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•综述•　中国野生脊椎动物鸣声监测与生物声学研究专题

网络分析法在动物声音通讯及生物声学研究中的应用与前景

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摘要: 动物社会网络分析法(animal social network analysis, ASNA)是一套用于研究动物社会性、量化个体间各种社会关系、揭示个体行为与社会结构动态之间联系的工具, 被广泛应用于多种动物类群的行为学研究。该分析方法所提供的一系列指标也非常适用于探究动物的声音交流及鸣声结构。在此, 本文首先简要介绍了网络分析法的基本概念及一些常用的指标; 然后基于野外和室内研究实例, 阐述了如何利用ASNA建立声音通讯网络、量化声音交流, 以及将ASNA与被动声学监测技术相结合的应用前景; 随后探讨了ASNA在分析鸣声相似性及鸣声地理变异中的优势; 最后概述了ASNA在解析鸣声结构和句法规则中的应用。ASNA为研究动物通讯网络以及声音信号的适应性进化提供了新的视角和新的思路。

关键词: 中心度; 声音通讯网络; 鸣声网络; 鸣声相似性; 鸣声序列; 传递模体

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Application and prospect of network analysis in the studies of animal vocal communication and bioacoustics

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ABSTRACT

Background & Aim: Animal social network analysis (ASNA) is a toolbox used to examine animal sociality, quantify various social relationships between individuals, and uncover links between individual behavior and dynamics of social structures, which is widely used in studies of animal behavior across a variety of taxa. In addition, a series of measurements in ASNA are very suitable for investigating vocal interactions and song structure. Here we reviewed the applications of ASNA in studies of animal vocal communication and bioacoustics.

Progress: Firstly, we introduced a description of basic concepts and some measurements. Secondly, we described the use of ASNA to construct vocal networks and quantify vocal interactions based on field and laboratory studies, and the application prospect of ASNA combined with passive acoustic monitoring technology. Thirdly, we discussed the advantages of ASNA in analyzing song similarity and geographic variation. Finally, we summarized the application of ASNA in the analysis of song structure and syntactical rules.

Conclusion: ASNA provides a comprehensive perspective and new ideas for studying animal communication networks and investigating the adaptive evolution of acoustic signals.

Key words: centrality; vocal communication network; song network; call similarity; vocal sequence; transition motif

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20世纪30年代, Moreno (1935)在探索群体关系如何影响个体行为时, 首次使用了“社群图”, 即用“点”代表个体, 用“线”表示个体之间的社会关系。由此, 社会网络分析法(social network analysis, SNA)的雏形诞生了。20世纪50年代, 人类学家Barnes首次提出了社会网络概念, 并将这一概念用于社会学研究(Barnes, 1954)。随着图论、矩阵算法和随机理论模型的出现和发展(Forsyth & Katz, 1946; Luce & Perry, 1949; Erdös & Rényi, 1959), SNA被广泛应用于信息科学、人类学、经济学、心理学和流行病学等不同研究领域(Otte & Rousseau, 2002; Smith & Christakis, 2008; Borgatti et al, 2009)。

在行为生态学领域, Sade (1965)率先利用手绘网络图的方法, 描述了猕猴(*Macaca mulatta*)理毛行为的社会关系。近10余年来, 随着社会网络理论的完善和计算机技术的发展(Girvan & Newman, 2002; Newman, 2006; Whitehead, 2008b; Sih et al, 2009; De Domenico et al, 2014), SNA逐渐被应用于兽类、鸟类、鱼类以及无脊椎动物等不同动物类群的行为学研究。动物社会网络分析法(animal social network analysis, ASNA)的出现和运用, 极大程度地推动了行为生态学的发展(Krause et al, 2007; Croft et al, 2008; 张鹏, 2013; Kurvers et al, 2014; 邓可等, 2019)。个体之间某种行为的发生频次和持续时间是量化互动强度的常用指标, 但这只能反映直接的社会关系。相较而言, ASNA的优势在于能够识别和量化社会关系中的独特属性, 从不同水平(从个体到群落)揭示目标对象之间的各类社会关系(如社会冲突、合作联盟), 并能通过可视化的网络图直观展示出来(Whitehead, 2008a; Krause et al, 2009)。基于网络分析法的理论框架和分析手段, 学者们得以更好地辨识和量化个体间直接或间接的社会关系(Brent, 2015; Maguire et al, 2021), 分析社会交往格局的形成机制及动态变化(Blonder & Dornhaus, 2011; Kurvers et al, 2014; Pinter-Wollman et al, 2014), 揭示事件或信息在群体中的传播途径(VanderWaal et al, 2014a; Fountain-Jones et al, 2017)。ASNA不仅增进了学者们对社会复杂性及其生态功能的理解, 也为探讨动物社会性的进化及维持提供了新的视角, 如今已成为动物行为学研究中极为实用的一套工具(Farine & Whitehead, 2015; Kulahci & Quinn, 2019; Meise et al, 2019)。近年来, 与ASNA有关的数据分析方法和研究方向仍在不断地拓展(Croft et al, 2016; Farine, 2017; Silk et al, 2018; Robitaille et al, 2019; Bonnell & Vilette, 2020; Finn, 2021; Farine & Carter, 2022)。

