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## Early survival in roe deer: causes and consequences of cohort variation in two contrasted populations

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**Abstract** Time- and sex-specific summer survival of roe deer fawns was estimated using capture-mark-recapture methods in two enclosed populations living in contrasting conditions. The population of Trois Fontaines (eastern France) was roughly constant in size throughout the study period, while in Chizé (western France), the population experienced frequent summer droughts and numbers decreased continuously during the study. Early survival of fawns was low and highly variable over the years at both Chizé and Trois Fontaines, and demonstrated marked variations between cohorts that need to be taken into account when modelling roe deer population dynamics. In Trois Fontaines, fawn survival was positively correlated with early body growth and total rainfall in May and June. In Chizé, fawn survival decreased with increasing density and tended to increase with increasing rainfall in May and June and adult female body mass. These factors explained more than 75% of the variability in early survival observed in both populations. Variation between cohorts had different consequences for the two populations. At Trois Fontaines, cohort variation was limited to a numerical effect on early survival. However at Chizé, cohort variation was long-lasting and affected the phenotypic quality of survivors at later ages, and thereby future survival and breeding abilities (both numerical and quality effects). Male and female fawns had similar survival over their first summer in both populations. This result contrasts with the lower survival of young males often observed in ungulates. Two ultimate causes can be proposed to account for the low and variable survival of roe deer fawns over the first summer: the high energy expenditures incurred by does during each breeding attempt and/or the low absolute body size of newborn roe deer fawns.

**Key words** Ungulates · Population dynamics · Density dependence · Environmental variation · Sexual selection

## Introduction

Survival patterns play a fundamental role in the evolution of life history strategies (see Stearns 1992 for a recent review). At the interspecific level, survival accounts for a large part of the variation observed in life history tactics (Partridge and Harvey 1988; Gaillard et al. 1989). Furthermore, both theoretical (Gillespie 1977: Tuliapurkar 1989) and long-term empirical studies (Clutton-Brocket al. 1982, 1992) have demonstrated the importance of variability in survival patterns in shaping population dynamics, and thereby the evolution of life history strategies. In vertebrates, age is a prime source of variability in vital rates (Charlesworth 1980), particularly in survivorship (Caughley 1966; Gaillard et al. 1993a). In large mammals such as ungulates, juvenile survival is generally lower and more variable than adult survival (see Fowler and Smith 1981 for a review). This variation in the survival of offspring from one reproductive attempt to the next is generally expected to induce a selective pressure for a longer reproductive lifespan (Murphy 1968; Gillespie 1977; but see Orzack and Tuljapurkar 1989 for possible exceptions).

Offspring survival is also one of the major components of the variation in lifetime reproductive success (Clutton-Brock 1988). For example, among female red

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