



研究论文 ORIGINAL PAPERS

滇蛙繁殖鸣声特征在城乡环境中的差异

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摘要

无尾两栖动物的鸣叫是两性在婚配行为中的主要通讯方式,其鸣声特征是否受城市化的影响尚待深入研究。本研究基于土地硬化比例,在昆明市周边划分“城市”“农村”“自然”三类生境,于2019年7—8月使用便携式录音机采集滇蛙(*Nidirana pleuraden*)鸣声,并对应测量录音个体的体长和体质量。共获取城市34只、农村30只、自然22只滇蛙的821条有效鸣声。鸣声由1~11个音节构成,其中,2、3、4音节鸣声占滇蛙鸣声总数的68.5%。鸣声特征分析表明,自然生境中滇蛙鸣声的主频、鸣声间隔、鸣声时长、音节时长和音节间隔均大于城市和农村生境;而城市个体的基频和音节数量大于其他两类生境,且城市个体的体质量极显著高于其他两类生境。相关性分析显示,体质量与基频、音节间隔呈显著正相关;体长与基频呈显著正相关,与鸣声时长、音节数呈极显著负相关。从鸣声结构上看,滇蛙鸣声第1音节振幅较其他音节小且音节时长最长;最后1节振幅大于第1音节小于其他音节,音节时长最短,该特征可用于区分滇蛙的每一条鸣声。总体而言,随着城市化程度的增加,滇蛙趋向于发出基频更高、鸣声时长更短、音节时长与音节间隔更小的鸣声,表明其鸣声特征在城市生境中具有明显的可塑性响应。

Differences in Reproductive Call Characteristics of Yunnan Pond Frogs Between Urban and Rural Environments

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Abstract: Amphibian calls are the primary communication method between the sexes during mating behavior. However, whether call characteristics are affected by urbanization requires further investigation. This study used the proportion of land hardening to define three environments around Kunming City: “urban”, “rural”, and “natural”. From July to August 2019, we recorded the calls of Yunnan pond frog (*Nidirana pleuraden*) in these three environments using a portable recorder and simultaneously measured the body length and mass of the recording individuals. A total of 821 calls from 34 “urban” frogs, 30 “rural” frogs and 22 “natural” frogs were analyzed. Each call consisted of 1 to 11 notes, with calls comprising 2, 3 and 4 notes accounting for 68.5% of the total. The dominant frequency, inter-call interval, call duration, note duration, and inter-note interval of Yunnan pond frogs in the natural environment were larger than those in the urban and rural environments. In contrast, the fundamental frequency and note number was higher in the urban environment than in the other two. Moreover, the body mass of urban individuals is significantly higher than that of the other two types of habitats. Body mass was positively correlated with fundamental frequency and inter-note intervals. Body length was positively correlated with fundamental frequency, and negatively correlated with call duration and note number. The results showed that the amplitude of the first note was smaller and its duration was the longest. The amplitude of the last note was larger than that of the first note and smaller than that of the others, and its duration was the shortest. These characteristics of the initial and terminal notes can be used to distinguish each call. With increasing urbanization, Yunnan pond frogs tend to produce calls with a higher fundamental frequency, but shorter call duration, note duration and inter-note intervals. It indicates that its call characteristics have obvious plastic responses in urban habitats.

全球两栖类物种数量超过8 000种,其中超过三分之一的物种面临威胁,种群呈急剧下降趋势^[1]。在众多影响因素中,声音通讯受干扰被认为是导致其衰退的重要原因之一^[2]。声音是两栖类信息传递的主要载体,直接影响繁殖成功率^[2]。动物的声音信号可以在栖息地之间远距离传播,用来吸引配偶和保护资源^[3]。在不同的环境中,动物繁殖期的鸣声呈现出对环境的特征适应^[4]。例如,鸟类和蛙类的繁殖鸣声在声谱和鸣叫时间特征上往往与栖息地的环境特性相匹配^[3]。在繁殖季节,多数两栖动物的雄性个体通过发出求偶鸣声进行通讯,雌性则可依据雄性鸣声特征识别同种雄性,并选择交配对象^[5]。鸣声的主频、时长等特征可能是雌体对雄性身体情况和所处环境的判别信号^[6]。同时,雄体鸣声也可向同种其他个体传递领域信息,以减少资源竞争^[7]。在不同的生境中,蛙类可通过改变鸣声频率、振幅、时长和音节数量等特征来增加声音信号的

