

Analyzing endocrine system conservation and evolution



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ABSTRACT

Analyzing variation in rates of evolution can provide important insights into the factors that constrain trait evolution, as well as those that promote diversification. Metazoan endocrine systems exhibit apparent variation in evolutionary rates of their constituent components at multiple levels, yet relatively few studies have quantified these patterns and analyzed them in a phylogenetic context. This may be in part due to historical and current data limitations for many endocrine components and taxonomic groups. However, recent technological advancements such as high-throughput sequencing provide the opportunity to collect large-scale comparative data sets for even non-model species. Such ventures will produce a fertile data landscape for evolutionary analyses of nucleic acid and amino acid based endocrine components. Here I summarize evolutionary rate analyses that can be applied to categorical and continuous endocrine traits, and also those for nucleic acid and protein-based components. I emphasize analyses that could be used to test whether other variables (e.g., ecology, ontogenetic timing of expression, etc.) are related to patterns of rate variation and endocrine component diversification. The application of phylogenetic-based rate analyses to comparative endocrine data will greatly enhance our understanding of the factors that have shaped endocrine system evolution.

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1. Introduction

Rates of evolution are tremendously disparate across organisms and their constituent traits. Understanding the basis of this variation can provide valuable insights into the biological constraints that restrict trait evolution, as well as factors that promote trait diversification (Raff, 1996; Kirschner and Gerhart, 1998; Carroll, 2005). Many components of endocrine systems are both multifunctional and essential, thus significant alterations to these systems can result in pervasive pleiotropic effects with deleterious consequences. This is exemplified by the deep evolutionary conservation of many endocrine system components and pathways (Gilbert, 2011; Norris and Carr, 2013). However, endocrine systems are known to be important regulators of growth, differentiation, reproduction, and behavior, which are among the major axes of metazoan evolution (Schluter, 2000; Streelman and Danley, 2003; Coyne and Orr, 2004; Gilbert, 2011; Norris and Carr, 2013). Therefore, variations in endocrine system components are likely to have been major drivers of metazoan diversification. Yet, relatively few comparative studies have quantified the conservation and evolutionary flexibility of endocrine system traits, or tested for the factors that promote their diversification.

Phylogenetic-based comparative analyses are critical for understanding patterns of trait evolution (Felsenstein, 1985; Harvey and Pagel, 1991). The sophistication of these methods and the diversity of questions that they can address have flourished over the last two decades. These include statistical phylogenetic methods to analyze the distributions of traits on a phylogeny, patterns of trait correlations, and rates of trait diversification (Garland, 1992; Martins, 1994; Pagel, 1994; Schluter et al., 1997; Pagel et al., 2004; O'Meara et al., 2006; Beaulieu et al., 2012; Hadjipantelis et al., 2013; Jones and Moriarty, 2013; Adams, 2014; Denton and Adams, 2015; Goolsby, 2015). These analyses have been heavily applied to morphological, physiological, and ecological traits, but rarely to endocrine system traits (some examples discussed below). This may be in part due to the fact that many endocrine system components are inherently dynamic across ontogeny, which challenges quantification. Furthermore, many methods used to quantify endocrine components yield values that are not directly comparable across species. Nucleotide and amino acid based components are, however, readily obtainable and can be directly comparable among even divergent taxa. In parallel with the development of phylogenetic comparative methods, the field of molecular evolution has produced statistical frameworks to analyze patterns and rates of nucleotide and protein substitutions among species (Yang and Bielawski, 2000; Lanfear et al., 2010). The application of high-throughput sequencing methods to the genomes

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and transcriptomes of even non-model species provides the opportunity to collect large-scale comparative data for many evolutionarily relevant endocrine variables (e.g., coding sequences, transcription factor binding locations, cis-regulatory sequences, micro-RNAs, and expression patterns). Consistent quantification of endocrine components across species and analyses of the rates of trait and molecular evolution will significantly enhance our understanding of the factors that drive endocrine system evolution.

This minireview highlights the multitude of points of potential evolutionary variation within endocrine systems, and shows how analyzing the evolutionary rates of endocrine traits, genes, and proteins (individually or across pathways) can elucidate patterns and drivers of endocrine systems conservation and evolution.

2. Endocrine system conservation and evolutionary flexibility

Our most intricate knowledge of molecular endocrine mechanisms is primarily based on studies of divergent model organisms, and broad-scale comparisons of these taxa have identified both highly divergent and strictly conserved components of the endocrine system (Heyland et al., 2005). Many features are similar (or identical) in structure or function among highly divergent species, in some cases showing conservation over hundreds of millions of years. For example, thyroid hormone-like molecules and thyroid hormone receptors can be traced to the common ancestor of bilaterians (~700 MYA; Wu et al., 2007; Laudet, 2011; Huang et al., 2015). Functionally, thyroid hormone control of postembryonic remodeling is evident across osteichthians (~430 MYA; Brown, 1997; Norris and Carr, 2013; Shi, 2013), and even short, orthologous genomic response elements for thyroid hormone receptors share gene regulatory mechanisms across divergent tetrapods (~350 MYA; Bagamasbad et al., 2015).

