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The effects of a severe drought on mouflon lamb survival

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The mouflon population of Caroux-Espinouse, southern France, inhabits a highly seasonal area with dry summers. We monitored summer lamb survival during a severe drought in 2003, from early June to late August. The survival of 35 radio-tagged lambs over nine two-week periods was strongly affected by the timing of rainfall. Survival depended on the amount of rainfall recorded at a given 14 day period and in the previous 14–21 day period. Survival was not influenced by the exceptionally high mean daily temperature recorded during some periods. Male lamb survival (0.68) tended to be less than female survival (0.81), although not significantly, possibly because of a low sample size. The high lamb mortality (25.7%) recorded during a four-month period is much higher than previous estimates of first-year mortality (less than 10%). We recommend accounting for climatic variation in summer when studying the population dynamics of ungulates.

Keywords: drought; summer lamb survival; mouflon; radio-tagged monitoring; Caroux-Espinouse massif

1. INTRODUCTION

Ungulate mortality is usually a result of either predation (Linnell *et al.* 1995) or starvation (Saether 1997), often interacting with population density or climate variation (Gaillard *et al.* 2000). In predator-free environments, several life-history traits such as body weight, fecundity or survival vary in relation to the variation in local or global climate (e.g. Coulson *et al.* 2000). Among large mammals, survival from birth to 1 year of age is the most sensitive vital rate for variation in weather and density (review in Gaillard *et al.* 2000). However, the timing of juvenile mortality may differ from that for the other age classes and depend more on the seasonal variation in the environment. Whereas most studies on ungulates document a strong impact of severe winters on juvenile survival in highly seasonal environments (e.g. Loison *et al.* 1999; Coulson *et al.* 2001), others suggest that spring–summer may also be a critical period, in some cases being even more important than winter (Saether *et al.* 1996; Gaillard *et al.* 1997). We document a die-off among lambs of mouflon (*Ovis gmelini musimon* × *Ovis* sp.) during the severe drought experienced in southern Europe in summer 2003. More specifically, based on the monitoring of 35 radio-tagged lambs, we addressed the following two questions. (i) Was the timing of lamb mortality synchronized with the timing of the drought? (ii) Was there any between-sex difference in lamb mortality rate?

2. MATERIAL AND METHODS

(a) *Study area*

The study site is on the southwestern border of the Massif Central, in southern France. The population of mouflons inhabits the Caroux-Espinouse massif (43°40′ N, 3°0′ E; elevation 150–1124 m). Weather conditions are variable because of the influence of three climatic regimes (oceanic, Mediterranean and mountain), with hot dry summers (average precipitation 115 ± 11 mm, mean daily temperature 17 ± 0.1 °C in July–August at 850 m), wet autumns and fairly cold winters.

(b) *Data collection*

Between 6 May and 6 July 2003, 19 male and 16 female lambs were trapped, weighed ($n = 31$), individually marked with a radio transmitter-collar (Biotrack) and released. Radio-collars were fitted with a mortality sensor set at 4 h to recover the collars and investigate the causes of death. Radio-tagged lambs were checked at least once a week (66 days of radio-tracking for 120 days of study). Carcasses that were sufficiently well preserved to determine cause of death were necropsied. Mouflons (mainly adults, 4 years or older, harvested from early September to late February) were also weighed to the nearest 0.5 kg with a spring scale.

(c) *Climatic variables*

Daily rainfall and mean daily temperature were obtained from Météo France weather stations, located in the western part of the study area: Cambon et Salvergues (CS) and Fraïsse sur Agoût (FA). CS and FA records were available from 1988 to 2003 and from 1976 to 2002 for rainfall, and from 1999 to 2003 and from 1990 to 2002 for temperature. The mean difference between FA and CS was 0.60 ± 0.02 °C for mean daily temperature and 1.21 ± 0.10 mm for daily rainfall.