复杂性。因此,两栖动物的鸣声特征既受生物个体因素影响,也受温度^[8-10]、人类活动和噪声^[3,11]等环境因素的影响。城市化进程快速改变了土地利用方式、气候条件和水体质量等环境因素^[12],导致动物的栖息环境发生转变^[13]。其中,道路的修建将两栖动物栖息地分割,使种群隔离开来^[14],动物的密度下降,并增加了同种个体间的通讯距离^[15];人为噪声则干扰了动物用于交流的声音信号,提升环境背景噪声水平^[16]。为应对噪声,两栖动物常通过增加鸣声振幅和复杂度来适应噪声水平^[11,17-18]。例如,Halfwerk *et al.*^[3]将雄性泡蟾(*Physalaemus pustulosus*)暴露于不同频率的噪声干扰中,结果发现其通过提高鸣声振幅、鸣叫频率和鸣声复杂性来应对低频噪声干扰。

滇蛙(*Nidirana pleuraden*)属于蛙科(Ranidae)琴蛙属(*Nidirana*),是中国特有种,主要分布于四川、贵州和云南等地^[19]。该物种多栖息于海拔1 150~2 600 m的小水塘和水稻田中。繁殖期在5—8月,其间雄蛙

发出连续性的“科~科~科”鸣声吸引雌蛙,从而完成交配产卵^[19]。滇蛙繁殖期鸣声响亮,繁殖期较长,是研究无尾两栖类鸣声特征参数的理想对象。目前,未见对该蛙鸣声特征的相关报道。为此,本研究以滇蛙为研究对象,基于昆明地区硬地面积比例划分“城市”“农村”和“自然”三类生境,通过分析其鸣声特征的差异,旨在探究两栖动物繁殖鸣声在不同城市化环境中的适应策略与声学响应。

1 研究方法

1.1 声音采集地点

根据滇蛙的生活习性,本研究选取了7个临时

水塘和永久性水塘为采样点。以每个采样点为中心,使用ArcGIS 10.02软件添加1 km × 1 km网格,并叠加2020年土地利用类型(Finer Resolution Observation and Monitoring-Global Land Cover, <http://data.ess.tsinghua.edu.cn/>),计算每个网格的硬地面积比例。将下载的人口分布数据(WorldPop: Population Counts, <https://www.worldpop.org/geodata>)导入ArcGIS后,提取网格内的人口密度,辅助判别城市化情况。硬地面积比例高于50%的为城市环境,30%~50%的为农村环境,低于30%的为自然环境(下文简称为“城市Urban”“农村Rural”和“自然Natural”)。采样点详情见表1。

表1 滇蛙鸣声采集地点

Table 1 Collection sites of *Nidirana pleuraden* calls

| 环境类型 Habitat type | 采样点 Sampling site | 起点 Starting point | 终点 End point | 人口密度/(人·km ⁻²) Population density | 水体类型 Waterbody type |
|----------------------|----------------------|---------------------------------|---------------------------------|--|------------------------|
| 城市 Urban | 月华街 | 24°50'46.88" N, 102°51'37.14" E | 24°50'49.68" N, 102°51'47.68" E | 1 299.80 | 永久水塘 |
| | 植物园 | 25°08'10.13" N, 102°44'35.53" E | 25°08'24.04" N, 102°44'34.42" E | 4 388.82 | 临时水塘 |
| | 西南林业大学 | 25°03'25.17" N, 102°45'29.83" E | 25°03'46.70" N, 102°45'28.56" E | 7 650.39 | 临时水塘 |
| 农村 Rural | 黄龙箐 | 25°05'9.69" N, 102°48'20.21" E | 25°05'08.05" N, 102°48'33.09" E | 200.28 | 临时水塘 |
| | 关山水库 | 24°49'34.27" N, 102°50'20.57" E | 24°49'20.66" N, 102°50'23.44" E | 567.87 | 永久水塘 |
| 自然 Natural | 三家村 | 25°02'29.94" N, 102°35'38.58" E | 25°02'44.00" N, 102°35'50.53" E | 40.62 | 永久水塘 |
| | 青山村 | 25°13'8.71" N, 102°20'53.35" E | 25°13'1.56" N, 102°20'42.60" E | 0 | 临时水塘 |