目前, 动物社交网络的建立主要基于直接观测数据(如个体间的理毛、打斗) (Madden et al, 2009; Brent et al, 2011; Xia et al, 2019)或基于标志重捕数据(Castles et al, 2014; Deng et al, 2017; 朱家贵等, 2022)。声音通讯是动物的重要交流方式之一, 在动物的生存和繁殖中起关键作用, 尤其是鸟类和蛙类(Gerhardt & Huber, 2002; Naguib et al, 2009)。对声音信号的传递模式及信号本身的研究, 有助于深入了解动物声音通讯及声音信号的适应性进化。本文简要介绍了网络分析法中常用的量化指标, 并根据现有的相关研究阐述了如何利用ASNA分析动物的声音交流过程、揭示鸣声相似性的地理格局、解析动物的鸣声结构, 强调了ASNA在动物声音通讯及生物声学研究中的优势。

1 网络分析法的常用指标

网络分析法的一大特点是利用可视化网络图直观展示目标个体间的关系, 图中的节点(nodes/vertices)通常代表个体, 它们之间的连线(edges/lines)则代表个体间的某种关系。研究者可根据实际所需给图中的点和线赋予多种信息, 比如以点的形状、大小、颜色等对不同个体属性加以区分(如性别、年龄), 以连线粗细反映关系的强弱, 以箭头表示行为或信息的传递方向(邓可等, 2019)。网络分析法的另一特点是它具有一系列量化个体或群体社会属性的指标, 个体水平指标用于反映目标个体与其他个体的直接或间接关系及紧密程度, 群体水平指标用于衡量群体的总体结构或稳定性。

中心度(centrality)是网络分析法中的一个基本概念, 它根据目标个体在网络中的位置来衡量其在群体结构中的重要性(Freeman, 1979; Friedkin, 1991)。常用的指标有节点中心度(degree centrality)、接近中心度(closeness centrality)、中介中心度(betweenness centrality)、特征向量中心度(eigenvector centrality)等。节点中心度基于与目标个

体直接相连接的个体数量，数量越多，中心度指数就越大。在有向网络(directed network)中，节点中心度又分为点入度(in-degree)和点出度(out-degree)，分别表示目标个体接收和发出的数量。交往强度(strength)是加权的节点中心度，它可以同时反映连接的数量及程度(如频次、持续时间)。节点中心度与交往强度量化了个体间的直接关系，接近中心度、中介中心度和特征向量中心度则是量化个体间间接关系的常用指标。接近中心度基于目标个体与其他所有个体的最短路径长度(shortest path length)之和(Freeman, 1979)，接近中心度高的个体，其信息传播能力更强、速度更快。中介中心度基于目标个体与网络中每两个个体最短路径长度之和(Freeman, 1979)，用于衡量个体的间接关系对其在群体结构中的位置的影响。特征向量中心度基于目标个体邻居的中心度之和，通过与目标个体所连接的个体的重要性来反映其自身的影响力(Newman, 2004)。这3个中心度指标所反映的个体属性具有相似之处，但每个指标都包含了某种特定信息，各自从不同的角度衡量个体在网络结构中的地位。

