

Original Article

Multilevel social organization and space use in reticulated giraffe (*Giraffa camelopardalis*)

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It is increasingly recognized that association patterns of most gregarious animals are nonrandom. However, nonrandom patterns can emerge in any population that exhibits spatial structure, even if individuals associate randomly. In species that lack clearly differentiated social relationships characteristic of socially complex mammals, space use patterns must be considered alongside association patterns in order to establish whether nonrandom association patterns are determined by underlying social structure or are merely an artifact of spatial structure. In this study, we simultaneously consider space use and association patterns for a wild population of reticulated giraffe. We examined whether the giraffe's flexible fission–fusion association patterns were embedded in higher levels of social organization. We identified multilevel social organization in which individuals were members of social cliques. Cliques were embedded in larger subcommunities, which in turn were embedded in communities. The frequency with which 2 individuals were observed together was positively correlated with the extent to which their home range overlapped, implying an underlying role of shared space use in determining association patterns. However, membership in cliques and subcommunities was relatively unrelated to space use patterns for males. For females, space use played a much larger role in determining multitiered social organization, which is consistent with a matrilineal-based society characterized by female philopatry. Although giraffe social interactions are highly fluid in nature, it is apparent that association patterns in giraffe are not the result of random fission–fusion events but are embedded within a structured social network characterized by multiple levels of organization.

Key words: association patterns, community structure, data cloud geometry, network analysis, social structure, spatial overlap.

INTRODUCTION

The ecological basis of social organization has had a long history of investigation in behavioral ecology, and it is now understood that ecological factors, such as predation and the distribution of resource, play a crucial role in shaping social structure (Alexander 1974; Rubenstein and Wrangham 1986; Isbell and Young 2002). Animal social structures that are characterized by fission–fusion dynamics exhibit frequent coalescing and dividing of group members into smaller subgroups (Langman 1977; Leuthold 1979; Couzin 2006; Aureli et al. 2008). Fission–fusion dynamics are thought to allow animals to respond to changing environmental conditions and

flexibly balance conflicting demands. They allow animals to form larger groups when there are reproductive, foraging, or antipredator benefits, but to minimize costs of intragroup competition if the benefits of grouping change. Flexible grouping dynamics are exhibited in a broad range of taxa, including shoaling fish (Hoare et al. 2004; Kelley et al. 2011), bats (Popa-Lisseanu et al. 2008; Kerth et al. 2011), primates (Kummer 1968; Symington 1990), carnivores (Schaller 1972; Wolf et al. 2007; Smith et al. 2003), ungulates (Aycrigg and Porter 1997; Cross et al. 2005; White et al. 2010), elephants (Moss 1988; Weitemeyer et al. 2005; Archie et al. 2006b), and marine mammals (Lusseau 2003; Pearson 2009).

Understanding how fission–fusion dynamics influence population structure has important implications for disease transmission (Keeling 1999; Craft et al. 2010; Griffin and Nunn 2012), information flow (McComb et al. 2001; Vital and Martins 2009), mating

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