1.2 鸣声采集与处理

于2019年7月6日—8月3日的晴朗夜晚(20:00—23:00),在距目标个体约1 m处,利用便携式录音机(SONY PCM-D100)采集滇蛙的鸣声。采用立体声模式、44.1 Hz和16 bit格式,对研究对象一对一录制。为避免人为因素干扰,在录音期间关闭光源。对每只滇蛙持续录制20~45 min,文件保存为wav格式。录音结束后捕捉该蛙,测量体长和体质量,完成后原地放归。

1.3 数据处理与分析

将wav格式的声音文件导入计算机后,首先进行降噪处理,随后使用Adobe Audition CS6软件和Praat软件提取鸣声的特征参数,包括主频、基频、鸣声时长、鸣声间隔、音节时长、音节间隔和音节数。鸣声波形图和语图的绘制使用Praat软件。使用Graph-Pad Prism软件进行单因素方差分析(ANOVA),以检验不同生境组间的鸣声特征差异。采用R 4.1.0软件中的ggstatsplot包进行体质量、体长与鸣声特征的相关性分析。在进行数据分析前,首先对数据进行

正态性检验,若数据符合正态分布,则选择Pearson相关分析;否则,采用Spearman相关分析。

2 结果

2.1 不同生境下滇蛙鸣声音节数的差异

野外共计录制到86只雄性滇蛙鸣声,其中59只被成功捕捉并测量。在城市、农村和自然生境中录制到的滇蛙鸣声个体数量分别34、30、22只。经分析后获得有效鸣声821条,构成鸣声的音节数为1~11个。滇蛙主要以2、3、4个音节构成一条鸣声,这类鸣声条数占总鸣声条数的68.5%,最常见的鸣声类型在不同生境下略有差异:在自然和农村生境中,2个音节的鸣声占比最高(分别为30.4%和31.8%);而在城市生境中,4个音节的鸣声最为常见(占比25.3%)。城市中4个音节是鸣声中最多的音节,而在自然和农村生境中,最多的是2个音节。此外,从平均音节数来看,城市生境(3.7) > 农村生境(3.5) > 自然生境(3.1),表明城市化程度可能与鸣声音节数量的增加存在关联(表2)。

表2 不同生境下滇蛙不同音节数鸣声的数量

Table 2 Number of calls with different note number in *Nidirana pleuraden* across different habitats

| 音节数量/个 Number of notes | 自然 Natural | | 农村 Rural | | 城市 Urban | |
|--------------------------------|-------------------------|--------------------|-------------------------|--------------------|-------------------------|--------------------|
| | 鸣声条数 Number of calls | 占比/% Percentage | 鸣声条数 Number of calls | 占比/% Percentage | 鸣声条数 Number of calls | 占比/% Percentage |
| 1 | 24 | 10.7 | 25 | 8.2 | 10 | 3.4 |
| 2 | 68 | 30.4 | 97 | 31.8 | 67 | 22.9 |
| 3 | 57 | 25.5 | 63 | 20.7 | 71 | 24.3 |
| 4 | 33 | 14.7 | 32 | 10.5 | 74 | 25.3 |
| 5 | 20 | 8.9 | 44 | 14.4 | 30 | 10.3 |
| 6 | 19 | 8.5 | 22 | 7.2 | 23 | 7.9 |
| 7 | 3 | 1.3 | 10 | 3.2 | 6 | 2.1 |
| 8 | 0 | 0 | 6 | 2.0 | 6 | 2.1 |
| 9 | 0 | 0 | 3 | 1.0 | 3 | 1.0 |
| 10 | 0 | 0 | 2 | 0.7 | 2 | 0.7 |
| 11 | 0 | 0 | 1 | 0.3 | 0 | 0 |
| 鸣声总条数 Total number of calls | 224 | | 305 | | 292 | |
| 总音节数 Total number of notes | 698 | | 1 064 | | 1 078 | |
| 平均音节/个 Mean number of notes | | 3.1 | | 3.5 | | 3.7 |