常用的群体水平指标有网络直径(diameter)、平均路径长度(average path length)和聚集系数(clustering coefficient)等。网络直径是网络中的最长路径，平均路径长度是指所有节点之间所有路径长度的平均值(Wey et al, 2008)。直径和平均路径长度都反映了网络中节点的总体连接程度，它们的值越小，连接越紧密。聚集系数描述的是目标个体周边个体的聚集程度，用于揭示网络中的“亚群体”结构(Wey et al, 2008)。关于网络指标，现有大量文献和专著对其概念和算法进行了更加全面完整的介绍(Croft et al, 2008; Makagon et al, 2012; Brent, 2015; Farine & Whitehead, 2015)。

2 网络分析法的应用

2.1 量化声音交流格局

声音通讯广泛存在于昆虫、蛙类、兽类、鸟类等不同动物类群(Gerhardt & Huber, 2002; Chen & Wiens, 2020)，在动物的社会交往及繁殖求偶中扮演着重要角色。由于声音信号能远距离传播，除了预期的信号接收者，范围内的所有同类都可能接收到声音信号所传递的信息，而个体对该信号的鸣叫回应本身又能引起更多个体的回应(Peake, 2005)。此外，声音信号的异种窃听(heterospecific eavesdropping)现象十分普遍，比如捕食者对猎物求偶信号的利用(Zuk & Kolluru, 1998)或个体利用异种的警报鸣叫提早发现并回避捕食者(Magrath et al, 2015)。因此，声音信号连接的往往不只是两个个体，而是多个个体所形成的网络，声音信号所携带的信息就在这个网络中传播。McGregor和Dabelsteen (1996)首次定义了通讯网络(communication network)，在随后的近10年里，学者们通过野外观察和回放等手段，从网络的视角探讨了远距离信号传递及信号窃听如何影响动物的行为决策(McGregor, 2005)。然而，将ASNA应用于声音通讯研究、建立并量化声音通讯网络(vocal communication network)，目前只有零星报道(Snijders & Naguib, 2017; Kulahci et al, 2018)。

理毛(grooming)是灵长类动物维系社会纽带的重要方式，该行为反映了个体间的社会关系(Silk et al, 2006; Lehmann et al, 2007)。人们认为，联系鸣叫(contact calls)也具有维系社会纽带的作用，可以看作是一种远距离的理毛行为(grooming-at-a-distance) (Dunbar, 2003)。Kulahci等(2015)利用ASNA分析了环尾狐猴(*Lemur catta*)的理毛行为与声音交流之间的关系，记录了每个事件中的行为发出者和接收者(即谁给谁理毛，谁发出鸣叫、谁给予了鸣叫回应)。结果显示，环尾狐猴的理毛网络与声讯网络显著相关(图1)，且相较于理毛对象，个体对鸣叫回应对象的选择性更强。回放实验进一步证实了个体在声音交流中倾向于回应之前有过理毛互动的群体成员，表明环尾狐猴的声音交流可用于衡量个体间的社会纽带(Kulahci et al, 2015)。声音信号所携带的信息本质上是一种公开信息，除了社群内部成员，群体外的个体也能获取并加以利用。Morino等(2021)收集了7个合趾猿(*Symphalangus syndactylus*)群体之间的鸣叫数据，利用ASNA探究了群体成员变化对声讯网络结构的影响。分析结果显示，相较于成员稳定的群体，成员组成发生了变化的群体能获得更多来自其他群体的鸣叫回应，证实了合趾猿能通过声音交流判断其他社群的稳定性(Morino et al, 2021)。动物的声音交流与社会交往密切相关，对声讯格局

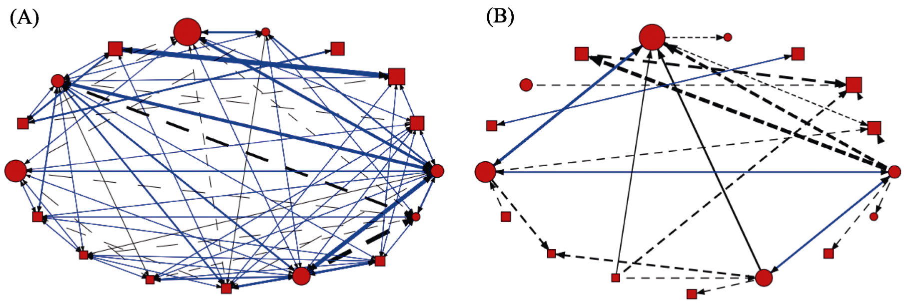

图1　环尾狐猴(*Lemur catta*)的理毛网络(A)与声讯网络(B)。圆圈代表雌性，矩形代表雄性，节点的大小代表年龄。线段的粗细代表互动频次，箭头指向的是被理毛或收到鸣叫回应的个体。蓝色实线表示相互理毛或鸣叫回应，黑色虚线则表示单向的理毛或鸣叫回应。改自Kulahci等(2015)。

