

# Dynamics of an introduced population of 2 mouflon (*Ovis aries*) on the sub-Antarctic archipelago of Kerguelen

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**Short title:** Irruptive dynamics of Kerguelen mouflon.

4 A commonly reported pattern in large herbivores is their propensity to  
irrupt and crash when colonizing new areas. However, the relative role of  
6 density-dependence, climate and cohort effects on demographic rates in  
accounting for the irruptive dynamics of large herbivores remains  
8 unclear. Using a 37-year time series of abundance in a mouflon (*Ovis*  
*aries*) population located on Haute Island, a sub-Antarctic islands of  
10 Kerguelen, (i) we investigated if irruptive dynamics occurred and (ii) we  
quantified the relative effects of density and climate on mouflon  
12 population dynamics. Being released in a new environment, we expected  
mouflon to show rapid growth and marked over-compensation. In  
14 support of this prediction, we found a two-phase dynamics, the first  
phase being characterised by an irruptive pattern best described by the  
16  $\theta$ -Caughley model. Parameter estimates were  $r_m = 0.29 \pm 0.005$   
(maximum growth rate),  $K = 473 \pm 45$  (carrying capacity) and  
18  $S = 2903 \pm 396$  (surplus) mouflon. With a  $\theta = 3.18 \pm 0.69$  our model also  
supported the hypothesis that density dependence is strongest at high  
20 density in large herbivores. The second phase was characterised by an  
unstable dynamic where growth rate was negatively affected by  
22 population abundance and winter precipitation. Climate, however, did  
not trigger population crashes and our model suggested that lagged  
24 density-dependence and over-grazing were the probable causes of mouflon  
irruptive dynamics. We compare our results with the Soay sheep  
26 population and discuss the possibility of a reversible alteration of the  
island carrying capacity after the initial over-grazing period.

Population dynamics of large herbivores results from complex interactions  
2 between per capita food and climate (Sauer and Boyce 1983, Portier et al.  
1998, Coulson et al. 2000), population age-structure (Coulson et al. 2001),  
4 diseases (Albon et al. 2002) and, when present, predation (Sinclair and Krebs  
2002). Consequently, a wide range of population dynamics has been  
6 documented (Clutton-Brock et al. 1996, Aanes et al. 2000, Solberg et al. 2001,  
Forchhammer et al. 2002, Coulson et al. 2004), determined mainly by the  
8 strength and shape of the relationships between demographic rates with density  
and environmental variations (Clutton-Brock and Coulson 2002, Turchin 2003).

10 In mammals, the response of demographic rates to density and  
environmental stochasticity is age-dependent (Gaillard et al. 2000, Eberhardt  
12 2002) and density-dependence is the strongest at high population densities  
(Fowler 1987, Sinclair 1989). Consequently, populations of large mammals grow  
14 close to their maximum growth rate ( $\lambda_m$ , *sensu* Caughley 1970) over a wide  
range of population densities, quickly reaching and sometimes exceeding the  
16 carrying capacity of their environment ( $K$ , Caughley 1977). A consistent  
observation in large herbivores is that many populations undergo so-called  
18 “irruptive dynamics” (Klein 1968, Caughley 1970, McCullough 1997, Forsyth  
and Caley 2006). An irruption is characterized by three distinct phases  
20 (Caughley 1970, McShea et al. 1997): (i) an exponential increase in population  
size up to a peak abundance followed by (ii) a population crash before (iii) a  
22 second increase to another peak of population size typically lower than the first  
peak of abundance.

24 Irruptive dynamics are expected to occur in newly introduced populations  
because of initially abundant food resources and habitat (Sinclair 1979, Gunn  
26 et al. 2003) but such dynamics can also occur in established populations

(Coulson *et al.* 2004). Diverse factors may trigger the irruption of large herbivores and McCullough (1997) identified three of them as critical: population confinement (see also White 2007), habitat modification, and decrease in predation (referring to both carnivores and humans). For instance, the seminal – though controversial – deer irruption documented by Leopold (1943) seems to have its roots in a combination of a change in the fire regime and an important reduction of predation pressure (Binkley *et al.* 2006). If, in irruptions, the causes of the marked increase in population size are reasonably well understood, the rapid die-off (with up to 90% of the individuals dead within a year) and subsequent dynamics are not (Gunn *et al.* 2003). Delayed density-effects on demographic parameters (Hutchinson 1948), the progressive change in plant structure and quality, a combination of both (Caughley 1977) or a particular combination of climatic events (Gunn *et al.* 2003) have all been suggested as possible mechanisms initiating a population crash.

The Kerguelen population of mouflon (*Ovis aries*) provides an interesting quasi-experimental setup, in a simple ecosystem, to test for the irruptive dynamics of large herbivores. Starting from the introduction of two mouflon to Haute Island, a 37-year time series of regular population surveys has been used to test seven competing models of population dynamics, following the approach of Forsyth and Caley (2006). Because of the high resource availability, we predict ( $H_1$ ) an irruption with a strong over-compensatory effect so that Caughley irruptive models provide the best description of the dynamics (see “Material and Methods” section). At high latitudes / elevations, winter severity prevails over early summer conditions as a limiting factor of ungulate populations (Solberg *et al.* 2001, Weladji *et al.* 2002, Sæther *et al.* 2007) either because of increased costs of locomotion in snow (Crête and Larivière 2003) or

because of food shortage (Albon *et al.* 2002). We then predict (H<sub>2</sub>) a negative  
2 relationship between population growth rate and winter severity measured by  
both local and global climatic indexes. Finally, because of the body size of  
4 mouflon (26 and 38 kg for females and males respectively, Boussès and Réale  
1996) and the sub-Antarctic location of Kerguelen, we predict (H<sub>3</sub>) similar  
6 effects of density and climate on population growth rate (Post 2005) as found  
in the Soay sheep population, the closest match to our study population in  
8 terms of species and climate (Coulson *et al.* 2000).

