

Phylogeny and evolution of rodent copulatory behaviour

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Abstract. Variation in rodent copulatory behaviour among species of neotomine-peromyscine rodents of the New World murids (Muridae: Sigmodontinae) was analysed from a phylogenetic perspective and found to be influenced by descent from common ancestry. A cladistic analysis revealed that behaviour was consistent with a phylogeny derived from morphological characters. Primitive species display a mechanical lock between partners, whereas more derived species show no lock but produce a copulatory plug. The more derived species also display increased complexity in the copulatory sequence. Phylogenetic patterns in rodent copulatory behaviour hold implications for our understanding of the evolution of copulatory behaviour in rodents and underscore the advantage of including rigorous phylogenetic analyses in studies of animal behaviour.

The morphology of male genitalia in animals displaying internal fertilization has long been recognized by systematists for its phylogenetic information. Morphological characters of the genitalia have been used to describe new species and delineate relationships within groups (for a review see Eberhard 1985). Hooper & Musser (1964a, b) applied the method to rodent systematics when they analysed relationships within neotomine-peromyscine species of the New World murid rodents. Within one genus, *Peromyscus*, the relationships based on morphology of male genitalia proposed by Hooper & Musser (1964b) were later substantiated and supported by genic and chromosomal analyses of the group by Stangl & Baker (1984).

Despite the relationship evident between phylogeny and the copulatory organ of rodents, no similar relationship was demonstrated between phylogeny and copulatory behaviour. Dewsbury (1975a) found only diversity and convergence in copulatory patterns among 31 species of murid rodents studied in his laboratory. He concluded that copulatory patterns may be evolutionarily labile and determined by selective pressures within the habitat. This disparity between morphology, behaviour and phylogeny is intriguing. Is the evolution of rodent copulatory behaviour uncoupled from the evolution of the copulatory organ? Is there any reason why one should expect morphology and

behaviour to evolve in tandem and copulatory behaviour to be influenced by phylogeny?

To examine these questions we re-analysed the diversity of rodent copulatory behaviour described by Dewsbury (1975a) from a phylogenetic perspective. Such a re-analysis is warranted for several reasons. First, since Dewsbury's analysis in 1975, new phylogenetic hypotheses have been proposed and the copulatory behaviour patterns of additional species have been described (e.g. Estep & Dewsbury 1976; Dewsbury 1979b). Second, because of the limited database, Dewsbury (1975a) examined patterns among species across several higher taxonomic assemblages. Parallel evolution among lineages can confound comparative analysis (Harvey & Mace 1982; Felsenstein 1985). Dewsbury's analysis across lineages may have obscured patterns that would be evident if the behaviour patterns were compared within a lineage. We had sufficient behavioural data for the monophyletic neotomine-peromyscines, a tribe of the subfamily Sigmodontinae in the family Muridae (Carleton & Musser 1984), to examine this possibility. Third, cladistic techniques, which traditionally have been used in the construction of phylogenies, are now being used by comparative biologists to analyse evolutionary patterns in behaviour and ecology (Lauder 1986; Coddington 1988; Sillén-Tullberg 1988). A cladogram is a hypothesis of evolutionary relationship and historical pattern among a given group of organisms. By