Fig. 1　The grooming network (A) and vocal network (B) from a group of ring-tailed lemurs (*Lemur catta*). Circles represents females and squares represents males. Size of the nodes indicates the age. Thickness of the lines indicates the frequency of the interactions and the arrows indicate the recipient of the grooming or vocal response. Solid (blue) lines visualize reciprocal grooming or vocal responses, while dashed (black) lines indicate nonreciprocal interactions or vocal responses. Adapted from Kulahci et al (2015).

的探究有助于深入了解个体间的社会关系，尤其是那些在野外难以直接观察和追踪的动物类群(McGregor & Peake, 2000)。不少研究表明，个体在社交网络中的位置与其适合度密切相关(Barocas et al, 2011; Formica et al, 2012; Wey & Blumstein, 2012)。那么，个体在声讯网络中的位置是否同样可以反映性别、年龄和社会地位等属性?中心度较高的个体能更快地获得和传播信息，它们是否因此而具有更高的适合度收益?对这些问题的回答，有助于全面揭示声音交流对动物生存和繁殖的影响。

蛙类的繁殖求偶高度依赖于声音通讯(Gerhardt & Huber, 2002)，求偶场中此起彼伏的鸣声形成了一个典型的声音通讯网络。雄蛙的广告鸣叫(advertisement calls)不仅是吸引配偶的关键信号，也是雄性竞争的重要手段。通常，雄蛙会窃听竞争对手的求偶信号进而调整自己的鸣叫策略，如改变鸣叫频次或鸣叫时机(Deng et al, 2020; Legett et al, 2021)。由此可见，蛙类的声讯网络结构可能受竞争环境影响。Deng和Cui (2019)利用ASNA定量研究了外来竞争者对仙琴蛙(*Nidirana daunchina*)种群原有鸣叫格局的影响，通过记录每次事件的鸣声发出者及回应者，作者发现尽管声讯网络的拓扑结构发生了改变，但群体水平的鸣叫活跃性、接近中心度和中介中心度在干扰前后无显著差异。雄性仙琴蛙具有在池塘边缘建造泥穴的习性，它们通常在洞穴内部或洞穴边鸣叫求偶(Cui et al, 2010, 2012)。因此，针对个体数量较少的自然种群，实验者通过方位和

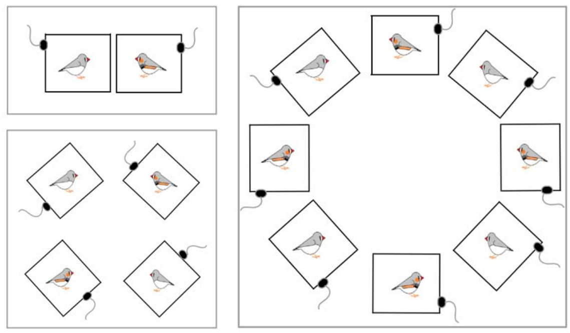

图2　群体大小和组成对鸣叫活动影响的实验装置示意。群体分别由2、4、8只斑胸草雀(*Taeniopygia guttata*)组成，每个笼子顶部装有麦克风。配对的雌雄个体被放置于相邻的笼子，以降低应激性。改自Fernandez等(2017)。

Fig. 2　Graphical representation of the experiment of the impact of group size and composition on vocal activity. Groups of two, four and eight zebra finches (*Taeniopygia guttata*) were formed, with one bird per cage and one microphone on the top of each cage. Pair mates were put in neighboring cages to reduce stress. Adapted from Fernandez et al (2017).