## Material and methods

### 10 Population studied

The Kerguelen mouflon population is located on Haute Island, a small  
12 sub-Antarctic island (8 km<sup>2</sup>) in the Kerguelen archipelago (48°25'–50° S,  
68°27'–70°35' E, Southern Indian Ocean). The climate is characterized by  
14 year-round precipitation (averaging 420 mm in winter and 330 mm in summer),  
strong winds, and an average temperature of 2°C in winter and 7.5°C in  
16 summer (Météo-France). The island landscape is treeless and dominated by  
rocky and bare soils (68%). An addition 26% is covered by swards and  
18 meadows and 6% by peat bogs (see Chapuis *et al.* 2001, for details). Meadows  
are composed of a few native (cushion plant *Azorella selago*, *Agrostis*  
20 *magellanica*) and introduced species since the XIX<sup>e</sup> century (annual blue grass  
*Poa annua* and dandelion *Taraxacum spp.*). In 1972, twelve additional fodder  
22 grasses were successfully introduced to increase the foraging resources of the  
island (Fig. 1). Some of them (orchard grass *Dactylis glomerata* and meadow  
24 fescue *Festuca pratensis*) have now formed meadows. Overall, half the sward

and meadow areas are dominated by introduced species (Boussès *et al.* 1994).

- 2 The diet of mouflon at our site is dominated by annual blue grass, rush *Juncus*  
3 *scheuchzerioides*, cushion plant and several mosses (Chapuis *et al.* 2001).  
4 Fodder grasses are now part of the mouflon diet on Haute Island but to a lower  
5 extent than the annual blue grass (Chapuis *et al.* 2001). At the same time,  
6 native species such as the dwarf shrub *Acaena magellanica* and the Kerguelen  
7 cabbage *Pringlea antiscorbutica* were grazed by mouflon and therefore kept at  
8 very low densities (Réale *et al.* 1996, p. 51).

The mouflon is a medium sized, grazing herbivore (Chapuis *et al.* 2001).

- 10 The species is polygynous and dimorphic in size, with males being 45% heavier  
11 than females (Boussès and Réale 1996). The rut takes place in May–June and  
12 birth occurs in October–November. Females breed for the first time as yearlings  
13 that produce singletons only, whereas adult females ( $\geq 2$  years of age) carried  
14 twins 36.4% of the time (Boussès and Réale 1998). Mouflon on Haute Island  
15 show the highest reproductive output ever reported in this species, a likely  
16 consequence of crossbreeding with domestic sheep (Boussès and Réale 1998,  
17 Garel *et al.* 2005). One male and one female mouflon were introduced in 1957  
18 to Haute Island (Boussès *et al.* 1994). The population then rapidly established  
19 and increased in size. In addition to mouflon, three reindeer (*Rangifer*  
20 *tarandus*) were successfully introduced on Haute Island in 1956. These animals  
21 established a population that became extinct in 1981 (Fig. 1). Reindeer  
22 abundance was made available to us by repeated surveys, which were first  
intended to monitor the mouflon population.

## Population abundance

2 Population abundance from 1957 to 1988 was obtained from hunting reports by  
volunteers and recorded at the scientific base of Port-aux-Français (data from  
4 Chapuis *et al.* (1994), completed by Réale (1996)). Surveys were performed in  
all but 7 of the 37 years (1975, 1976, 1978, 1981, 1982, 1986 and 1987). During  
6 this period, no standardized transect was used. Abundance of mouflons on the  
island was estimated during the Austral summer (from December to March).  
8 Hunting was allowed and abundance at time  $t$  was estimated by summing the  
number of counted and culled individuals (see White *et al.* 2007, for a similar  
10 approach). During that period hunting did not occur every year and harvest  
size was generally low (10–20 per year) but peaked twice at 50 individuals in  
12 1972 and 1988. We assumed that the density-dependent processes on survival  
and fecundity occurred on the pre-winter population size in April, *i.e.* the  
14 post-breeding population size.

From 1989 to 1995, hunting was forbidden and surveys were standardized.  
16 Two observers walked a unique transect covering 90% of the island in late  
summer, excluding a plateau of high elevation. The rarity of tracks and  
18 droppings observed at high elevation indicated that this area was almost never  
used by mouflon (Réale *et al.* 1996). We acknowledge the low quality of our  
20 data (especially between 1957 and 1988) but, in many respects, they are similar  
to other studies (*e.g.* Sæther *et al.* 2007, White *et al.* 2007).