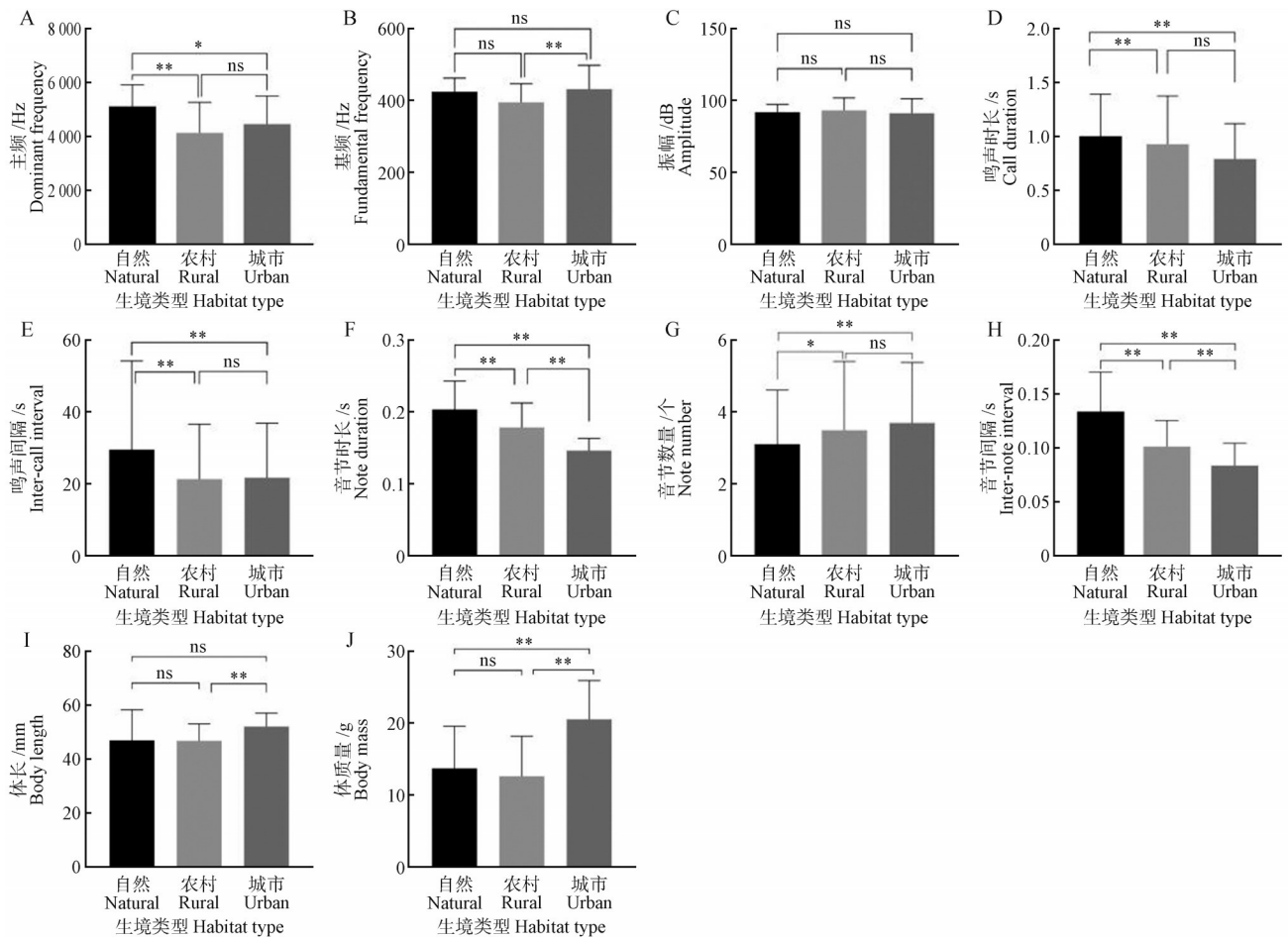
2.2 不同生境下滇蛙鸣声特征与体型指标的差异

单因素方差分析表明,滇蛙的鸣声特征和体型指标在不同生境间存在显著差异(图1)。主频以自然生境高,其次是城市,农村最低($F_{(2,81)} = 5.98$),自然与城市差异显著($P < 0.05$),自然与农村差异极显著($P < 0.01$)。鸣声时长在自然生境中最长,其次是农村,城市最短($F_{(2,757)} = 18.46$),自然与农村、城市差异极显著($P < 0.01$)。鸣声间隔在自然生境中最大,其次是城市,农村最小($F_{(2,696)} = 13.65$),自然与城市、农村差异极显著($P < 0.01$)。音节时长在自然生境中最长,其次是农村,城市最短($F_{(2,2790)} = 768.20$),三类生境间均存在极显著差异($P < 0.01$)。音节间隔在自然生境中最长,其次为农村,城市最短($F_{(2,2015)} = 525.90$),三者间差异均极显著($P < 0.01$)。基频以城市生境最高,其次是自然,农村最低($F_{(2,83)} = 3.75$),城市与农村差异极显著($P < 0.01$)。音节数量在城市生境中最多,其次是农村,自然最低($F_{(2,818)} = 7.48$),自然与城市差异极显著($P < 0.01$)。体长方面,城市生境个体体长