鸣声特征就能实现个体识别并记录鸣叫互动(Deng & Cui, 2019)。为研究室内小种群的声讯网络，研究人员开发了相应的设备和技术，以便人为控制参与声音交流的成员或声音信号的传递路径(Fernandez et al, 2016; Rychen et al, 2021)。比如，Fernandez等(2017)将斑胸草雀(*Taeniopygia guttata*)单笼放置，在每个笼子的顶部安装麦克风，并设置了不同群体大小和成员组成(图2)。相邻笼子之间的距离相等，以此控制个体间的距离。通过分析个体间的声音交流，Fernandez等(2017)探究了群体大小和成员组成是否影响个体鸣唱的同步化，以及配对关系和空间距离对两两个体间鸣唱互动的影响。

在自然条件下, 动物声音交流的动态过程要复杂得多: 参与声音交流的个体数量较多、空间距离较远, 个体所处的位置不断变化, 不同个体的鸣声会出现不同程度的重叠等等。Jenikejew等(2020)以焦点动物法记录了白犀牛(*Ceratotherium simum simum*)的发声行为及叫声类型, 设定与焦点动物的距离不超过3 m (1只成年白犀牛的最大体长)的个体均为声音信号的接收者。该研究展示了如何基于个体的空间距离建立声讯网络, 但由于数据收集方式的局限性, 不可避免地会漏掉部分交流事件, 从而无法全面、准确地揭示群体成员的声音交流格局。对于自然种群, 想要准确识别每个个体、明确信号的发出者与接收者, 仅通过实验者直接观察或依靠一两个监测设备是难以实现的, 而这些信息恰好是利用ASNA建立声音通讯网络的必要前提。

被动声学监测(passive acoustic monitoring)技术被广泛用于陆生动物的声学研究、物种多样性调查及活动监测(Blumstein et al, 2011; Pérez - Granados & Traba, 2021), 麦克风阵列(microphone array)能大范围同时记录多个体的鸣声, 并根据声音信号抵达时间的差异定位每个个体(McGregor, 2005; Jones & Ratham, 2009)。另一方面, 随着算法的发展, 人们可基于鸣声特征识别类群、物种、性别、个体以及鸣叫类型(Terry et al, 2005; Bedoya et al, 2014; Gibb et al, 2018)。理论上, 利用被动声学监测技术能准确识别信号的发出者及回应者, 从而记录群体内的声音交流过程, 为全面揭示声讯网络格局的动态变化提供技术支持。

2.2 分析鸣声相似性

ASNA不仅能用于量化各种社交互动(如肢体接触、声音交流、聚群行为), 实际上, 它能量化个体间的任意一种共享属性, 如遗传关系、共享病原体(Rollins et al, 2012; VanderWaal et al, 2014b; Arnberg et al, 2015), 甚至鸣声相似性(Deng et al, 2021)。动物的鸣声特征通常存在个体差异, 这与个体的体型、年龄、性别等都有一定关系。在更大的空间尺度上, 动物鸣声的地理变异也普遍存在。一方面, 环境异质性产生的不同选择压力导致了鸣声的局部适应性进化(Branch & Pravosudov, 2020); 另一方面, 动物的配偶选择或社会学习过程促进了鸣声的地理变异(Henry et al, 2015; Araya-Salas et al, 2019)。方言和文化差异形成后, 性选择压力会增加鸣声的分化程度, 在地理隔离的作用下可能最终导致物种分化(Slabbekoorn & Smith, 2002; Gerhardt, 2013; Wilkins et al, 2013; Wang et al, 2022)。

在现有的相关研究中, Mantel tests (Mantel, 1967)常被用于分析个体(群体)的鸣声相似性与空间距离之间的关系(Akçay et al, 2014; Sosa-López & Mennill, 2014), 判别分析或分层聚类则常被用于评估个体(群体)在鸣声特征上的"聚集"程度(Pérez-Granados et al, 2015; Branch & Pravosudov, 2020)。前者基于空间距离矩阵和鸣声相似性矩阵揭示鸣声的地理格局, 后者则基于鸣声参数的相似性对目标对象进行归类。然而, 仅依靠Mantel tests分析来探究某种特征与鸣声相似性的关系并不总是适用, 而判别或聚类分析无法揭示鸣声相似格局的形成原因。ASNA不仅包含了上述两类分析手段, 还提供了更完善的理论框架和更全面的分析方法, 可用于探究鸣声特征多样化的进化过程, 并通过可视化的网络图予以呈现。