## 22 Models of population dynamics, model fitting, and selection

All mechanisms expected to produce irruptive dynamics can be expressed with  
24 a discrete time span by difference equation models (three models were reviewed  
by Forsyth and Caley 2006), making use of the generalized logistic growth

model (or  $\theta$ -logistic model, Gilpin and Ayala 1973) as a basis, *i.e.* with no  
 2 delayed density effects and no alteration of the carrying capacity (see Boyce  
 1989, for an application on elk *Cervus canadensis*). This basic model of  
 4 population growth suitable for the dynamics of large herbivore populations can  
 be written:

$$N_{t+1} = N_t \times \exp \left( r_m \left( 1 - \left[ \frac{N_t}{K} \right]^\theta \right) \right) \quad (1)$$

6 where  $N_t$  and  $N_{t+1}$  are the population sizes at time  $t$  and  $t + 1$ ,  $r_m$  is the  
 intrinsic rate of increase,  $K$  is the carrying capacity, and  $\theta$  is the shape  
 8 parameter influencing the form of density dependence. The delayed  $\theta$ -logistic  
 model has the same structure as the above  $\theta$ -logistic but includes an additional  
 10 time lag ( $T$ ) in the effect of population size on the population growth rate:

$$N_{t+1} = N_t \times \exp \left( r_m \left( 1 - \left[ \frac{N_{t-T}}{K} \right]^\theta \right) \right) \quad (2)$$

Forsyth and Caley (2006) recently developed two variants of these models to  
 12 account for different mechanisms supposed to generate the irruptive dynamics  
 of large herbivores. First, they added a term  $S$  that simulates a linear decline  
 14 in the resource “surplus” from time of introduction  $t = 0$  to time  $t = t_K$ , *i.e.*  
 the time at which all the “surplus” is consumed. This threshold model (referred  
 16 to as the “Leopold model”) is:

$$\begin{cases} N_{t+1} = N_t \times \exp \left( r_m \left( 1 - \left[ \frac{N_t}{K+S(1-t/t_K)} \right]^\theta \right) \right) & \text{for } t \leq t_K, \\ N_{t+1} = N_t \times \exp \left( r_m \left( 1 - \left[ \frac{N_t}{K} \right]^\theta \right) \right) & \text{for } t > t_K. \end{cases} \quad (3)$$

Second, they defined the “Caughley model” by adding a time lag  $T$  to the  
 18 Leopold model thus accounting for the possibility of approaching the post-crash

equilibrium via dampened oscillations once all the surplus was consumed:

$$\begin{cases} N_{t+1} = N_t \times \exp \left( r_m \left( 1 - \left[ \frac{N_{t-T}}{K+S(1-t/t_K)} \right]^\theta \right) \right) & \text{for } t \leq t_K, \\ N_{t+1} = N_t \times \exp \left( r_m \left( 1 - \left[ \frac{N_{t-T}}{K} \right]^\theta \right) \right) & \text{for } t > t_K. \end{cases} \quad (4)$$

2 Seven models were fitted (Table 1) using a maximum likelihood procedure  
 with all errors ( $\sigma$ ) log-normally distributed (Forsyth and Caley 2006): the  
 4  $\theta$ -logistic model, the delayed  $\theta$ -logistic model with  $\theta$  fixed to one (Forsyth and  
 Caley 2006) and estimated (White 2007), the Leopold model with  $\theta$  fixed to  
 6 one and estimated (Forsyth and Caley 2006, White 2007) and the Caughley  
 model with  $\theta$  fixed to one and estimated (Forsyth and Caley 2006, White  
 8 2007).

Model likelihoods were optimized using the `nlminb` function in the package  
 10 `stats` (R Development Core Team 2007) to test  $H_1$ . Parameters  $r_m$ ,  $K$ ,  $S$  and  
 $\theta$  were all constrained within a range of biologically plausible values to avoid  
 12 false convergence. We allowed time lags ( $T$ ) to vary up to five years. For the  
 Caughley models, a grid search was used to identify the best combination of  $T$   
 14 and  $t_K$ . Potential values for  $t_K$  were set within the range of 15-25 years, *i.e.*  
 covering both sides of the first peak of the mouflon dynamics in 1977 ( $t = 20$   
 16 years). We used Akaike's Information Criterion corrected for sample size ( $AIC_c$ ,  
 Burnham and Anderson 2002) to rank the seven models and provided Akaike  
 18 weights ( $w_i$ , Burnham and Anderson 2002) to assess their relative statistical  
 support. We reported parameter estimates for all models but standard errors  
 20 for the best model only.

## Assessing the effects of climate

2 Analysis of density-dependent and density-independent components of the time  
series of population abundance was restricted to the post first-crash period  
4 (1983-1995,  $n = 9$  years with 3 missing values). The brevity of the time series  
and the missing values prevented the fitting of autoregressive models (AM,  
6 *sensu* Royama 1992). The response variable was the annual population growth  
rate calculated as  $\log_e \lambda_t = X_{t+1} - X_t$  (where  $X_t = \log_e$  [population size at time  
8  $t$ ]). We quantified the effect of climate on population dynamics by fitting  
standard linear models ( $\log_e \lambda_t = \beta_0 + \beta_1 \times X_t + \beta_2 \times \log_e(\text{climate}) + \sigma^2$ ). We  
10 fitted different models where population size ( $\log_e(N_t) = X_t$ ) and climate  
indices interact on  $\log_e \lambda_t$  (model  $X_t \times \text{climate}$ ), are additive on  $\log_e \lambda_t$  (model  
12  $X_t + \text{climate}$ ), or are incorporated as simple effects (model  $X_t$ , model climate) or  
not (null model).

