 实验和分析方法

1.1 实验动物与饲养环境

本研究所采用的实验动物为齐齐哈尔市龙沙公园所饲养的健康成年丹顶鹤。此实验动物共分 3 组(3 对),分别记为 1 号鹤(RC-1)、2 号鹤(RC-2)和 3 号鹤(RC-3)。其中 RC-1 的雄鹤 1998 年丧偶,1999 年人为给它配一只成年雌鹤并单独笼养,当年未发情。2000 年,这两只鹤有发情鸣叫、对舞、交配行为,产下 1 枚卵,但未受精。2001 年,该对鹤发情表现明显,交配正常并产下 2 枚卵。RC-2 是经过自由选择配对的已有多年繁殖史的优秀繁殖种鹤。RC-3 是 2001 年经自由选择配对的新鹤。实验时间为 2001-03-24～06-30;2002-03-24～06-30。3 对鹤分别饲养在 3 个并排的笼舍内,每个笼舍内设砖砌的避风舍,面积为 3m×1.5m,运动场是由 5m×3m ×2m 的铁丝网围成的封闭式笼舍,内部并设有供夏季炎热天气洗浴用的水池,地面是沙土地。

1.2 观察方法

本实验通过从清晨到傍晚,每天 16h 的全天候直接观察和摄像机重点跟踪录制法对繁殖行为及鸣声进行记录。所使用的摄像机是日本松下公司出品的 Panasonic NV-VX22EN 型摄像机。

1.3 分析方法

将摄像机上的声信号输入计算机,通过 MATLAB 分析软件(中国科学院生物物理研究所提供)处理,给出观察动物各类鸣声的声图、示波图和功率谱,据此可得到各个鸣声的频域、时域 和强度特性。所取的数据全部采用 SAS 软件包(Ver 6.12 for Windows, Statistical Analysis Institute, 1996)进行处理,平均过程计算平均数及标准差,ANOVA 过程进行数据的方差分析及均数的多重比较。

2　结果

2.1　性活动的声行为模式

在繁殖期内,丹顶鹤的性活动可分为 4 个阶段,依次是:雄鹤求偶期(courtship phase, CP),即雄鹤在雌鹤面前点头炫耀、叨草跳跃、跳跃飞舞的挑斗行为期;雌鹤对雄鹤求偶的应答期(answered spouse phase, ASP),即雌鹤在雄鹤的挑斗下与之共舞的和谐行为期;两性交配期(mating phase, MP),即从雄鹤跳跃雌鹤背上到两性泄殖腔对接,雄鹤尾部振动射精后跳下的行为期;交配完结期(finishing phase, FP),雄鹤跳下后,两性进行高声对唱和对舞的行为期。相应的鸣声模式分别为雄性的求偶鸣声、雌性择偶的应答声和两性的对鸣声、两性对唱的交配声和两性的高声合唱。

求偶期(CP)雄性求偶鸣声,是继求偶炫耀之后而昂头挺胸,跟随雌鹤发出"嘎! 嘎!! 嘎!!! ……"逐渐升高的单音节连续鸣叫声。其声学模式[14](图 1)为 2 个单次叫声(SS_1 和 SS_2),每个单次叫声都含有 3 个音节(S_1～S_3),并含 7 个频带(FB_1～FB_7),每个音节展开后可见由 3 个声脉冲(P_1～P_3)组成。图 C 中,只显示 1 个频带(FB_1),声图中其它 6 个频带(FB_2～FB_7)的能量很小,而无显示。

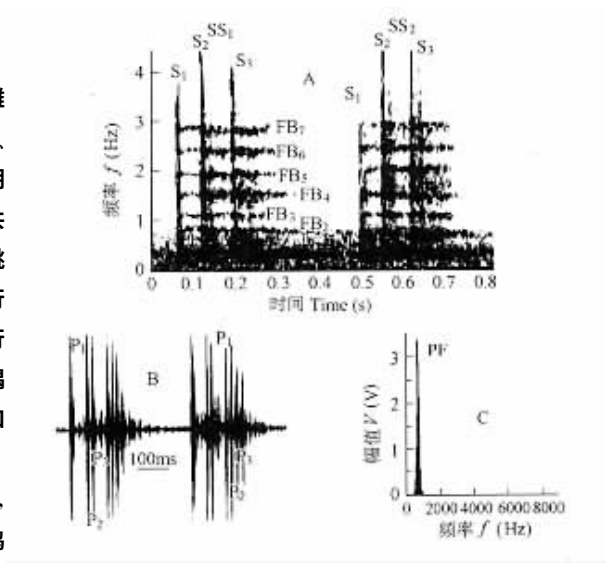

图 1　RC-2 雄鹤求偶鸣声

Fig. 1　Courtship song of male in RC-2

A 和 B　声图和示波图 Sonogram and oscillogram;1～7,频带 FB_1～FB_7;SS_1、SS_2,单次叫声 Single calling song;S_1～S_3,音节 Syllable;C 频谱 Frequency spectrum;*PF*,主频率 Principal frequency