To assess the range and magnitude of the drought in 2003, we estimated a summer drought index, calculated as the daily rainfall minus twice the mean daily temperature (Gaillard *et al.* 1997). We then plotted the mean (± s.d.) of daily summer drought indices recorded for 1990–2002 at FA against the daily summer drought index from CS for 2003.

(d) *Statistical analyses*

We estimated lamb survival (denoted by Φ in the following) over two-week periods, using capture–mark–recapture models. The study period extended from the first capture (6 May) to the end of the summer drought (28 August, see § 3), or nine 14 day periods (5 May to 7 September). Based on the monitoring of the radio-tagged animals, we knew whether each lamb survived or died within every two-week interval. The day of death was estimated based on the state of the carcass. We used the staggered entry models (Pollock *et al.* 1989), because captures lasted over several weeks. We tested for the effects of lamb sex, time, trap date and climatic variables (drought index, precipitation and temperature at CS). Because there could be a time delay between drought and death, we tested for the effects of climatic variables in the current 14 day period, and from the previous 7 day periods (see table 1). All analyses used MARK 3.2 (White & Burnham 1999).

Model selection was based on the corrected Akaike Information Criterion (AICc) with a second-order adjustment of the AIC to correct for small-sample bias (Burnham & Anderson 1998). The most-parsimonious model (i.e. lowest AICc) was selected as the best model. When the difference in AICc between two models was greater than 2, we concluded that the models were different, and when the difference was less than 2 we kept the model with the least number of parameters (Burnham & Anderson 1998). We used likelihood-ratio tests among nested models to test specific hypotheses (Lebreton *et al.* 1992).

We compared between-sex differences in lamb body mass (after accounting for differences of date of capture), and the mean adult body mass recorded during the three last hunting seasons, with that recorded in 2003–2004 after the drought period using one-way ANOVAs.

3. RESULTS

The exceptional drought of 2003 occurred between 3 June and 28 August, when the summer drought index was

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Table 1. Modelling summer lamb survival (Φ) of the Caroux-Espinouse mouflon population during the summer drought of 2003 in relation to sex (Φ_{sex}), time (Φ_t), and climatic conditions (precipitation, mean daily temperature, mean daily summer drought index—calculated as rainfall minus twice mean daily temperature; see Gaillard *et al.* (1997)).
(We tested for the effects of the climatic variables of the current two-week period (t), and previous 7 day periods. For the best models, we report (in parentheses) the AICc of a corresponding model without considering the current two-week period. +, additive effect; *, interaction between factors; the number of days of weather records before the current interval are indicated by subscripts. The selected models (lowest AICc) are in bold.)

biological hypothesis	models	AICc
sex effect	$\mathbf{\Phi_t}$	**71.19**
	Φ_{t+sex}	72.65
	Φ_{t*sex}	90.14
timing effect of climatic conditions		
rainfall effect	Φ_t	65.50
	$\Phi_{7\ days}$	63.57
	$\mathbf{\Phi_{14\ days}}$	**57.34 (61.93)**
	$\mathbf{\Phi_{21\ days}}$	**58.68 (63.22)**
	$\Phi_{28\ days}$	66.25
summer drought index effect	Φ_t	73.38
	$\Phi_{7\ days}$	75.52
	$\Phi_{14\ days}$	74.31
	$\Phi_{21\ days}$	74.02
	$\Phi_{28\ days}$	74.66
temperature effect	Φ_t	77.10
	$\Phi_{7\ days}$	76.57
	$\Phi_{14\ days}$	75.93
	$\Phi_{21\ days}$	75.54
	$\Phi_{28\ days}$	75.39

above the range of values recorded between 1990 and 2002 (figure 1). In 2003, rainfall between June and August (52.8 mm) was less than one-third of the average June–August rainfall in 1976–2002 (184.1 ± 17.0 mm), whereas the mean daily temperature (20.0 ± 0.3 °C) was approximately one-third higher than the average (16.0 ± 0.1 °C) in 1990–2002. The pattern of rainfall during the nine 14 day periods of study differed from that recorded between 1976 and 2002 (see figure 2).