14 To test  $H_2$ , we retained local and global climatic variables all related to the  
annual winter climate severity (Table 2). Large-scale climate indices are  
16 expected to better predict the impact of climate on population dynamics than  
are local weather indices (Hallett *et al.* 2004, Stenseth and Mysterud 2005) but  
18 since contrasting results exist (*e.g.* Mysterud *et al.* 2007, on bison *Bison*  
*bonasus*) we used both large-scale and local climatic variables in the analyses.  
20 Firstly, we used the Southern Oscillation Index (SOI,  
<http://www.bom.gov.au/climate/current/soi2.shtml>) and the Antarctic  
22 Oscillation Index (AAOI,  
[http://gcmd.gsfc.nasa.gov/records/GCMD\\_NOAA\\_NWS\\_CPC\\_AAO.html](http://gcmd.gsfc.nasa.gov/records/GCMD_NOAA_NWS_CPC_AAO.html)) as  
24 large-scale climatic indices. We derived winter (w) values for SOI and AAOI by  
calculating the mean of monthly SOI and AAOI values from May to October.  
26 SOI<sub>w</sub> and AAOI<sub>w</sub> values were then regressed on the annual population growth

rate. Secondly, we used three local climatic indices (Météo France): (i) the  
2 temperature  $T^\circ$  in Celsius ( $^\circ$ ); (ii) the windchill index  $WCI$ , calculated as  
 $WCI = 13.12 + 0.6215 \times T^\circ - 11.37 \times W^{0.16} + 0.3965 \times T^\circ \times W^{0.16}$  where  $T^\circ$  is  
4 the air temperature and  $W$  is the wind speed in kilometers per hour ( $\text{km.h}^{-1}$ )  
(Osczevski and Bluestein 2005); (iii) the effect of precipitation assessed using a  
6 precipitation index  $PI$  calculated as the total number of days with  
precipitation  $PI = ndr + nds$ , where  $ndr$  is the number of days with rainfall  
8  $> 1$  mm and  $nds$  is the number of days with more than 50% of the soil surface  
covered with snow. We used the mean of the monthly values during winter  
10 (May-October) for  $T^\circ$ ,  $WCI$  and  $PI$ . The values of  $T^\circ$  and  $PI$  were  
 $\log_e$ -transformed before their use in the models.  $WCI$  was not  $\log_e$ -transformed  
12 because of negative values.

The selection of linear models with and without direct effect of the climate  
14 was evaluated using  $AIC_c$  and Akaike weights. Model likelihoods were  
calculated using the R software (R Development Core Team 2007).

## 16 Results

### Population trajectory

18 The Kerguelen mouflon population grew rapidly for 12 years following the  
introduction of two individuals in 1957. From 1969 to 1972 the population  
20 stabilized at 100–130 mouflon (Fig. 1). From then, the population grew  
exponentially to a maximum size of 700 individuals at the end of the 1970's  
22 and then crashed dramatically before increasing again to approximately 600  
mouflons, following the predicted sequence of events of a typical irruption ( $H_1$ ).  
24 Afterward, the population entered an unstable phase fluctuating around a size

of 400–500 individuals. Therefore, we identified two phases in the population  
 2 dynamics: one phase before the first crash in 1977–1978 and a second phase  
 that includes the subsequent variations.

#### 4 Irruptive models

In support of  $H_1$ , the best model describing our data was the irruptive  
 6  $\theta$ -Caughley model with time lag  $T = 1$  year and the time at which all the  
 “surplus”  $S$  is consumed of  $t_K = 21$  years ( $w_i = 0.70$ , Table 1). This model  
 8 gave estimates of the intrinsic rate of increase,  $r_m = 0.29 \pm 0.005$ , a carrying  
 capacity of  $K = 473 \pm 45$  mouflons, a surplus of  $S = 2903 \pm 396$  mouflons and a  
 10 shape parameter influencing the form of density dependence of  $\theta = 3.18 \pm 0.69$   
 (Fig. 2, Table 1). We found a clear pattern as the  $\theta$ -Caughley model has at  
 12 least 4 times more statistical support than any other competing model  
 (Table 1). Parameter estimates were consistent among the  $\theta$ -logistic, the  
 14 delayed  $\theta$ -logistic, the  $\theta$ -Leopold and the  $\theta$ -Caughley models except for  $\theta$  and  $S$   
 (Table 1).

#### 16 Climate effects on population dynamics

In agreement with our second hypothesis ( $H_2$ ), winter severity decreased the  
 18 annual population growth rate particularly with respect to the number of days  
 with precipitation (rain or snow). The best model included the additive effects  
 20 of population size and  $PI$  on  $\log_e \lambda_t$  ( $w_i = 0.74$ ,  $R^2 = 0.92$ ; Table 2, Fig. 3).

The second and third best models, respectively, included the simple effects of  
 22  $PI$  ( $w_i = 0.22$ ,  $R^2 = 0.81$ ) and population size on  $\log_e \lambda_t$  ( $w_i = 0.01$ ,  $R^2 = 0.65$ ;  
 Table 2). Supporting our third prediction ( $H_3$ ), the effects of  $N_{t-1}$  (scaled  
 24 coefficient:  $\beta_1 = -0.292 \pm 0.09$ ) and  $PI$  (scaled coefficient:  $\beta_2 = -0.282 \pm 0.05$ )

on population growth rate ( $\log_e \lambda_t$ ) were of similar magnitude.