雌鹤对雄鹤求偶的应答期(ASP)中,雌鹤对雄鹤求偶的应答声和两性对鸣声,是雌鹤随着雄鹤求偶鸣叫而发出"咕噜…咕噜…咕噜…"的多音节应答鸣声和两性对鸣声。其声学模式(图 2)为 2 个单次叫声(SS_1 和 SS_2);第 1 个单次叫声中含有 15 个音节(S_1～S_{15}),前 3 个音节(S_1～S_3)和后 3 个音节(S_{13}～S_{15})为雄鹤鸣叫声,中间 9 个音节(S_4～S_{12})为雌鹤叫声;第 2 个单次叫声共含有 22 个音节(S_1～S_{22}),前 3 个音节(S_1～S_3)为雄鹤鸣叫

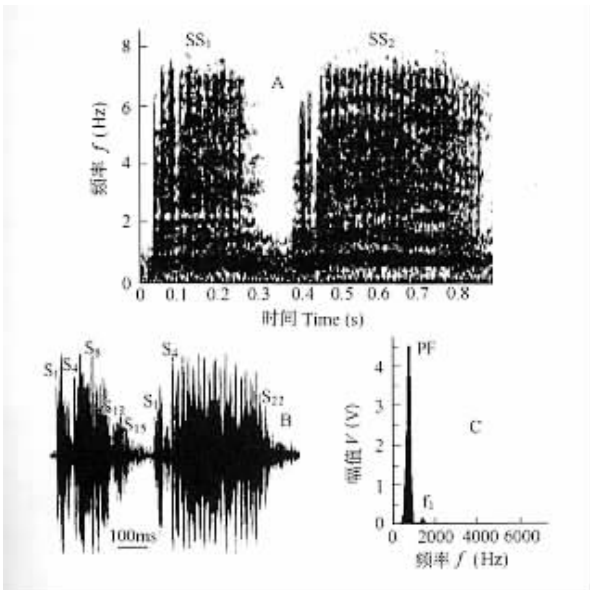

图 2　RC-1 雌鹤对雄鹤求偶的应答声和两性对鸣声

Fig. 2　Antiphonal song of both sexes in female answered spouses for RC-1

A 和 B　声图和示波图 Sonogram and oscillogram;SS_1、SS_2,单次叫声 Single calling song; S_1～S_{15},音节 Syllable;C 频谱 Frequency spectrum;*PF*,主频率 Principal frequency;f_1,次峰频率 Sub-peak frequency

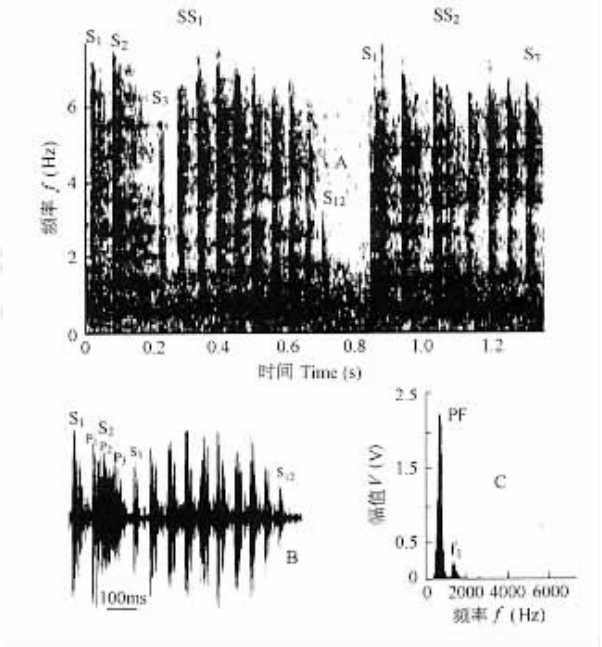

图 3　RC-1 两性交配的对鸣声

Fig. 3　Antiphonal song of both sexes mating in RC-1

A 和 B 声图和示波图 Sonogram and oscillogram;SS_1～SS_3,单次叫声 Single calling song; S_1～S_{18},音节 Syllable;C 频谱 Frequency spectrum;*PF*,主频率 Principal frequency;f_1,次峰频率 Sub-peak frequency