最长,农村与城市差异极显著($P < 0.01$)。体质量以城市最高,其次是自然,农村最低($F_{(2,56)} = 10.04$),城市与自然、农村差异极显著($P < 0.01$)。平均振幅在3种生境间均无显著差异。综上所述,自然生境中的滇蛙鸣声具有最高的主频,以及最长的鸣声时长、鸣声间隔、音节时长和音节间隔;而城市生境中的个体则表现出最高的基频和最多的音节数量,但鸣声时长、音节时长及音节间隔较短。

从滇蛙鸣声的波形图和语图(图2)可以看出,在滇蛙的多音节鸣声中,起始音节的振幅通常相对较小,且持续时间往往相对较长;终止音节的振幅通常大于起始音节但小于中间的音节,其持续时间则相对较短。这种在时间与振幅维度上具有特定模式的起始和终止结构可以用于区分滇蛙的每一条鸣声。

对体长和体质量与鸣声特征进行相关性分析(图3),体质量与基频和音节间隔均呈显著正相关($P < 0.05$);体长与基频呈显著正相关($P < 0.05$),与鸣声时长和音节数呈极显著负相关($P < 0.03$),表明体型越大,基频越高。



A. 主频, $F_{(2,81)} = 5.98$; B. 基频, $F_{(2,83)} = 3.75$; C. 振幅, $F_{(2,82)} = 0.46$; D. 鸣声时长, $F_{(2,757)} = 18.46$; E. 鸣声间隔, $F_{(2,696)} = 13.65$; F. 音节时长, $F_{(2,2790)} = 768.20$; G. 音节数量, $F_{(2,818)} = 7.48$; H. 音节间隔, $F_{(2,2015)} = 525.90$; I. 体长, $F_{(2,56)} = 2.25$; J. 体质量, $F_{(2,56)} = 10.04$; *. 差异显著 ($P < 0.05$); **. 差异极显著 ($P < 0.01$).

A. Dominant frequency, $F_{(2,81)} = 5.98$; B. Fundamental frequency, $F_{(2,83)} = 3.75$; C. Amplitude, $F_{(2,82)} = 0.46$; D. Call duration, $F_{(2,757)} = 18.46$; E. Inter-call interval, $F_{(2,696)} = 13.65$; F. Note duration, $F_{(2,2790)} = 768.20$; G. Note number, $F_{(2,818)} = 7.48$; H. Inter-note interval, $F_{(2,2015)} = 525.90$; I. Body length, $F_{(2,56)} = 2.25$; J. Body mass, $F_{(2,56)} = 10.04$; *. Significant difference ($P < 0.05$); **. Highly significant difference ($P < 0.01$).