Potvin等(2019)利用ASNA研究了13个灰胸绣眼鸟(*Zosterops lateralis*)种群的鸣唱共享(song sharing)格局, 他们首先通过鸣唱网络图直观展示了处于相似经度的种群比处于相似纬度的种群有着更高的共享水平。为了探究空间距离能否反映种群间的鸣唱相似性, 他们估算了每个种群的特征向量中心度, 作为衡量目标种群的鸣唱曲目与其他所有种群的总体相似度的指标, 并利用多元回归二次分配程序(multiple regression quadratic assignment procedure, MRQAP)分析了鸣唱共享水平是否受种群间的空间距离、遗传关系及生境类型的影响(Potvin et al, 2019)。MRQAP是常见的网络分析方法, 它是一种特殊形式的Mantel tests, 可以同时检验一个因变量与多个自变量之间的关系(Dekker et al, 2003, 2007)。此外, 根据不同音节是否共同出现在某一种群, Potvin等(2019)建立了音节网络(syllable network)并以模块化(modularity)反映音节的聚集程度, 进而探究聚在一起的音节是否具有相似的特征(如带宽)。

Yoktan等(2011)探究了北非橙簇花蜜鸟(*Nectarinia osea*)方言的地理格局, 发现鸣唱的聚集模式与种群的地理分布部分相关, 表明种群的拓殖

历史在方言的形成中起到一定作用。特征向量中心度较高的种群可以看作是方言的传播者(起源地), 中心度最高的3个种群分布在不同的地理位置, 加之种群的遗传距离与方言地理格局的相关性并不显著, 暗示了社会学习是方言形成与维持的主要驱动力(Yoktan et al, 2011)。除了研究鸣声相似性的地理格局, ASNA也能用于建立个体间的鸣声网络。为了探究个体在鸣声网络中的位置是否影响其繁殖成功, Potvin等(2019)建立了歌带鹀(*Melospiza melodia melodia*)的音节共享网络, 并估算了每个个体的特征向量中心度和中介中心度, 结果显示歌带鹀的中心度与孵化的雏鸟数量、离巢的雏鸟数量的相关性均不显著。在该研究中, 特征向量中心度反映了目标个体与其他所有个体音节的整体相似度, 而中介中心度则用于衡量目标个体在群体中传递信息的重要性。

2.3 解析鸣声结构

鸟类和兽类通常拥有相对丰富的曲目(repertoire), 许多物种会利用功能性参照鸣叫(functionally referential calls)向同类或异种个体警示特定的危险(Casar & Zuberbuhler, 2012; Suzuki, 2018, 2020)。另一方面, 不同鸣叫以一定顺序排列组合后能表达某种特定的含义, 甚至形成句法(syntax) (Arnold & Zuberbuhler, 2006; Ouattara et al, 2009; Suzuki et al, 2018)。鸟类的鸣唱尤为复杂多变, 某些物种的鸣声由一些以固定的顺序重复出现的单一的音节(syllables)或短语(phrases)组成, 而某些物种的鸣声则由数十个、数百个不同音节或短语组合而成, 且随着社会环境的变化呈现不同的组合方式(Okanoya, 2004)。动物的声音信号常被用于雄性竞争、吸引配偶和社会交往, 由于鸣声结构与其功能密切相关, 对鸣声结构的解析有助于深入理解动物的竞争策略以及声音通讯的进化。

在早期关于鸣声复杂性的研究中, 人们通常关注于单一鸣声参数, 如曲目大小(即不同音节、短语或鸣声类型的总数量)。然而, 单一鸣声参数无法准确、全面地描述具有较大曲目物种的鸣声特征及复杂程度。此外, 马尔科夫链分析(Markov chain analyses)被用于研究不同鸣声单元之间的转换率, 在一定程度上揭示鸣声单元间的传递规律(Bernal et al, 2009; Markowitz et al, 2013; Bhat et al, 2022)。尽管如此, 由于该方法难以清晰反映鸣声序列结构, 以及鸣声单元传递模式与鸣声序列结构间的关系, 因此在分析具有较大曲目的鸣声结构时存在局限性。基于图论和数学模型的ASNA为研究动物鸣声结构提供了新的视角。首先, 利用ASNA可以将一段鸣声序列以网络图的形式呈现, 图中的节点可以代表任意水平的鸣声单元, 如音节、短语或某种叫声。比如, 图3(A)是加州弯嘴嘲鸫(*Toxostoma redivivum*)的鸣唱频谱图, 鸣唱时长为20 s, 共包含71个短语(共25种类型)。图3(B)和图3(C)分别是基于鸣唱序列建立的无向网络图和有向网络图。鸣声网络图直观展示了短语之间的连接模式和传递顺序, 以及短语的聚集程度(Sasahara et al, 2012)。