声，后 19 个音节(S_4～S_{22})为雌鹤鸣叫声，每个音节展开后可见由 3 个声脉冲(P_1～P_3)组成。

交配期(MP)中，雌雄交配对鸣声，是两性交配时发出的似哨声的两性对鸣声。其声学模式(图 3)为 2 个单次叫声(SS_1 和 SS_2)，第 1 个单次叫声中前 3 个音节(S_1～S_3)为雄鹤鸣声，第 4 音节至第 12 音节(S_4～S_{12})为雌鹤鸣叫声中的音节；第 2 个单次叫声中第 3 个音节为雌雄鸣声融合的音节，其前两个音节为雄鹤鸣声，其后面的音节为雌鹤鸣声，每个音节展开后可见由 3 个声脉冲(P_1～P_3)组成；其频谱(时域为 0.8 秒)中是以主频率为主，只带一个次峰频率。

交配完结期(FP)中，雌雄鹤对鸣高唱声，是指交配完成后，雄鹤挺胸抬头仰对天空高唱，同时雌鹤则挺胸目视前方与之对鸣形成的具有情歌韵味的鸣唱声。其行为模式(图 4)为 1 个单次叫声，雌雄鹤鸣叫声交叉在一起，形成许多个谐频，很难从中分辨出雄鹤鸣唱声单次叫声的音节数；其频谱(时域为 1.6s)中显示 1 个主频率和 5 个较高能量的次峰频率。

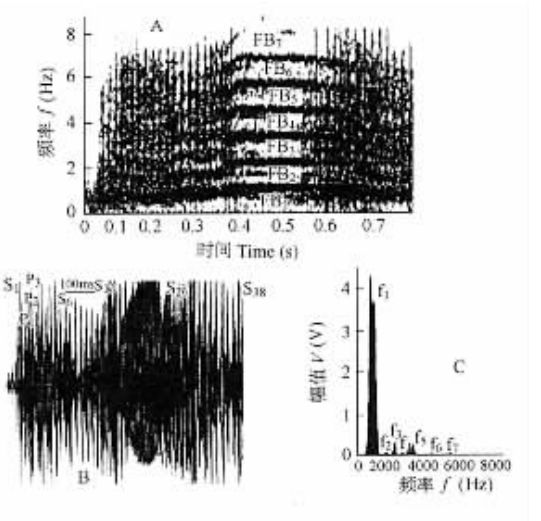

图 4 RC-1 交配后两性高声对唱鸣声

Fig. 4 Loud-antiphony song of both sexes after mating in RC-1

A 声图 sonogram; B 示波图 oscillogram; C 频谱 frequency spectrum; PF，主频率 principal frequency; f_1～f_5，次峰频率 sub-peak frequency

2.2 性活动鸣声的特性

由性活动 4 个阶段鸣声的声图、示波图和频谱，可给出相应的声学特性，主频率(PF)、次峰频率(f_n)、f_n 的相对幅值[RA_n (dB)=20log(V_n/V_0)，V_n 和 V_0 为频谱中 f_n 和 PF 的电压幅值]、品质因数[$Q_{3dB}=PF/PF$ 下降 $3dB$ 的带宽]和声脉冲重复频率(RFP)[14,15]，见表 1 和表 2。

表 1 雄鹤求偶鸣声、雌鹤对雄鹤求偶的应答声与两性对鸣声的声学特性

Table 1 Acoustic properties of courtship song of male, antiphonal song of both sexes in female answered spouses