## 2 Discussion

As expected for herbivores introduced to new locations, the Kerguelen mouflon population showed an irruptive population dynamics following their introduction to Haute Island in 1957. We document a population crash 21 years after introduction (with 71% fewer mouflon in two years) that was best modeled as a function of lagged density-dependence and an exhaustion of available resources ( $\theta$ -Caughley model). The same patterns of population dynamics have been documented for domestic sheep in Australia (Forsyth and Caley 2006, but note that the  $\theta$ -Caughley model was not fitted in that study). We also show that the mouflon population of Kerguelen shared similarities with the unstable Soay sheep dynamics of St Kilda (Clutton-Brock and Pemberton 2004).

### 14 Irruptive potential and dynamics

The time series of the mouflon population size reinforces the idea of the importance of irruptive dynamic in introduced and recolonizing populations in simple ecosystems, especially for large herbivores, even with contrasting life histories (reindeer: Scheffer 1951; tahr *Hemitragus jemlahicus*: Caughley 1970; white-tailed deer *Odocoileus virginianus*: McCullough 1997; Sika deer *Cervus nippon*: Kaji et al. 2004; ibex *Capra ibex*: Toïgo 1998, Sæther et al. 2002).

Exponential growth started immediately following the introduction but suddenly increased in intensity following the addition of new forage resources – due to introduced fodder grasses in 1972 – as well as the release of the

interspecific competition with reindeer in the mid 1970s (Fig. 1). In line with  
2 previous studies (McCullough 1997), introduction to a new range and  
improvement of available resources are likely causes of the exponential growth  
4 of the Kerguelen mouflon population. Our study could also suggest that release  
from interspecific competition promoted the constant increase of mouflon  
6 population size over 20 years. This hypothesis is, however, less plausible given  
the large mouflon number supported for several years before the first crash  
8 happened ( $> 500$  individuals) and the relatively small number of reindeer  
( $< 150$  individuals, Fig. 1). Furthermore, it is likely that the exponential  
10 growth phase would have occurred with only one or none of these factors  
(Sinclair 1979, Gunn et al. 2003; see also Aanes et al. 2000 for an example on  
12 Svalbard reindeer).

As expected for large herbivores, the shape parameter of the  
14 density-dependence function, (estimated from our best model,  $\theta$ -Caughley), is  
far greater than 1 ( $\theta = 3.18 \pm 0.69$ ) and slightly greater than the estimated  $\theta$   
16 for Soay sheep ( $\theta = 2.30$ , Lande et al. 2003, p. 41).  $\theta$  falls within the range of  
observed values for large herbivores (ibex:  $\theta = 1.54$ , Sæther et al. 2002; elk:  
18  $\theta = 3.50$ , Boyce 1989; wildebeest *Connochaetes taurinus*:  $\theta = 5.94$ , Fryxell  
et al. 2007), confirming the contention that density dependence is strongest at  
20 high population density in large mammals (Fowler 1987, Sinclair 1989).

The combination of the high intrinsic rate of increase and the pervasive  
22 cohort effects generating delayed responses of demographic rates to changing  
density (see Gaillard et al. 2003a, for a review) favored a strong  
24 over-compensatory density-dependence. The exponential growth and the first  
crash of the mouflon population was perfectly captured by the  $\theta$ -Caughley  
26 model (Fig. 2), which probably was the main reason for its selection (Table 1).

Population abundance was indeed found to be lower after the first crash than  
2 after subsequent crashes, as predicted by the Caughley models.

According to the  $\theta$ -Caughley model (Caughley 1970), density-dependent  
4 processes should lead the mouflon population to converge toward the carrying  
capacity through dampened oscillations once the surplus of vegetation becomes  
6 exhausted after the first crash (after year 21). However, following the first peak  
and crash sequence, the population achieved abundances close to the maximum  
8 of 1977 several times (1988, 1992 and 1994, see Fig. 1), dynamics that were  
poorly explained by the  $\theta$ -Caughley model (Fig. 2). The observed pattern  
10 suggests that successive irruptions may occur rather than dampened oscillations  
(hypothesis 4 & 5 in McCullough 1997, p. 79), as documented in Soay sheep  
12 (Clutton-Brock et al. 1991). The very high reproductive potential of the  
mouflon (twinning rate up to 36.4%), in association with delayed  
14 density-dependent processes on demographic rates, may explain the relatively  
high intrinsic rate of increase ( $r_m = 0.29$ ), therefore allowing the population to  
16 recover rapidly (within 2–3 years) after a winter crash. Nevertheless, successive  
irruptions and quick recoveries at a similar abundance might occur only if the  
18 decrease in carrying capacity following the initial over-grazing period was  
reversible (Mysterud 2006). Feeding primarily on grass species, sheep could  
20 have altered plant composition of the island, selecting for plants highly tolerant  
to herbivory. Such a progressive change in plant composition could have  
22 improved the carrying capacity over the years following the first crash (Fig. 1).

## Mouflon and the climate of Kerguelen

24 Another factor that could account for the poor fit of the  $\theta$ -Caughley model  
after the first crash (1977–1978, Fig. 2) could be climate. There was evidence

that after the first crash, population growth rate was not only linked to  
2 population density but also to  $PI$ , in an additive way. Our model did not take  
into account climatic indices that affect population growth rate (Fig. 3b) and  
4 generate noise around the predicted population size. As expected at this  
latitude ( $50^{\circ}\text{S}$ ), density-independent factors affected demographic rates to  
6 reduce population growth rate to the same extent as density (Fig. 3) – so that  
winter severity may result in strong limitation of large herbivore populations  
8 (*e.g.*, Caughley and Gunn 1993, Duncan and Forsyth 2006).