图1 不同生境下滇蛙的鸣声特征差异

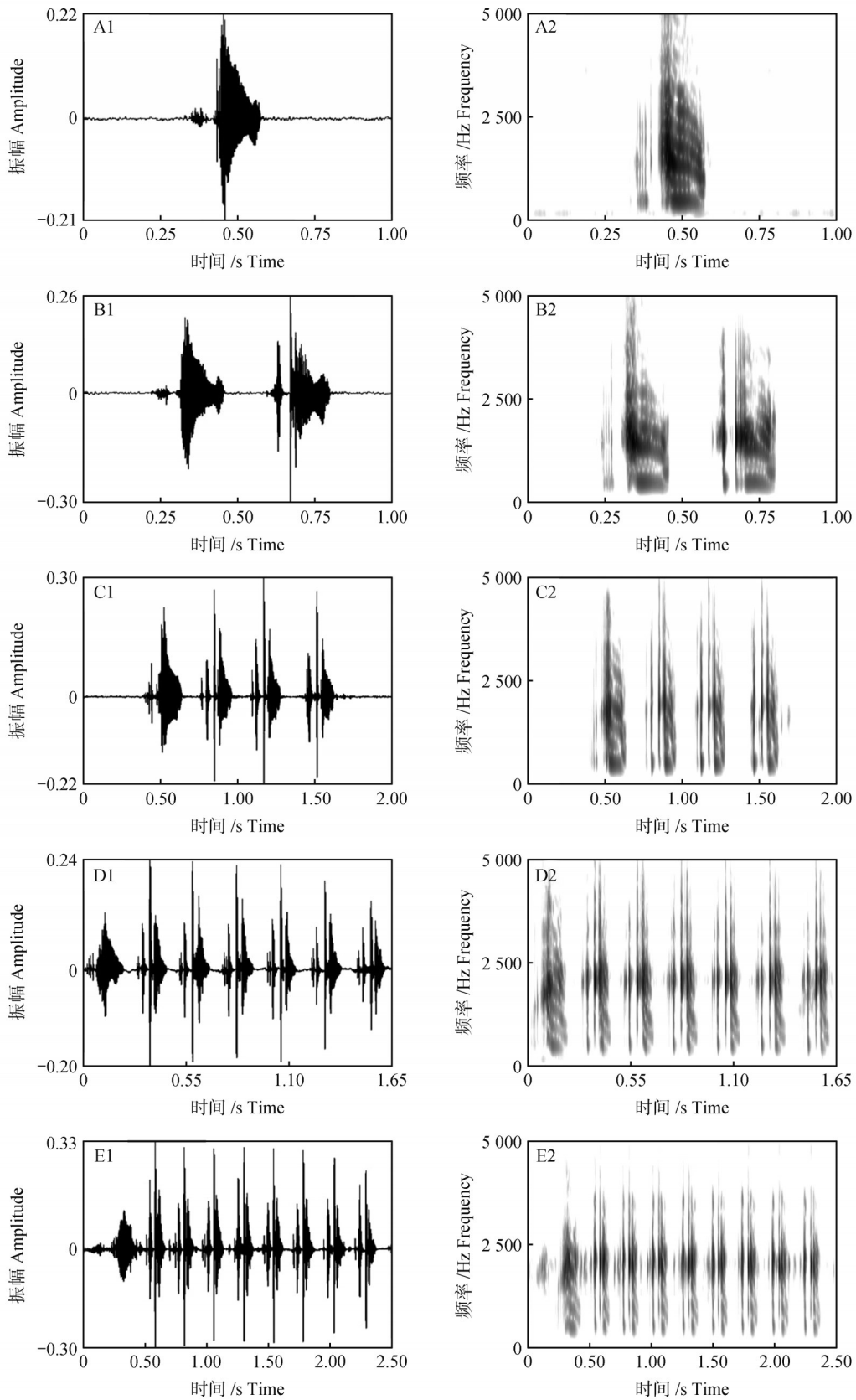
Figure 1 Differences in call characteristics of *Nidirana pleuraden* across different habitats

3 讨论

3.1 滇蛙鸣声特征的城乡差异

两栖动物常通过调整它们的鸣叫行为和策略来适应不同的生境^[20]。本研究也观察到相应结果,滇蛙鸣声的主频、鸣声间隔、音节时长和音节间隔均为自然生境中最大;而城市生境中基频最大,鸣声时长、音节时长和音节间隔较小。滇蛙通过改变鸣声特征适应环境,这样的声音特征可能更利于其提高在复杂生境中的通讯效率^[20-21]。但是,城市环境对野生动物的干扰是综合性的,包括噪声污染、栖息地碎片化导致的个体间距离增加等。物种需有效应对这些复合压力方能生存,而表型可塑性(phenotypic

plasticity)在此适应过程中常扮演关键角色^[22-24]。城市和自然种群间的表型差异正是这种可塑性的直接体现^[23,25-26],鸣声特征的改变也是表型可塑性的一方面。城市环境中的蛙类经常受到人为噪声的干扰,如交通噪声会干扰雌性柯氏灰树蛙(*Hyla chrysoscelis*)判别雄蛙方位,促使雄蛙发出更高频率的鸣声^[27];Zhao *et al.*^[17]的研究表明飞机起飞和降落产生的噪声使机场附近的蛙类比其他地点蛙具有更高频的鸣声;Sun *et al.*^[16]的研究结果也表明,摩托车行驶时产生的低频噪声可导致黑带水蛙(*Hylarana nigrovittata*)、粗皮姬蛙(*Microhyla butleri*)和花狭口蛙(*Kaloula pulchra*)鸣声频次下降。此外,在噪声、交通等干扰影响后,雄性两栖动物可能倾向于发出持