	实验动物 E. A	观察日期 O. D	主频率 PF(Hz)	次峰频率 f_1～f_4(Hz)	重复频率 RFP(Hz)	相对幅值 $(RA_1$-$RA_4)/dB$	品质因数 Q_{3dB}
雄鹤求偶鸣声 Courtship song of male	RC-1	04-06	621	1186/1560	175	−19.9/−19.9	3.7
		04-08	615	1397/2010	175	−14.4/−17.9	3.5
		04-15	620		148		6.9
		04-16	615		169		3.7
		04-19	621	1158	175	−21.4	5.9
		04-21	680	1300	169	−12.4	6.8
	RC-2	04-09	680	1130/1420	169	−18.8/−16.3	5.0
		04-10	680	1470	168	−17.6	5.4
		04-11	680		169		6.0
		04-15	690		169		6.9
		04-17	615	1070/1400	135	−18.2/−13.0	3.9
		04-22	690	1450/2230/2960/3680	237	−15.0/−34.6/−28.0/−34.0	5.1
	RC-3	04-10	630	1290/1900/2520	169	−28.8/−38.3/−34.8	4.8
		04-14	780	1400	169	−18.5	8.6
		04-22	870	1450	169	−38.9	5.2
		04-24	620	1330/2550	153	−28.5/−34.8	3.9
		04-27	880	1390	225	−19.4	9.9
		04-28	610	1310/2570	169	−28.8/−3.6	3.8
雌鹤对雄鹤求偶的应答声与两性对鸣声 Autiphonal song of both sexes in femal answered spouses	RC-1	04-06	782	1400	263	−28.1	4.7
		04-08	718	1380	296	−34.6	4.3
		04-15	700	1400	263	−27.1	6.2
		04-16	690	1410	239	−14.2	4.4
		04-19	780	1420	225	−31.5	8.6
		04-21	680	1300	225	−12.4	6.7
	RC-2	04-09	715	1540/2240/3000	296	−30.3/−38.2/−34.7	3.4
		04-10	715	1470/2210/3020	225	−22.0/−22.0/−19.5	6.4
		04-11	780	1280/1560/1880	238	−28.6/−30.6/−34.6	3.7
		04-15	690		169		6.9
		04-17	615	1070/1400	135	−18.2/−13.0	3.9
		04-22	690	1450/2230/2960/3680	237	−15.0/−34.6/−28.0/−34.0	5.1
	RC-3	04-10	860	1400/1900/2520	159	−21.6/−20.5/−40.7	5.1
		04-14	780	1480	178	−38.2	3.6
		04-22	870	1450	168	−38.9	5.2
		04-24	840	1400/1660	176	−43.0/−43.0	5.4
		04-27	780	1470	176	−39.1	5.3
		04-28	850	1470	176	−41.1	5.4

表 2　雌雄交配对鸣声和交配完后两性高声对唱鸣声的声学特性

Table 1　Acoustic properties of antiphonal song of both sexes mating and loud-antiphony song of both sexes after mating

	实验动物 E. A	观察日期 O. D	主频率 PF(Hz)	次峰频率 $f_1\sim f_4$(Hz)	重复频率 RFP(Hz)	相对幅值 $RA_1\sim RA_4$(dB)	品质因数 Q_{3dB}
雌鹤交配对鸣声 Autiphonal song of both sexes mating	RC-1	04-06	780	1186/1560	175	−19.9/−19.9	3.7
		04-08	623	1397/2010	175	−14.4/−17.9	3.5
		04-15	690		148		6.9
		04-16	625		169		3.7
		04-19	670	1158	175	−21.4	5.9
		04-21	690	1300	169	−12.4	6.8
	RC-2	04-09	682	1130/1420	169	−18.8/−16.3	5.0
		04-10	773	1470	168	−17.6	5.4
		04-11	680		169		6.0
		04-15	780		169		6.9
		04-17	780	1070/1400	135	−18.2/−13.0	3.9
		04-22	784	1450/2230/2960/3680	237	−15.0/−34.6/−28.0/−34.0	5.1
	RC-3	04-10	686	1370	177	−37.4	8.6
		04-14	706	1120	169	−21.8	7.8
		04-22	727	1250/1510/2220	159	−23.1/−24.9/−35.7	4.3
		04-24	690	1380	175	−37.4	4.3
		04-27	680	1120	169	−21.8	8.6
		04-28	710	1220/1440/2150	187	−23.3/−24.7/−36.4	8.7
交配后两性高声对唱鸣声 Loud-antiphong song of both sexes after mating	RC-1	04-06	780	1186/1560	175	−19.9/−19.9	3.7
		04-08	623	1397/2010	175	−14.4/−17.9	3.5
		04-15	690		148		6.9
		04-16	625		169		3.7
		04-19	670	1158	175	−21.4	5.9
		04-21	690	1300	169	−12.4	6.8
	RC-2	04-09	682	1130/1420	169	−18.8/−16.3	5.0
		04-10	773	1470	168	−17.6	5.4
		04-11	680		169		6.0
		04-15	780		169		6.9
		04-17	780	1070/1400	135	−18.2/−1	3.9
		04-22	784	1450/2230/2960/3680	237	−15.0/−34.6/−28.0/−34.0	5.1
	RC-3	04-10	686	1370	177	−37.4	8.6
		04-14	706	1120	169	−21.8	7.8
		04-22	727	1250/1510/2220	159	−23.1/−24.9/−35.7	4.3
		04-24	690	1380	175	−37.4	4.3
		04-27	680	1120	169	−21.8	8.6
		04-28	710	1220/1440/2150	187	−23.3/−24.7/−36.4	8.7

