

Correlated evolution of maternally derived yolk testosterone and early developmental traits in passerine birds

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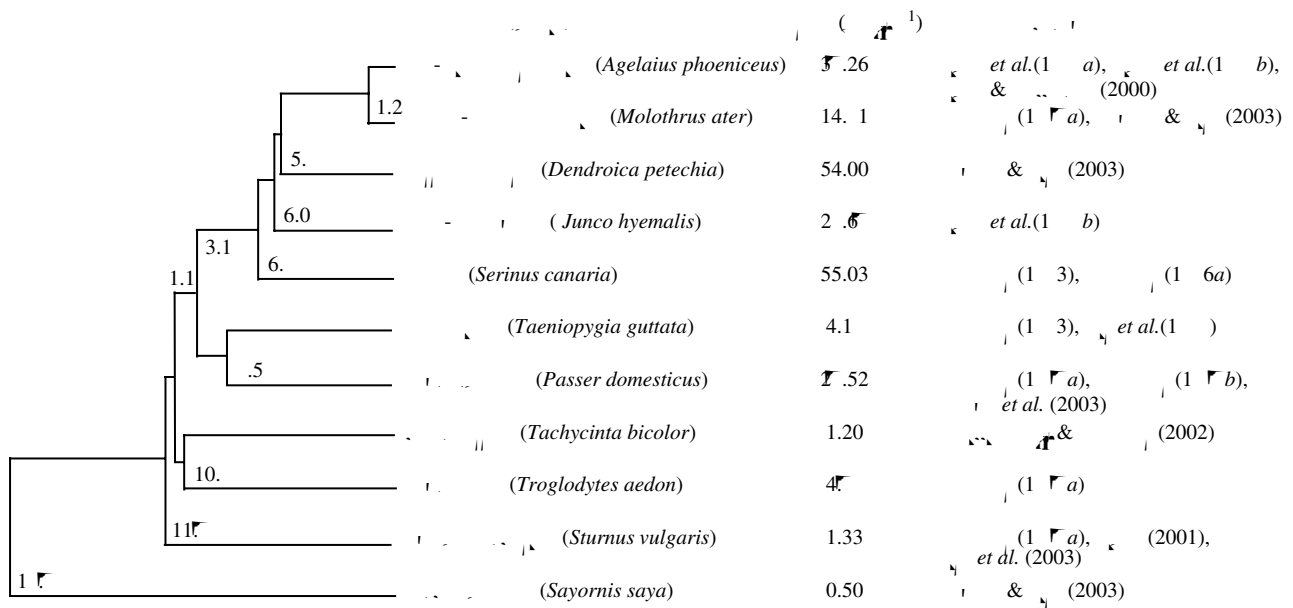
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Recent studies on hormone-mediated maternal effects in birds have highlighted the influence of variable maternal yolk androgen concentration on offspring phenotype, particularly in terms of early development. If genetic differences between laying females regulate variation in yolk hormone concentration, then this physiological maternal effect is an indirect genetic effect which can provide a basis for the co-evolution of maternal and offspring phenotypes. Thus, we investigated the evolutionary associations between maternally derived yolk testosterone (T) and early developmental traits in passerine birds via a comparative, phylogenetic analysis. Our results from species-correlation and independent contrasts analyses provide convergent evidence for the correlated evolution of maternal yolk T concentration and length of the prenatal developmental period in passerines. Here, we show these traits are significantly negatively associated (species-correlation: $p < 0.001$, $r^2 < 0.85$; independent contrasts: $p < 0.005$). Our results highlight the need for more studies investigating the role of yolk hormones in evolutionary processes concerning maternal effects.

Keywords: maternal effects; yolk hormones; testosterone; early development; independent contrasts

1. INTRODUCTION

Recent work on maternally derived yolk hormones in avian syyDUCTION



(b) Data analysis

We used species-correlation and independent contrasts analyses to test for evolutionary associations between maternally derived yolk T concentration and offspring early developmental traits. Species-correlation analyses assume inter-specific data are phylogenetically independent (Martins 2000) and describe current associations between extant taxa (Price 1997). Independent contrasts analyses incorporate phylogenetic information into comparative data to control for the statistical problems associated with species-relatedness (Felsenstein 1985; Martins 2000), and are therefore more conservative. We report the results of both analyses as similarity in

results is suggestive of robust relationships, while discrepancies may be biologically relevant (Ricklefs & Stark 1996; Price 1997).

We derived phylogenetic relationships from the DNA-DNA hybridization phylogeny reported by Sibley & Ahlquist (1990; Figure 1) for use in independent contrasts analyses. COMPARE software 4.5 (Martins 2003) was used to produce independent contrasts of maternal yolk T and offspring early developmental trait data. Adequate standardization of independent contrasts was tested by regression of the absolute value of the contrasts by their standard deviation (Garland et al 1992). All contrasts were adequately standardized for all analyses ($p < 0.05$). Species-correlation and

independent contrasts analyses were analysed using linear regression models in JMP 4.0 (2001). Independent contrasts analyses forced the regression line through the origin (Garland et al 1992).

3. RESULTS

(a) Species-correlation analyses

Linear regression analyses of species yolk T concentration and length of the prenatal developmental period indicated these traits were significantly negatively related ($p < 0.001$; $r^2 = 0.85$; [figure 2 a](#)). Furthermore, species yolk T concentration was significantly negatively associated with length of the postnatal developmental period ($p < 0.02$; $r^2 = 0.49$; [figure 2 b](#)).