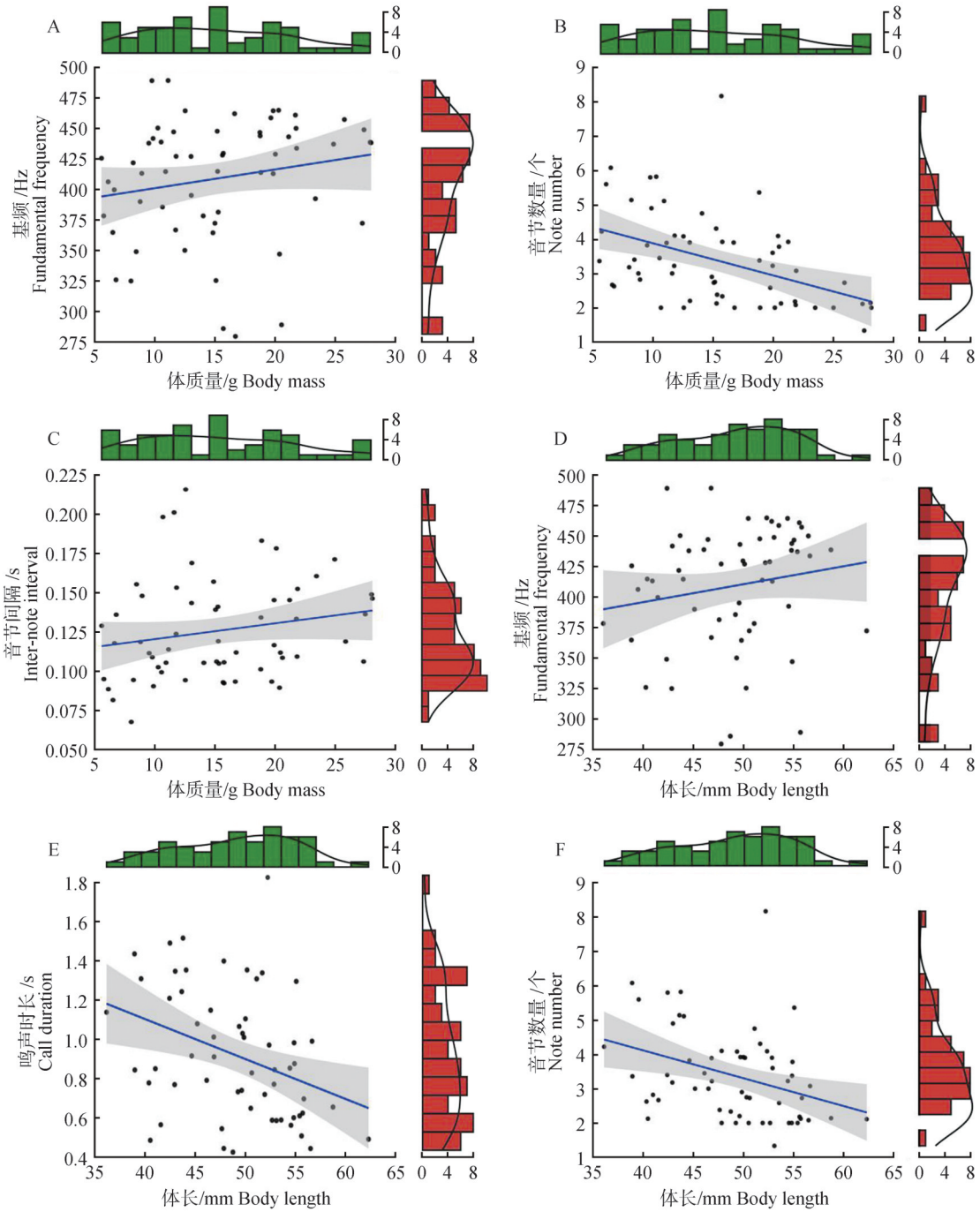


A. 1个音节; B. 2个音节; C. 4个音节; D. 7个音节; E. 9个音节; 1. 波形图; 2. 语图。

A. One-note call; B. Two-note call; C. Four-note call; D. Seven-note call; E. Nine-note call; 1. Waveform; 2. Sonogram.

图2 滇蛙鸣声的波形图和语图

Figure 2 Waveform and sonogram of calls from *Nidirana pleuraden*



上方柱形图为横坐标的数据分布图,右方的柱形图为纵坐标的数据分布图;数字表示样本量。

The histograms at the top and on the right represent the data distribution along the x-axis and y-axis, respectively. The tick labels indicate the sample size.