4 个阶段鸣声都是以基本音的主频率(PF)为主音的单音调声,前 3 个阶段都带数个近似 $f_n=nf_0$ 关系的低幅值谐频成分,第 4 个阶段带数个近似 $f_n=nf_0$ 关系的高幅值谐频成分;品质因数(Q_{3dB})多半为 4～6,声脉冲重复频率(RFP)一般为 150～180Hz,而第二阶段声脉冲重复频率(RFP)一般为 180～260Hz。

2.3　性活动中鸣声的统计特性

由表 1 和 2,可得到性活动不同阶段鸣声的统计特性,分别见表 3、4 和 5。

主频率中,RC-1 第 1、2 阶段除与第 3 阶段差异不显著外,与其它阶段间差异均显著;RC-2 只有第 1、2 阶段和第 2、3 阶段间不存在显著差异;RC-3 第 1 阶段除与第 3 阶段不存在显著差异,与其它阶段均存在显著差异。

RC-1 与 RC-2 的主频率在第 3 阶段,次峰频率在第 2 阶段差异显著;RC-1 与 RC-3 的主频率在第 2 阶段差异显著;RC-2 与 RC-3 的主频率在第 2 阶段,次峰频率在第 3 阶段差异显著;声脉冲重复频率:RC-1 与 RC-3 和 RC-2 与 RC-3 在第 2、3 和 4 阶段都存在显著差异。

3　讨论

雌雄鹤鸣叫时,通过人耳是无法分辨其鸣声的特点与区别,但通过鸣声图及其声学特性可知,雌雄鹤鸣声有明显的不同,即雄性鸣叫发出的声音比较单一,鸣声特性是每个单次叫声中含有的音节数较少,一般不超过 4 个;而雌性鸣叫发出的声音比较复杂,鸣声特性是每个单次叫声中含有的音节数较多,一般都在 7～8 个以上,多者达 11～19 个。因此,在两性对鸣高唱声中可以清晰地分辨出雄鹤鸣唱声频率变化幅度较小,而雌鹤鸣唱声频率变化规律是由小到大达到高峰后又开始下降。通过对鸣唱声频率变化分析可对鹤的性别进行鉴定。

雌雄鸣声的共同特性是每个音节都是由 3 个声脉冲组成,这与声脉冲具有种的特异性是相一致的[15]。4 个阶段的鸣声都具有较好共鸣,所以听起来较为好听。只有第 2 阶段发声运动较快,其它阶段发声运动都比较缓慢。而且发现雄鹤鸣唱单次鸣叫声

的音节数“增多”,一方面是因为与雌鹤鸣唱声融合所至,另一方面是由于声音持续时间延长所至,在这方面还没有准确的依据可寻,因而暂时无法定论,有待于进一步研究探讨。

表 3 不同阶段内 RC-1～RC-3 鸣声的主频率、重复频率、品质因数、次峰频率和相对幅值的统计结果

Table 3 Statistical results of principal frequency (PF), repetition frequency (RFP), quality factor (Q_{3dB}), sub-peak frequencies ($f_{1\text{-}2}$) and relative amplitudes ($RA_{1\text{-}2}$) of songs of RC-1～RC-3 in different stage