Despite the deep conservation of some endocrine components, this multi-faceted system offers a wealth of material for evolution. Components can diversify along at least two dimensions: (1) through duplication to produce paralogous components, and (2)

through the modification of a given homologous (orthologous) component among species (Fig. 1; Table 1). Even a relatively simple endocrine pathway includes dozens of components that could be changed in composition, direction, magnitude, or ontogenetic timing (Table 2). The composition of components available to an organism is also shaped by the loss (extinction) of ancestral components (Fig. 1), and collectively these evolutionary changes (duplication, modification, and loss) can lead to major phenotypic consequences. Analyzing evolutionary rates of paralogous and orthologous endocrine components (traits) across species in a phylogenetic context allows for a variety of evolutionary inferences, including what factors drive their conservation and diversification.

3. Diversification of endocrine traits

Ordinary statistical analyses of trait or genome evolution among species are encumbered by the fundamental problem of phylogenetic non-independence of data points (Felsenstein, 1985). This has been addressed through the development of a variety of phylogenetic comparative methods that can be used to analyze trait or genome evolution while correcting for relatedness of species. Several studies have used phylogenetic comparative methods to test whether variations in endocrine traits are correlated with other phenotypic traits. These include tests for relationships between growth factor levels with life history (Stuart and Page, 2010; Swanson and Dantzer, 2014), reproductive hormones with mating strategies (Garamszegi et al., 2005), and “stress” hormones with ecology (Brischoux et al., 2015), morphology (Lendvai et al., 2013), and social interactions (Abbott et al., 2003). The theory and application of phylogenetic correlation tests to endocrine (signal) data have been recently reviewed (Swanson and Snell-Rood, 2014). Here I review a different, but intimately related, set of phylogenetic comparative analyses that are used to compare rates of trait evolution across clades (Garland, 1992; O’Meara et al., 2006). In the simplest sense, evolutionary rate analyses are based on the premise that trait variation has the potential to change over time. However, biological constraints can restrict trait evolution, whereas the removal (or circumvention) of constraints can provide opportunities for traits to vary (Raff, 1996; Kirschner and Gerhart, 1998; Carroll, 2005). In other words, comparatively low rates of trait evolution (conservation) indicate the action of biological constraints from stabilizing selection, while relatively high rates of trait evolution (flexibility) may indicate relaxed constraints and/or strong directional selection. Analyzing rates of trait evolution across species can be used to test for factors associated with trait conservation and evolution.

The application of phylogenetic-based rate analyses to endocrine traits can address many outstanding questions in endocrine system evolution. For example, how has ecology influenced the diversification of endocrine components? This analysis requires: (1) continuous data that represent variation in an endocrine trait across at least several species (see Table 2 for trait examples), (2) categorical ecological data for the same set of species (aquatic vs. terrestrial in the example; Fig. 2), and (3) a phylogeny for these species with branch lengths that approximate time. Procedurally, the categorical trait (in this case ecology) is stochastically mapped onto the phylogeny in repetition (Nielsen, 2002). These maps are based on the branching structure (topology) of the phylogeny and the distribution of the categorical trait among the included species. In total, the maps represent an estimate of the collective amount of history (t , time) that the lineages (included in the phylogeny) have exhibited each ecological trait. In other words, the total amount of evolutionary time that one ecological trait was exhibited compared to another across the clade. The rates of change of the continuous trait (in this case the endocrine component) can then be calculated for each ecological category across

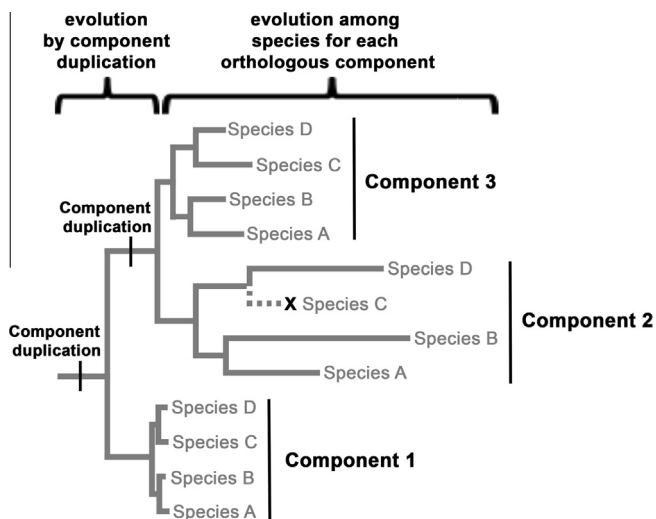


Fig. 1. Dimensions of component evolution. The two levels of component evolution are by component duplication, and by modification of orthologous components among species. In this example, there were two duplication events in the common ancestor of species A, B, C, and D that resulted in components 1, 2, and 3. Components 1, 2, and 3 have evolved at different rates. Component 1 is the most conserved (shortest branch lengths among species) and component 2 is most variable. Branch lengths represent number of changes. Species C lost component 2 (signified by the X), and therefore only retains components 1 and 3. Functionally equivalent components can also be independently derived in a system through *de novo* evolution (see Section 5).

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