其次, ASNA提供了一系列量化鸣声网络结构的指标, 如网络直径、平均路径长度、聚集系数等。在鸣声网络中, 平均路径长度的值越大, 意味着鸣声序列中音节(或短语等任意的鸣声单元)的序列相对固定; 值越小, 则意味着鸣声更加灵活多变, 音节重复出现的次数较多。聚集系数反映了不同音节在鸣声序列中同时出现、形成小群体的总体趋势, 它的值在0到1之间, 0表示没有形成小群体, 1表示整个网络图形成了一个群体, 即任意两个音节都是相连接的(Deslandes et al, 2014)。利用聚集系数和平均最短路径(average shortest path), 可以得到一个评估整体网络结构的指标——小世界系数(small-world coefficient, *S*), 计算公式为:

$$S = \frac{C / C_{rand}}{L / L_{rand}} \quad (1)$$

其中, C和L分别为观测数据得到的聚集系数和平均最短路径, C_{rand}和L_{rand}分别为随机化网络得到的聚集系数和平均最短路径。若小世界系数的值大于1, 且聚集的音节在一定程度上形成了模块化, 则表示鸣声网络中存在小世界(Humphries & Gurney, 2008; Cody et al, 2015)。小世界的存在表明某些鸣声单元之间的路径较短、连接紧密, 这意味着它们在鸣声序列中经常“扎堆”出现。Allen等(2019)利用连续13年的监测数据分析了座头鲸(*Megaptera novaeangliae*)的鸣声结构, 发现每年的鸣声网络都能形成明显的小世界网络, 表明座头鲸具有稳定的鸣声结构特征。

上述指标从不同角度揭示了网络中鸣声单元之间的连接性(connectivity)，传递性(transitivity)则是另一个量化鸣声结构的重要指标(Sasahara et al, 2012; Deng et al, 2022)。一个复杂的网络通常包含了反复出现的模式，被称为网络模体(network motif) (Milo et al, 2002)。在鸣声网络中，模体则是反复出现的一段鸣声序列。如果一个特定的鸣声单元总是出现在某些鸣声单元之后，便会形成确定性模体(deterministic motif，图4A，B)，反之则为非确定性模体(non-deterministic motif，图4C，D) (Sasahara et al, 2012)。因此，传递模体(transition motif)反映了鸣声单元在出现顺序上的变异性。由于传递具有方向性，所以在分析鸣声单元传递模式时通常使用有向网络(directed network)。每个鸣声单元之前或之后都可能连接着其他不同的单元，根据每个鸣声单元的点入度和点出度所占的比例，便可以估算出鸣声序列的传递模体(Weiss et al, 2014)。对鸣声单元连接方式及传递模式的比较研究，为进一步探究鸣声的功能、句法以及动物的语音学习(vocal learning)奠定了基础。