实验动物	求偶活动	主频率	重复频率	品质因数	次峰频率		相对幅值	
E. A	C. A	PF(Hz)	RFP(Hz)	Q_{3dB}	f_1(Hz)	f_2(Hz)	RA_1 dB	RA_2 dB
RC-1	CP	$629^{c}\pm25$	$169^{b}\pm11$	$5.1^{b}\pm1.6$	$1260^{a}\pm110$	$1785^{a}\pm318$	$-17.0^{a}\pm4.3$	$-17.15^{a}\pm3.9$
	ASP	$725^{b}\pm45$	$252^{a}\pm28$	$5.8^{b}\pm1.7$	$1385^{a}\pm44$		$-24.7^{ab}\pm9.2$	
	MP	$680^{bc}\pm57$	$86^{c}\pm25$	$5.3^{a}\pm0.7$	$1360^{a}\pm70$	$1733^{a}\pm92$	$-30.9^{b}\pm8.2$	$-37.1^{b}\pm7.9$
	FP	$987^{a}\pm95$	$89^{c}\pm9$	$4.3^{ab}\pm2.8$	$1551^{a}\pm452$	$2086^{a}\pm458$	$-17.1^{a}\pm10.9$	$-31.5^{ab}\pm5.9$
RC-2	CP	$673^{c}\pm29$	$175^{b}\pm34$	$5.2^{b}\pm0.8$	$1280^{a}\pm209$	$1683^{d}\pm474$	-17.4 ± 1.67	$-20.3^{a}\pm9.9$
	ASP	$727^{bc}\pm44$	$241^{a}\pm28$	$4.9^{b}\pm1.2$	$1494^{a}\pm37$	$2112^{b}\pm270$	-27.4 ± 8.9	$-33.7^{b}\pm7.8$
	MP	$745^{b}\pm51$	$73^{c}\pm16$	$7.1^{a}\pm2.0$	$1462^{a}\pm103$	$2555^{a}\pm205$	-25.9 ± 8.2	$-35.7^{b}\pm2.8$
	FP	$898^{a}\pm53$	$94^{c}\pm21$	$6.3^{ab}\pm1.5$	$1508^{a}\pm441$	$2014^{c}\pm435$	-33.4 ± 16.5	$-35.3^{b}\pm4.4$
RC-3	CP	$732^{c}\pm127$	$176^{b}\pm25$	$6.0^{a}\pm2.6$	1368 ± 71	$2225^{a}\pm460$	$-28.7^{a}\pm8.3$	$-36.6^{d}\pm2.5$
	ASP	$830^{b}\pm40$	$172^{b}\pm8$	$5.0^{a}\pm0.7$	1443 ± 40	$1680^{c}\pm0$	$-32.9a^{b}\pm9.8$	$-20.5^{a}\pm0$
	MP	$702^{c}\pm18$	$173^{b}\pm9$	$7.1^{a}\pm2.2$	1247 ± 125	$1510^{d}\pm0$	$-27.4^{b}\pm8.7$	$-24.9^{c}\pm0$
	FP	$931^{a}\pm57$	$225^{a}\pm0$	$6.3^{a}\pm1.3$	1435 ± 329	$2102^{b}\pm163$	$-18.3^{a}\pm16.1$	$-21.2^{b}\pm28.0$

* E. A. **实验动物** Experimental animal, C. A. **求偶活动** Courtship action, CP **求偶期** Courtship phase, ASP **应答期** Responding phase to spouse, MP **交配期** Mating phase, FP **完结期** Finishing phase, a、b、c **和组合表示差异性的显著水平** a, b, c and composing upper the corner express striking lever of differences

表 4 相同阶段内 RC-1～RC-3 鸣声的 PF、RFP、Q_{3dB}、$f_{1\text{-}2}$和 $RA_{1\text{-}2}$的统计结果

Table 4 Statistical results of principal frequency (PF), repetition frequency (RFP), quality factor (Q_{3dB}), sub-peak frequency ($f_{1\text{-}2}$) and relative amplitudes ($RA_{1\text{-}2}$) of songs for RC-1～3 in the same stage

