



Circadian activity rhythms in relation to season, sex and interspecific interactions in two Mediterranean voles

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Although environmental conditions and biotic interactions are widely recognized as key sources of variation in circadian activity rhythms of a broad array of vertebrates, information on their actual significance outside experimental settings remains scarce. We investigated changes in circadian activity rhythms of free-ranging Cabrera voles, *Microtus cabreræ*, and water voles, *Arvicola sapidus*, in highly seasonal Mediterranean environments, and analysed how such changes were further affected by intersexual and interspecific interactions. Cabrera voles were largely diurnal, with a unimodal peak around midday during the wet season, whereas during the dry season activity was reduced during the hot midday period and increased strongly at dawn and dusk. Water voles also had a marked bimodal crepuscular pattern during the dry season, but this was much attenuated during the wet season, when they were comparatively more diurnal. Activity patterns varied little between the sexes, although with a tendency for higher overall activity by male Cabrera voles (dry season only) and water voles, possibly because of intersexual interactions involving seasonal shifts from monogamy to facultative polygyny in Cabrera voles, and year-round polygyny in water vole. Within each season, Cabrera voles appeared to change their activity patterns in the presence of water voles, reducing overall activity and shifting activity peaks towards diurnal (dry season) or crepuscular (wet season) time periods less used by water voles. Overall, this study provides evidence for the strong role of seasonal changes in environmental conditions and interspecific interactions in driving variation in the activity patterns of Mediterranean voles under natural conditions.

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Circadian activity rhythms are part of the adaptations of a species to its environment, reflecting the adjustments in animals' physiology and behaviour to the diel changes in environmental conditions (e.g. Beltrán & Delibes 1994; Erkert & Kappeler 2004). These adjustments probably result from interactions between a number of exogenous abiotic and biotic factors (zeitgebers) and an endogenous biological clock or circadian pacemaker (Goldman 2001; Mistlberger & Rusak 2005), which have been described for a broad array of vertebrates (McNab 2002), including amphibians (Chiba et al. 2003), reptiles (Minutini et al. 1995), birds (Ebihara & Kawamura 1981) and mammals (Halle & Stenseth 2000). The daily light:dark (LD) cycle is a virtually universal zeitgeber for the circadian rhythms displayed by most species (Daan & Aschoff 1975; Bertolucci et al. 1999), implying

that animals that do not live on or near the equator may experience seasonal changes in daylength that require flexible behavioural adjustments to their seasonal circadian activity rhythms (Erkert & Kappeler 2004).

To date, most illustrative examples showing the influence of seasonal changes on species' circadian activity rhythms have used small mammals, and experimental photoperiod treatments designed to identify the outcomes of physiological optimization processes (Halle & Stenseth 2000; Kronfeld-Schor & Dayan 2008). While laboratory studies provide useful information to understand the relative role of endogenous biological clocks and exogenous stimuli in producing seasonal variation in activity timing (Halle & Stenseth 2000), there is mounting evidence that rhythm patterns often differ between captivity and natural settings (e.g. Larrucea & Brussard 2009; Scheibler & Wollnik 2009). This may be related, at least in part, to the matching between seasonal variation in photoperiod and in other environmental conditions such as temperature and food availability, which may produce distinct rhythm patterns from those resulting from simple variation in daylength (Kronfeld-Schor & Dayan 2008). Furthermore, individuals under natural conditions are involved in complex intraspecific and interspecific relations, which

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