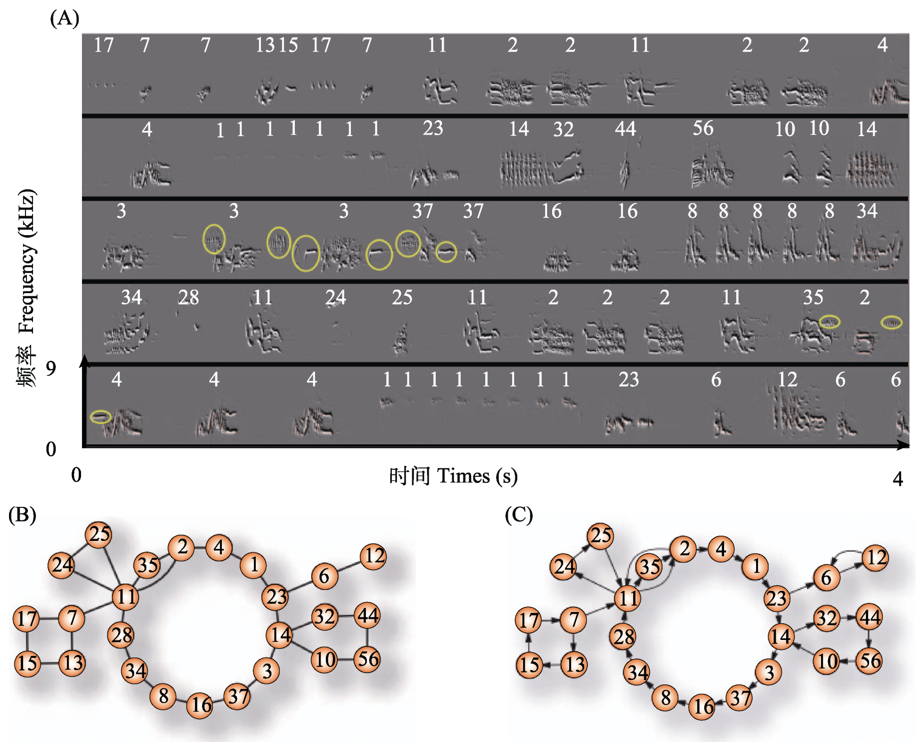

图3　加州弯嘴嘲鸫(*Toxostoma redivivum*)的一段鸣唱序列。(A)鸣唱序列的频谱图，每个短语有特定的数字编号，黄色圆圈中是其他个体的鸣声。(B)和(C)是基于鸣唱序列建立的无向网络和有向网络，展示了短语的传递模式(省略了短语的自身传递)。改自Sasahara等(2012)。

Fig. 3　Song fragment from a California thrasher (*Toxostoma redivivum*) recording. (A) Sound spectrogram of part of a song. Phrases are labeled with their ID numbers. Yellow circles denote background singing of other birds. (B) and (C) are song undirected and directed networks constructed from the song fragment shown in A, which represent transition patterns of phrases (self-transitions are omitted). Adapted from Sasahara et al (2012).

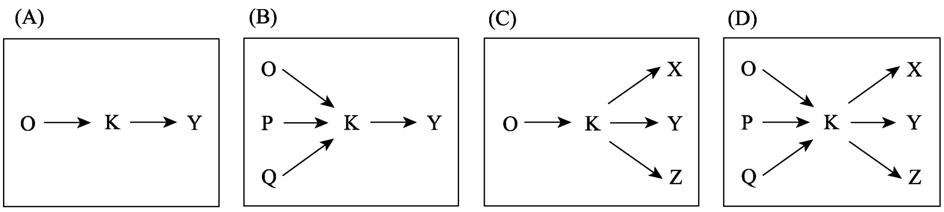

图4　四种传递模体的图示。字母代表不同的鸣声单元，箭头表示传递方向。(A)单向型；(B)瓶颈型；(C)树枝型；(D)沙漏型。

Fig. 4　Diagrams representing the four types of transition motifs. Letters indicate different acoustic units, and arrows indicate transition direction between units. (A) One-way; (B) Bottleneck; (C) Branch; (D) Hourglass.

3 结语

本文结合现有的研究实例，阐述了ASNA在动物声音交流、鸣声相似性及鸣声结构研究中的应用。对动物声音通讯的研究最初只是基于由信号发出者、传播媒介和信号接收者组成的小系统，20世纪90年代起，人们开始关注由多个信号发出者和多个接收者组成的通讯网络(McGregor & Peake, 2000)。然而，长期以来对动物声音通讯网络的探讨，基本停留在理论描述阶段，或只有一些简单的分析(McGregor, 2005)。ASNA是一套综合了图论及数学模型的分析工具，能够真正从“网络”的视角量化动物的声音交流过程，评估个体在声讯网络中的重要性，分析个体在信息传递过程中的作用。利用ASNA研究动物的声讯网络尚处于起步阶段，被动声学监测技术的发展有望促进ASNA在更多动物类群声音交流研究中的应用，进而增进人们对个体间甚至物种间声音通讯的理解。近年来，学者们提出了时序网络(time-ordered networks)、多层网络(multilayer network)等概念，并开发出了相应的分析和作图软件(Blonder et al, 2012; Finn et al, 2019; Finn, 2021)，可用于揭示动物声音通讯格局的动态变化。对声音信号自身的研究，如分析鸣声的相似性或差异性、解析鸣声的序列特征，ASNA也展现出优于传统分析方法之处。利用ASNA提供的一系列指标量化鸣声的个体差异或种群差异、识别独特的鸣声结构，将为理解动物方言的形成机制以及信号复杂性的进化过程提供启示。

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