实验动物	求偶活动	主频率	重复频率	品质因数	次峰频率		相对幅值	
C. A	E. A	PF(Hz)	RFP(Hz)	Q_{3dB}	f_1(Hz)	f_2(Hz)	RA_1 dB	RA_2 dB
CP	RC-1	629 ± 25	169 ± 11	5.1 ± 1.6	1260 ± 1110	1785 ± 318	-17.0 ± 4.3^{a}	-18.9 ± 1.4
	RC-2	689 ± 53	175 ± 33	5.4 ± 1.0	1284 ± 182	1683 ± 474	-16.8 ± 2.0^{a}	-20.3 ± 9.9^{a}
	RC-3	732 ± 127	176 ± 25	5.8 ± 2.3	1362 ± 62	2340 ± 381	-27.2 ± 7.5^{b}	-36.4 ± 1.8^{b}
ASP	RC-1	725 ± 45^{b}	252 ± 28^{a}	5.8 ± 1.7	1388 ± 46^{b}		-24.7 ± 9.2^{a}	
	RC-2	727 ± 44^{b}	241 ± 28^{a}	4.9 ± 1.2	1627 ± 308^{a}	2020 ± 330	-27.6 ± 8.0^{ab}	-33.2 ± 7.1
	RC-3	830 ± 40^{a}	172 ± 7^{b}	5.0 ± 0.7	1445 ± 36^{ab}	1670 ± 14	-37.0 ± 7.7^{b}	-31.8 ± 15.9
MP	RC-1	680 ± 58^{b}	86 ± 25^{b}	5.3 ± 0.7	1360 ± 70^{ab}	1733 ± 92.4^{b}	-25.9 ± 20.1	-37.1 ± 7.9
	RC-2	745 ± 51^{a}	73 ± 16^{b}	7.1 ± 2.0	1447 ± 105^{a}	2555 ± 205^{a}	-25.9 ± 8.2	-35.7 ± 2.8
	RC-3	702 ± 18^{ab}	173 ± 9^{a}	7.1 ± 2.2	1243 ± 115^{b}	1475 ± 50^{b}	-27.5 ± 7.7	-24.8 ± 0.1
FP	RC-1	987 ± 95	89 ± 9^{b}	4.3 ± 2.8	1552 ± 451	2087 ± 457	$-17.1^{a}\pm10.9$	-31.5 ± 5.9
	RC-2	898 ± 53	98 ± 25^{b}	6.1 ± 2.2	1420 ± 149	1982 ± 373	-33.4 ± 16.5^{b}	-36.6 ± 4.6
	RC-3	931 ± 57	221 ± 6.3^{a}	6.1 ± 1.3	1340 ± 308	2027 ± 223	$-18.3^{a}\pm16.1$	-31.0 ± 5.2

* E. A. **实验动物** Experimental animal, C. A. **求偶活动** Courtship action, CP **求偶期** Courtship phase), ASP **应答期** Answered spouse phase, MP **交配期** Mating phase, FP **完结期** Finishing phase, a、b、c **和组合表示差异性的显著水平** a, b, c and composing upper the corner express striking lever of differences

表 5 相同阶段内 RC-1～RC-3 鸣声次峰频率($f_{3\text{-}7}$)和相对幅值($RA_{3\text{-}7}$) 的统计结果

Table 5 Statistical results of sub-peak frequency ($f_{3\text{-}7}$) and relative amplitudes ($RA_{3\text{-}7}$) of songs for RC-1～RC-3 in the same stage

求偶活动	实验动物	次峰频率					相对幅值		
C. A	E. A	F_3(Hz)	f_4(Hz)	f_5(Hz)	f_6(Hz)	f_7(Hz)	RA_3/dB	RA_4/dB	RA_5/dB
MP	RC-1	2610 ± 0^{b}					-36.0 ± 0		
	RC-2	4720 ± 0^{a}					-40.3 ± 0		
	RC-3	2185 ± 50^{b}					-36.1 ± 0.5		
FP	RC-1	2775 ± 627	3683 ± 1016	0 ± 1050	4600 ± 0		-30.2 ± 6.7^{ab}	-33.1 ± 5.2^{b}	-29.2 ± 4.5^{b}
	RC-2	2310 ± 389	3198 ± 732	3703 ± 1063	4082 ± 905	4600 ± 20	-38.3 ± 10.7^{b}	-35.3 ± 4.7^{b}	-40.3 ± 5.0^{c}
	RC-3	2588 ± 401	3173 ± 91	3623 ± 39	4195 ± 506	4975 ± 312	-24.3 ± 6.4^{a}	-23.4 ± 0.3^{a}	-18.5 ± 3.3^{a}
			RA_6/dB	RA_7/dB					
	RC-1		-40.8 ± 0						
	RC-2		-36.6 ± 3.7	-41.9 ± 1.0^{b}					
	RC-3		-29.5 ± 6.2	-25.7 ± 7.8^{a}					

* E. A. **实验动物** Experimental animal, C. A. **求偶活动** Courtship action, CP **求偶期** Courtship phase, ASP **应答期** Answered spouse phase, MP **交配期** Mating phase, FP **完结期** Finishing phase, a、b、c **和组合表示差异性的显著水平** a, b, c and composing upper the corner express striking lever of differences

由鸣声的统计结果来看,不同组鹤间在性活动的四个时期的某一个阶段的某些声学特性存在着显著差异,表明不同组鹤配偶间的鸣声具有代表各自身份的某些声学特性,配偶间就是通过这些特性进行个体识别[4,6],才使得达到性成熟的鹤一旦性选择成功,则通过鸣声来保持长期的配偶关系,完成性活动过程,进行交配繁衍后代。此结论与 Isabelle Charrier 等人得出的南极贼鸥的求偶和联络鸣叫比警告鸣叫具有较高的个体识别信号潜能结果相一致[16]。另外,通过对不完整的性活动记录可知,在四个阶段的鸣声中,求偶鸣叫期和求偶应答与对鸣期构成丹顶鹤的性选择过程,是每对鹤顺利完成性活动不可缺少的关键环节,即没有性选择过程,则配偶间就不能达到发情同步而完成交配过程。

References:

[1] Shang Y C. *Behavioral Ecology*. Beijing:Beijing University Press, 1999.