Capture date did not influence lamb survival (Φ. versus Φ_{date}: $\chi^2 = 2.31$, d.f. = 1, $p = 0.13$). As expected, lamb survival varied over time (Φ. versus Φ_t: $\chi^2 = 21.17$, $d.f. = 8$, $p = 0.007$). All mortalities occurred within one month, between 18 June and 25 July (figure 1). Median mortality date was 14 July (±12 days). Starvation was the underlying cause of death of the two dead lambs autopsied.

During the study period, six males (32%) and three females (19%) died, but survival rates did not differ statistically between sexes (table 1). As expected in dimorphic ungulates, male lambs tended to be heavier than female lambs at a given date of capture (9.2 ± 0.4 kg and 7.7 ± 0.5 kg on 2 June, $F_{1,27} = 3.72$, $p = 0.06$). Models with the lowest AICc included the amount of rainfall recorded during the current interval and during the previous 14–21 day period. For clarity, we chose to report estimated parameters of model $\Phi_{14\ days}$. Rainfall had a positive effect on lamb survival (logistic slope = 0.14, 95%

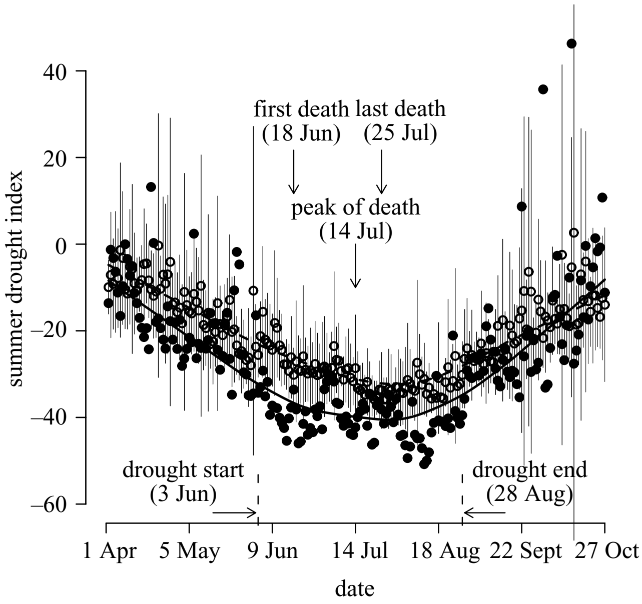

Figure 1. Mean daily summer drought indices (± s.d.) recorded between 1990 and 2002 (normal years, open circles and vertical segments) and in 2003 (drought year, filled circles) from 1 April to 27 October. The summer drought index was estimated as $Pr - 2T$ where Pr and T are precipitation (millimetres) and mean daily temperature (degrees Celsius), respectively (see Gaillard *et al.* 1997). The fitted locally weighted regression for each dataset is shown (smooth span = 0.4, normal years, dashed line; drought year, solid line). Peak of death was calculated following Caughley & Caughley (1974). One value was an outlier in 2003 and was not reported for the sake of clarity.

