

DO LIFE HISTORIES SHAPE VOCAL PRODUCTION LEARNING DIFFERENCES IN BIRDS? AN EXPLORATORY APPROACH

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1. Introduction

Vocal production learning (VPL) is the ability to change vocal output as a result of experience (e.g. auditory, be it through modification of spectral and/or temporal aspects of vocalizations or completely novel calls (see (Janik & Slater, 2000) for an influential definition). Despite the structural differences between the human cortex and the avian pallium, similar neural pathways have been proposed for VPL (Fitch, 2017; Jarvis, 2007), involving a direct forebrain (primary motor cortex/arcopallium) projection to the phonatory muscles (larynx/syrinx). Higher encephalization has been associated with complex behavioral traits (Isler & Schaik, 2009), including VPL (Liu, Wada, Jarvis, & Nottebohm, 2013). Charvet and Striedter (2011) proposed that the telencephalic expansion undergone by VPL birds is the result of delayed and protracted neurogenesis in this brain region, with a major effect in some song nuclei during song learning (Liu et al., 2013). In turn, this form of post-hatching maturation of the telencephalon would be promoted by an altricial developmental mode (Charvet & Striedter, 2011). In summary, prolonged brain maturation is likely to lead to an extended developmental period that would benefit the development of complex behavioral traits including VPL. Defining VPL is a non-trivial issue, which we put aside in the present work, which is of an exploratory nature. With this in mind, we opt for a bottom-up approach in which we aim to explore whether differences between birds considered to be VPL and non-VPL naturally emerge from other data. For example, life histories are affected by body mass, such that larger species mature more slowly (Minias & Podlasczuk, 2017). Avian species that learn their vocalizations tend to have relatively small body sizes (Liu et al., 2013). These species would be expected to group closer together by virtue of their small body size. The goals of the present work are the following: i) to explore whether groups reflecting divisions based on VPL/Non-VPL profiles emerge from avian life history traits (i.e., development

trajectories) and two biometric measures, brain mass and body mass; ii) to test whether differences in (adult) relative brain mass (measure here by the ratio of brain-to-body mass) are related to life history traits and contribute to shaping the differences between the groups obtained above.

2. Methods

Data. Six developmental variables representative of life history were used: incubation period, fledging age, period of post-fledging parental care, age of sexual maturity for males and for females, and maximum lifespan. Absolute body size and brain mass were used as biometric variables, as well as the brain-to-body mass ratio (as an approximate measure of relative brain mass). **Sample.** These data were extracted for 1498 species (34 orders) from the literature and public databases (Hoyo et al., 1992; Iwaniuk & Nelson, 2003; Striedter & Charvet, 2008; Myhrvold et al., 2015). After excluding species with missing or unclear data, the final sample consists of 179 species (96 thought to be vocal learners) with several orders and families represented. **Analyses. clustering** In order to explore how VPL and non-VPL birds grouped as a function of their life histories and biometric measures, we ran a hierarchical clustering analysis. Since developmental traits are correlated with one another, we specified Spearman correlation coefficients as the distance metric between clusters. Two hierarchical clusters were built by using the average and Ward's methods (average method: 0.674, Ward's method: 0.657). Non-hierarchical methods were also used to determine whether the groups obtained above emerged naturally from the data (e.g. k -medoid clustering using Partitioning Around Medoids (PAM). Different statistics were calculated over a range of 2 to 7 possible k values. **Permutation.** In order to extend the descriptive results, we tested the different groups obtained for significant differences using a permutation test ($n = 19999$, no replacement). When statistically significant differences were found, Monte Carlo-based permutation was used ($n = 9999$) to assess the effect of random shuffling. Since avian life history traits are correlated with relative brain size, we tested whether the groups obtained in the hierarchical clustering analysis differed in life history traits when controlling for brain-to-body mass ratio ($n = 10000$).

3. Results & discussion

Our analyses yielded the following 3 meaningful clusters: VL (vocal learners, 30 species), NVL (non-VL, 31 species), and a mix of both (MIX, 118 species, 66 vocal learners) (see supplementary materials). VL emerged as the most consistent group throughout our different analyses. Our findings suggest body size to range too widely to be a predictor of bird vocal VPL abilities. We found brain-to-body mass ratio to be related to all life history traits, but it has a significant effect in distinguishing the three groups when related to period of incubation and age of

sexual maturity. We discuss the implications of our results for the study of VPL in birds, and perhaps other species, as well as some cautionary notes.

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