[2] Liu R S, *et al* eds. *Bird Vocal Research*. Beijing:Science Press, 1998.

[3] Eens M, Pinxten R, Verheyen R F. Male song as a cue for mate choice in the European starling. *Behavior*, 1991, **116**:210～238.

[4] Mountjoy D J. Male song and sexual selection in the European starling. In:Ph. D. thesis, Mc. *Gill University*, *Montreal*, *Canada*, 1994.

[5] Searey W A. Song repertoire and mate choice in birds. *Am. Zool.*, 1992, **32**:71～80.

[6] Thierry L, Thierry A, Pierre J, *et al*. Acoustic communication in a king penguin colony; importance of bird location within the colony and of the body position of the listener. *Polar Biology*, 1999, **21**(4):262～268.

[7] Concha M, Juan C. Effects of male dominance and courtship display on female choice in the ring-necked pheasant. *Behavioral Ecology and Sociobiology*, 1999, **45**(3-4):235～244.

[8] David J W, Andrew P K, Meredith J W. Facultative development of courtship and communication in juvenile male cowbirds(Molothrus ater). *Behavioral Ecology*, 2002, **13**(4):487～496.

[9] Li P X, Yu X F, Li F M. Territorial songs and individual identification within species of yellow throat bustards in the breeding season. *Chinese Study on Zoology*, 1991, **12**(2):163～168.

[10] Jiang J C, Xu M L, Chen H, *et al*. Study on vocal behavior of budgerigar(Mefopsittacus undelafus). *Acta Zoological Sinica*, 1992, **38**(3):286～297.

[11] J iang S R, Ding P, Zhu G Y, *et al*. Characteristics of songs of the Chinese bulbul(Pycnonotus sinensis) in the breeding season. *Acta Zoological Sinica*, 1996, **42**(3):253～258.

[12] Jiang S R, Ding P, Zhu G Y. Analysis on sound spectrum of short wing tree warbler using computer. In: *Proceedings of the one hundredth birth anniversary of professor Chen Z at the sixtieth anniversary of Chinese Academy of Animals*. Beijing:Chinese Science Technology Press, 1994. 370～376.

[13] Zhang L. Preliminary analysis on songs of red-crowed cranes in artificial reared conditions. *Chinese Wildlife*, 2001, **4**:15～16.

[14] Jiang J C. *Songs and Sound Production of Cicadas*. Beijing:Earthquake Press, 2002.

[15] Ma D Q, *et al*, eds. *Acoustic Handbook*. Beijing:Science Press, 1983.

[16] Isabelle C, Pierre J, Nicolas M, *et al*. Individual identity coding depends on call type in the South Polar skua Catharacta maccormicki. *Polar Biology*, 2001, **24**(5):378～382.

参考文献:

[1] 尚玉昌著. 行为生态学. 北京:北京大学出版社, 1999.

[2] 刘如笋,等主编. 鸟声研究. 北京:科学出版社, 1998.

[9] 李佩　,于学峰,李方满. 繁殖期黄喉　的领域鸣唱及其种内个体识别. 动物学研究, 1991, **12**(2):163～168.

[10] 蒋锦昌,徐慕玲,陈浩,等. 虎皮鹦鹉声行为的研究. 动物学报, 1992, **38**(3):286～297.

[11] 姜仕仁, 丁平,诸葛阳,等. 白头鹎繁殖期的声行为的研究. 动物学报, 1996, **42**(3):253～258.

[12] 姜仕仁,丁平,诸葛阳. 短翅树莺鸣声的计算机声谱分析. 见:中国动物学会编, 中国动物学会成立 60 周年:纪念陈桢教授诞辰 100 周年论文集. 北京:中国科学技术出版社, 1994. 370～376.

[13] 张玲. 人工饲养条件下丹顶鹤鸣声的初步分析. 野生动物, 2001, **4**:15～16.

[14] 蒋锦昌著. 蝉的鸣声与发声. 北京:地震出版社, 2002.

[15] 马大猷,等编著. 声学手册. 北京:科学出版社, 1983.