A. $\log_e(S) = 10.14, P = 0.047, \hat{\rho}_{\text{Spearman}} = 0.26, \text{CI}_{95\%}[0.02, 0.47], n_{\text{pairs}} = 59$; B. $\log_e(S) = 10.83, P < 0.001, \hat{\rho}_{\text{Spearman}} = -0.48, \text{CI}_{95\%}[-0.66, -0.25], n_{\text{pairs}} = 59$; C. $\log_e(S) = 10.15, P = 0.047, \hat{\rho}_{\text{Spearman}} = 0.25, \text{CI}_{95\%}[-0.01, 0.47], n_{\text{pairs}} = 59$; D. $\log_e(S) = 10.12, P = 0.034, \hat{\rho}_{\text{Spearman}} = 0.28, \text{CI}_{95\%}[0.03, 0.49], n_{\text{pairs}} = 59$; E. $\log_e(S) = 10.71, P = 0.004, \hat{\rho}_{\text{Spearman}} = -0.37, \text{CI}_{95\%}[-0.58, -0.12], n_{\text{pairs}} = 59$; F. $\log_e(S) = 10.77, P = 0.003, \hat{\rho}_{\text{Spearman}} = -0.38, \text{CI}_{95\%}[-0.58, -0.14], n_{\text{pairs}} = 59$ 。

图3 滇蛙体质量、体长与声音特征的相关性

Figure 3 Correlations of body mass and body length with call characteristics in *Nidirana pleuraden*

续时间长、音节数较多、频率较低及重复程度高的鸣声,如雄性黑带水蛙会增加鸣叫次数,并发出强度低、持续时间短和重复性高的鸣声^[16]。然而,鸣叫行为本身消耗能量巨大,且重复鸣声不仅增加能量支出,也增加了被捕食或寄生的风险^[28]。因此,城市环境中滇蛙通过提高基频,同时缩短音节时长和音节间隔来适应环境,而非单纯增加鸣叫时长或重复率。与鸟类相比,蛙类和蟾蜍发出的鸣声相对单调,如圆蟾舌蛙(*Phrynoglossus martensii*)仅以单一音节不断重复^[29]。然而部分蛙类如仙琴蛙(*Nidirana daunchina*)也可发出由多音节组成的复杂鸣声^[30]。本研究中,城市及周边自然环境中的滇蛙鸣声则以2~4音节为主,最多可达11个音节。多音节鸣声中起始的第1节振幅小、音节时长最长,最后1节振幅小、音节时长最短,可以区分滇蛙每一次鸣叫的起始和终止。这种清晰的起始-终止结构,类似于鸟类鸣声中的“句子”。性选择压力常驱动动物声音信号的进化^[31],激烈的配偶竞争往往促使雄性发出包含更多音节的鸣声来获得更多交配机会^[32]。但是,更多音节意味着更高的能量消耗和天敌暴露风险。因此,在繁殖成功率、能量消耗和天敌压力多重因素权衡下,以2~4音节为主的鸣声可能是滇蛙的适应策略。综上所述,滇蛙适应城市化的鸣叫策略是发出更高基频,较短鸣声时长、音节时长和音节间隔的鸣声。

3.2 滇蛙鸣声与体质量和体长的相关性

无尾两栖类个体的性成熟度和体型等信息可以通过鸣声传递,体型大小可影响其鸣声特征^[29]。本研究结果显示,滇蛙鸣声的基频均与体质量和体长呈显著正相关,即体型越大,基频越高。该结果与圆蟾舌蛙^[29]和日本雨蛙(*Hyla japonica*)鸣声特征^[33]的研究结果相反。这表明体长和体质量较大的滇蛙可能通过提高鸣声基频来增加声音信号的传播效率。然而,蛙类的体质量、体长等生物因素并非总是与鸣声特征存在显著相关。本研究中滇蛙的其他鸣声特征与体质量和体长相关性较弱,这些特征可能受环境的影响更大。例如,陈平等^[34]发现棘胸蛙(*Quasipaa spinosa*)求偶鸣声特征受环境温度调控,而与体型无显著关联。结合已有研究^[8-9]可知,滇蛙的鸣声特征可能同时受生物因素和非生物因素的共同影响^[8-9]。因此,结合城乡差异结果可以推断人类活动对滇蛙的鸣声特征有一定影响。

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