At high latitude, or in mountainous areas, winter precipitation is known to  
10 negatively impact annual population growth rates in several species (Coulson  
et al. 2001, Kaji et al. 2004, Mysterud et al. 2007, Sæther et al. 2007). Difficult  
12 access to an already limited food resource (ice-blocking event following rainfall  
and freezing, Aanes et al. 2000, Skogland 1978) or increased costs of  
14 locomotion (Crête and Larivière 2003) are commonly reported causes of death.  
In the Kerguelen archipelago, snow depth never exceeded 20 cm during our  
16 study which limits its negative effect on mouflon (Telfer and Kelsall 1984).

That  $PI$ , a proxy of the number of days mouflons faced with wet conditions,  
18 decreased population growth rate supports the hypothesis of thermoregulation  
costs through heat loss (Cuyler and Øritsland 2004) for lambs. In our study,  
20 windchill ( $WCI$ ) was not correlated to growth rate but an index combining  
precipitation and wind could be more relevant. For instance, in Soay sheep,  
22 living in open habitat under a similar climatic regime as the Kerguelen islands,  
the combination of wet and windy periods was the main mortality source  
24 induced by climate (Coulson et al. 2001).

In contradiction with Hallett et al. (2004), large-scale climatic indices (SOI  
26 and AAOI) had no detectable effect on population growth rate despite the

strong relationship between  $\lambda_t$  and *local* weather (PI, Fig. 3; see also Mysterud  
2 et al. 2007). However, although the mouflon population responded to *PI*, we  
could not link the four crashes to any particular environmental event such as a  
4 sequence of harsh winters (Fig. 1) contrary to Gunn et al. (2003)'s hypothesis  
that crashes are determined by climate. Therefore, we could not disentangle  
6 climate from over-compensation as the most likely cause of population crashes  
in Kerguelen mouflon.

## 8 **Methodological considerations**

Relatively coarse population counts might have limited our ability to capture  
10 fine-scale aspects the population dynamics. The lack of information on  
sampling error, which both limits the interpretation of the parameter estimates  
12 and increases the probability of detecting false density-dependence, may have  
altered parameter estimates (Freckelton et al. 2006). Freckelton et al. (2006),  
14 however, argued that the probability of detecting false density-dependence is  
low for short time series (here 8 years in our case) and that it is still  
16 appropriate to use time series without sampling error estimates when there is a  
non-linear density-dependent response ( $\theta = 3.18 \pm 0.69$  in our study). Although  
18 our estimates may have a low accuracy, they do seem to have been sufficient to  
identify the major drivers of mouflon dynamics.

20 Another pitfall of using count data is that we may over-estimate population  
growth rate, as suggested by a few biologically unrealistic estimates, such as  
22  $r > 0.4$  in 1958, 1967, 1969, 1974 and 1994. Males are part of all counts but the  
population growth rate is defined as the recruitment of new females per female  
24 (Caswell 2001). However, because of higher male than female mortality during  
die-offs, the population sex-structure can change dramatically (Klein 1968, Kaji

et al. 2004). The estimate of  $r_m$  is then based almost on females only at low  
2 density but males make a substantial part of the population once the  
population has recovered. Without any information on the population  
4 sex-structure, parameter estimates may be biased or inaccurate so that two-sex  
models are required for sexually dimorphic species such as mouflon (Mysterud  
6 et al. 2002, Gaillard et al. 2003b).

## Conclusion

8 Our time-series of mouflon abundance supports the occurrence of irruptive  
dynamics in populations of large herbivores introduced to new range and in the  
10 absence of harvesting (Forsyth and Caley 2006). From 1983 to 1995, population  
growth rate was negatively related to population abundance in the preceding  
12 year and to winter severity, both of which also generate unstable dynamics in  
domestic sheep. An additional characteristic of the unstable mouflon dynamics  
14 of Kerguelen was the quick recovery to high population abundance during the  
90ies, close to the initial peak. This suggests that the carrying capacity ( $K$ )  
16 remained at similar levels since 1977 and has not been permanently affected by  
the mouflon irruption (Mysterud 2006). Our study therefore challenges the idea  
18 of a necessary control of introduced populations of large herbivores to prevent  
habitat degradation (Gunn et al. 2003).

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Table 1. Comparison of the seven candidate models explaining the dynamics of the Kerguelen mouflon population from 1957 to 1995.  $k$  is the number of estimated parameters of the  $i$ -th model;  $\Delta\text{AIC}_c$  is the difference in  $\text{AIC}_c$  between the best model and the  $i$ -th model;  $w_i$  is the Akaike weight. See text for the definition of the different models and the definition of  $r_m$ ,  $K$ ,  $\theta$ ,  $T$ ,  $t_K$ ,  $S$  and  $\sigma$ . The \* superscript indicates that the parameter has been fixed in the model.