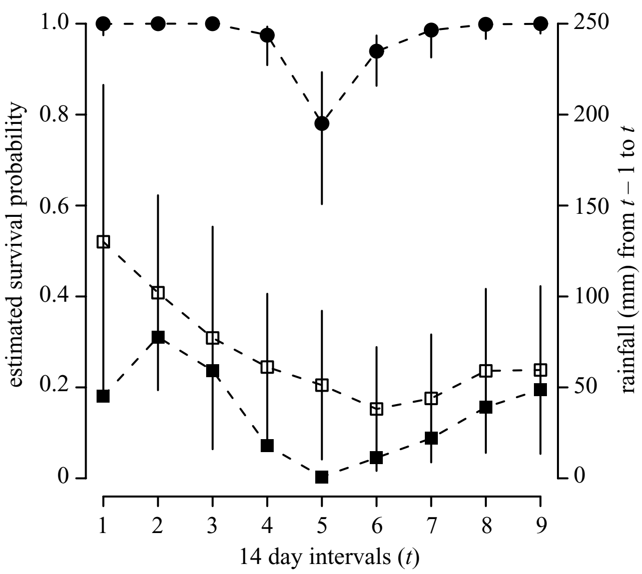

Figure 2. Estimated summer lamb survival (with 95% CI, filled circles) of Caroux-Espinouse mouflons from the selected model $\Phi_{14\ days}$ (see table 1) between 5 May and 7 September (nine 14 day intervals, t) during the severe drought of summer 2003. Rainfall corresponds to the total amount of precipitation (millimetres) recorded from $t - 1$ to t in 2003 (filled squares) and between 1976 and 2002 (open squares, ± s.d.).

CI: 0.05–0.23; figure 2). Models that included the effects of temperature or the summer drought index had much higher AICc than models including rainfall only (table 1).

During the three previous hunting seasons, adult females and males (females: 18.9 ± 0.8 kg, $n = 40$; males: 30.9 ± 0.6 kg, $n = 89$) were heavier than during the season after the drought (females: 17.0 ± 0.6 kg, $n = 13$; males: 27.0 ± 0.7 kg, $n = 46$; $F_{1,184} = 19.35$, $p < 0.001$). The decrease was similar for both sexes (-3.4 ± 0.8 kg, $F_{1,184} = 1.46$, $p = 0.23$).

4. DISCUSSION

First-year survival of ungulates has been repeatedly reported to depend on spring rainfall (e.g. Owen-Smith 1990; Gaillard *et al.* 1997; Portier *et al.* 1998), but rarely on summer drought (Saether *et al.* 1996). Moreover, few studies have analysed the influence of the timing of rainfall upon juvenile survival within a given cohort. We found that the amount of rainfall in the current interval of study, and in the two to three previous weeks, had an immediate positive effect on mouflon lamb survival in a drought year. Our data suggest a short-term and immediate effect of rainfall on lamb survival, with a probable cumulative effect which explains that the last death recorded occurred approximately one month before the end of the drought. Although temperature was much higher in 2003 compared with 1990–2002, only rainfall influenced summer lamb survival. Lamb mortality was therefore more likely to have been caused by the negative effects of water shortage on food biomass and quality, and therefore on animal condition, rather than by heat stress. The decline of mouflon body mass after the drought and the underlying cause of lamb death support this interpretation.

The lack of between-sex difference in summer survival in our population was consistent with previous observations on the long-term study of collared animals (Cransac *et al.* 1997; $n = 346$), but contrasts with the higher survival of young females reported during periodic food shortage in the Kerguelen archipelago (Boussès *et al.* 1994), and in other highly dimorphic and polygynous ungulates (see, for example, Loison *et al.* 1999), especially during stress periods (see, for example, Clutton-Brock *et al.* 1985). The absence of between-sex differences in early survival of mouflon, despite a marked tendency for males to die more than females, is probably due to our small sample size.

The low survival rate recorded for both sexes over nine two-week intervals contrasts with the low first-year mortality reported in this population from collared lambs during previous years ($\Phi_{\text{male}} = 0.92 \pm 0.42$, $\Phi_{\text{females}} = 1$ between 1986 and 1993; Cransac *et al.* (1997)). By contrast, none of the adults radio-monitored throughout summer 2003 died ($n = 13$). Lambs allocate the greatest part of their energy to growth and, having less body reserve than adults, are more likely to die from starvation when environmental conditions become harsh. These results demonstrate that the first months after birth are a critical period in the life history of ungulates (Saether 1997; Gaillard *et al.* 2000). As the European climate becomes warmer and drier than it has been in the past (Hurrell 1995), we recommend considering variation in summer climatic conditions when assessing the population dynamics of ungulates.

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