Brain size evolution in pipefishes and seahorses: the role of feeding ecology, life history and sexual selection

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Abstract
Brain size varies greatly at all taxonomic levels. Feeding ecology, life history and sexual selection have been proposed as key components in generating contemporary diversity in brain size across vertebrates. Analyses of brain size evolution have, however, been limited to lineages where males predominantly compete for mating and females choose mates. Here, we present the first original data set of brain sizes in pipefishes and seahorses (Syngnathidae) a group in which intense female mating competition occurs in many species. After controlling for the effect of shared ancestry and overall body size, brain size was positively correlated with relative snout length. Moreover, we found that females, on average, had 4.3% heavier brains than males and that polyandrous species demonstrated more pronounced (11.7%) female-biased brain size dimorphism. Our results suggest that adaptations for feeding on mobile prey items and sexual selection in females are important factors in brain size evolution of pipefishes and seahorses. Most importantly, our study supports the idea that sexual selection plays a major role in brain size evolution, regardless of on which sex sexual selection acts stronger.

Introduction
Brain size is remarkably variable among vertebrates (Jerison, 1973). This variation has been proposed to be formed through adaptations to different ecological and social environments (Jerison, 1973; Striedter, 2005) and the costs of developing and maintaining a larger brain (Aiello & Wheeler, 1995). Phylogenetic comparative studies have revealed three particular aspects that are related to brain size evolution (Striedter, 2005). First, various aspects of feeding ecology have been shown to be associated with relative brain size (i.e. brain size after controlling for body size), such as consumption of food items that are cognitively challenging to find or catch (Cluttonbrock & Harvey, 1980; Garamszegi et al., 2002; Hutcheon et al., 2002), wide diet breadth (MacLean et al., 2014) and propensity for consuming novel food items (Garamszegi et al., 2005; Lefebvre et al., 2016). These studies indicate that selection for the ability to explore and exploit food resources may be a common underlying force for adaptive brain size evolution (Striedter, 2005; MacLean et al., 2014). However, the advantages of having large brains come with increased energetic costs of brain development and maintenance (Mink et al., 1981). An increase in brain size over evolutionary time (encephalization) should therefore be accompanied by modifications in energy allocation (Isler & van Schaik, 2009; Tsuboi et al., 2015, 2016) and/or acquisition of more energy rich food resources (Aiello & Wheeler, 1995). Second,