Model	$k$	$\Delta\text{AIC}_c$	$w_i$	$r_m$	$K$	$\theta$	$T$	$t_K$	$S$	$\sigma$
$\theta$ -logistic	4	2.9	0.16	0.28	444	6.60	–	–	–	0.29
Delayed logistic	4	7.44	0.02	0.30	437	1*	0	–	–	0.31
Delayed $\theta$ -logistic	5	11.87	0.00	0.30	435	5.09	1	–	–	0.31
Leopold	5	5.57	0.04	0.29	440	1*	–	19	3784	0.29
$\theta$ -Leopold	6	4.86	0.06	0.29	421	6.51	–	21	2185	0.28
Caughley	6	8.8	0.01	0.29	428	1*	1	20	6078	0.30
$\theta$ -Caughley	<b>7</b>	<b>0</b>	<b>0.70</b>	<b>0.29</b>	<b>473</b>	<b>3.18</b>	<b>1</b>	<b>21</b>	<b>2903</b>	<b>0.25</b>

Table 2.  $\Delta\text{AIC}_c$  values and Akaike weight ( $w_i$ ) in brackets for the linear models  $\log_e \lambda_t = \beta_0 + \beta_1 \times X_t + \beta_2 \times \log_e(\text{climate variable}) + \sigma^2$  where  $X_t = \log_e(\text{abundance at time } t)$  ( $n = 9$  years). The most parsimonious model is shown in bold. For each model, the climate variable can be either  $T^\circ$ ,  $PI$ ,  $WCI$ ,  $\text{SOIw}$  or  $\text{AAOIw}$ .  $T^\circ$  stands for monthly average temperature in Celcius,  $PI$  for precipitation index,  $WCI$  is the wind chill index,  $\text{SOIw}$  is the winter Southern Oscillation Index and  $\text{AAOIw}$  is the winter Antarctic Oscillation Index. Note that  $WCI$  was not  $\log_e$ -transformed.

Model	Climate variable					
	$T^\circ$	$PI$	$WCI$	$\text{SOIw}$	$\text{AAOIw}$	none
$X_t \times \text{climate variable}$	21.10 (0.00)	10.33 (0.00)	19.06 (0.00)	20.70 (0.00)	27.16 (0.00)	–
$X_t + \text{climate variable}$	10.88 (0.00)	<b>0.00 (0.74)</b>	8.96 (0.01)	11.78 (0.00)	15.24 (0.00)	–
$X_t$	–	–	–	–	–	8.04 (0.01)
climate variable	17.42 (0.00)	2.44 (0.22)	16.86 (0.00)	18.59 (0.00)	15.77 (0.00)	–
null	–	–	–	–	–	13.94 (0.00)

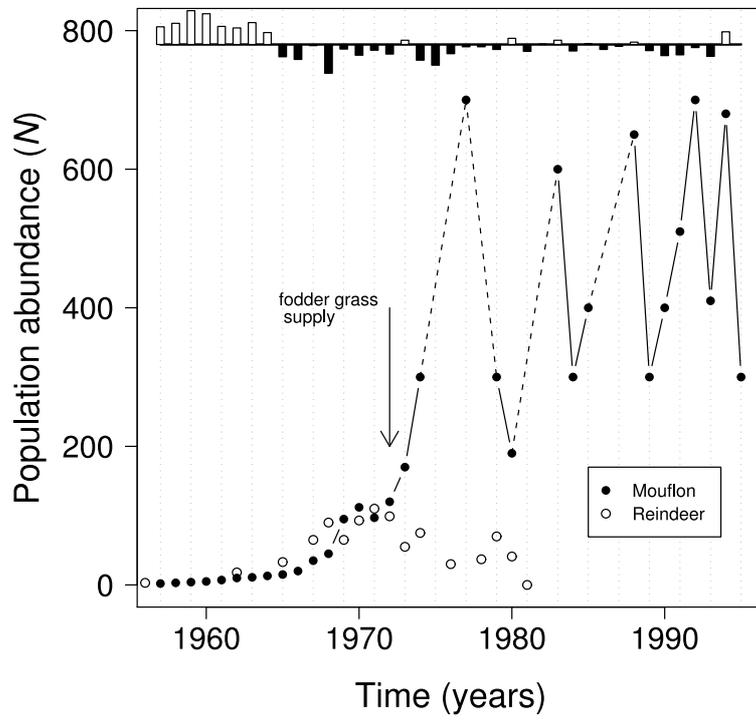
## Figure captions

2 **Fig. 1.** Time series of mouflon (1956–1995) and reindeer abundances  
 (1956–1981) on Haute Island, Kerguelen (48°25′–50° S, 68°27′–70°35′ E,  
 4 Southern Indian Ocean). Dashed lines link discontinuous years because of  
 missing values. The top bars represent climate winter anomalies (standardized  
 6 deviation from the mean) as measured by the precipitation index *i.e.*, the  
 number of days rainfall and snow fall from May to October (white bars:  
 8 positive anomalies; black bars: negative anomalies).

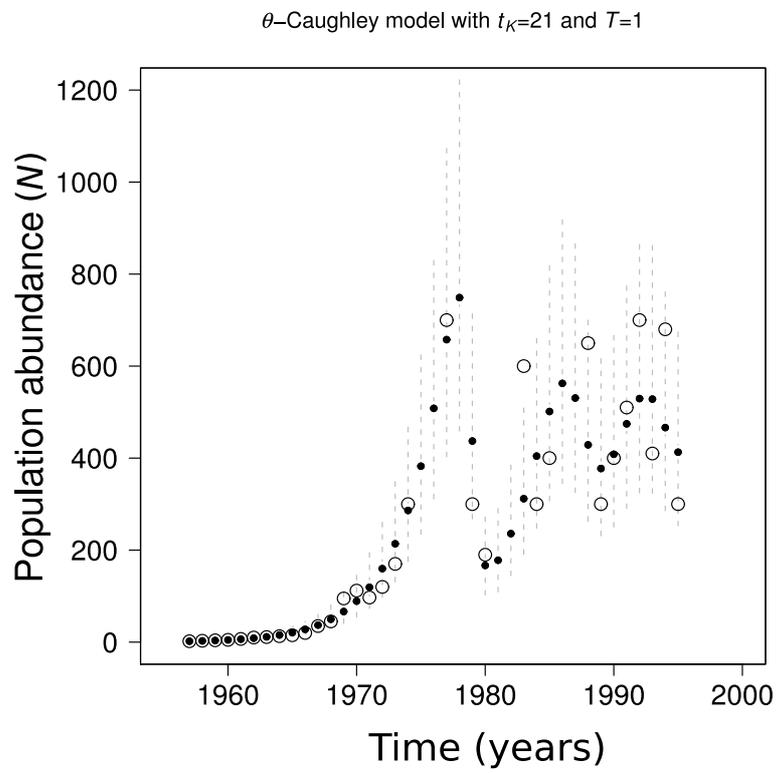
**Fig. 2.** Population abundance for Haute Island mouflon as observed (open  
 10 circles) and predicted (black dots), with 95% confidence limits (gray dashed  
 lines) from the  $\theta$ -Caughley model of irruptive dynamics.  $T$  is the time lag in  
 12 the effect of population size on the population growth rate and  $t_K$  is the time  
 at which all the “surplus”  $S$  is consumed (see Material and Methods).

14 **Fig. 3.** (a) Relationship between annual population growth rate ( $\log_e \lambda_t$ ) and  
 $\log_e$ -transformed mouflon abundance. (b) Relationship between annual  
 16 population growth rate  $\log_e \lambda_t$ , accounting for the density effect (*i.e.* residual  
 effect), and the  $\log_e$ -transformed precipitation index ( $PI$ ) for the period  
 18 (1983–1984 / 1988–1995). The regression lines represent the values (and  
 corresponding 95% confidence limits) predicted by the model  
 20  $\log_e \lambda_t = \beta_0 + \beta_1 \times N_{t-1} + \beta_2 \times PI + \sigma^2$ . The selected model explains 92% of the  
 observed variance in  $\log_e \lambda_t$ .

**Fig. 1**

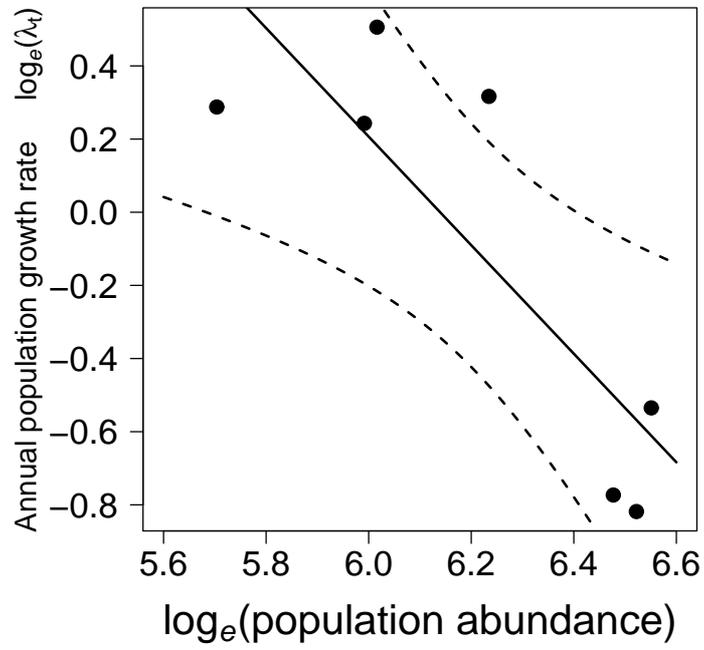


2

**Fig. 2**

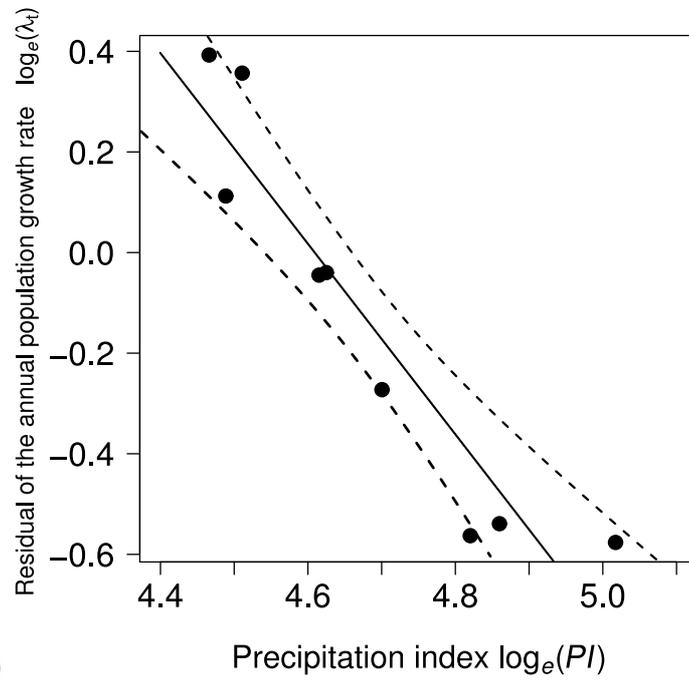
2

**Fig. 3**



2

(a)



(b)