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SELECTIVE HARVESTING AND HABITAT LOSS PRODUCE LONG-TERM LIFE HISTORY CHANGES IN A MOUFLON POPULATION

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Abstract. We examined the long-term effects (28 years) of habitat loss and phenotype-based selective harvest on body mass, horn size, and horn shape of mouflon (*Ovis gmelini musimon*) in southern France. This population has experienced habitat deterioration (loss of 50.8% of open area) since its introduction in 1956 and unrestricted selective hunting of the largest horned males since 1973. Both processes are predicted to lead to a decrease in phenotype quality by decreasing habitat quality and by reducing the reproductive contribution of individuals carrying traits that are targeted by hunters. Body mass and body size of both sexes and horn measurements of males markedly decreased (by 3.4–38.3%) in all age classes from the 1970s. Lamb body mass varied in relation to the spatiotemporal variation of habitat closure within the hunting-free reserve, suggesting that habitat closure explains part of these changes. However, the fact that there was no significant spatial variation in body mass in the early part of the study, when a decline in phenotypic quality already had occurred, provided support for the influence of selective harvesting. We also found that the allometric relationship between horn breadth and horn length changed over the study period. For a given horn length, horn breadth was lower during the second part of the study. This result, as well as changes in horn curve diameter, supports the interpretation that selective harvesting of males based on their horn configuration had evolutionary consequences for horn shape, since this phenotypic trait is less likely to be affected by changes in habitat characteristics. Moreover, males required more time (approximately four years) to develop a desirable trophy, suggesting that trophy hunting favors the reproductive contribution of animals with slow-growing horns. Managers should exploit hunters' desire for trophy males to finance management strategies which ensure a balance between the population and its environment. However, for long-term sustainable exploitation, harvest strategy should also ensure that selectively targeted males are allowed to contribute genetically to the next generations.

Key words: body mass; Caroux-Espinouse; France; habitat loss; horn measurements; mouflon; Ovis gmelini musimon × Ovis *sp.; selective hunting; wildlife management.*

Introduction

Disentangling human effects from natural processes is a challenging task for population biologists (Ashley et al. 2003). Human activities influence habitat fragmentation (Hanski 1999), climate changes (Gitay et al. 2002), and markedly increase evolutionary changes in animal species (Palumbi 2001).

Research on harvested populations has traditionally placed great emphasis on the demographic consequences of exploitation (e.g., Ginsberg and Milner-Gulland 1994). The hunting of large vertebrates usually leads to lower population density, a female-skewed adult sex ratio, and a younger age distribution, all of which are known to influence markedly life history traits such as body mass, reproductive allocation, and survivorship (Clutton-Brock and Lonergan 1994, Langvatn and Loison 1999, Singer and Zeigenfuss 2002, Solberg et al. 2002, Garel et al. 2006).

While fishery studies have shown that selective harvests may elicit an evolutionary response in wild stocks (Sutherland 1990, Law 2000, Ratner and Lande 2001, Conover and Munch 2002), the potential selective effects of sport hunting on wild ungulates in which large-horned or large-antlered males are selectively targeted by hunters have only been recently highlighted (see Harris et al. 2002, Festa-Bianchet 2003). Both body size and horn or antler size have high heritabilities (Williams

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et al. 1994, Réale et al. 1999, Kruuk et al. 2002, Coltman et al. 2003), so that selective harvests may select against large males and produce morphological changes in the opposite direction of the harvest bias (e.g., Coltman et al. [2003] in bighorn sheep, *Ovis canadensis*). Such changes might then have indirect effects on population dynamics, since genetic correlations may exist between the selectively targeted morphological characteristics and fitness related-traits (Hartl et al. [2003] in red deer, *Cervus elaphus*; Coltman et al. [2005] in bighorn sheep).

Wild sheep are likely to be highly susceptible to the effects of selective hunting because (1) there is usually no limit on the maximum horn size which can be harvested (e.g., Singer and Zeigenfuss 2002, Whitfield 2003), (2) horn size differences among males are very obvious to hunters, and (3) rams with fast-growing horns may become "desirable" as trophies before their large horns help them to achieve high reproductive success (e.g., Coltman et al. 2002), hence before they have contributed significantly in genetic terms to the next generation (Coltman et al. 2003). However, studies aimed at assessing the effect of selective hunting on animal morphology are still scarce (Festa-Bianchet 2003).

Habitat loss is also a major threat to wild sheep populations (e.g., Wakelyn 1987). Wild sheep are grazers (Hofmann 1989), selecting grass-rich open areas and high-visibility habitats near escape terrain (Risenhoover and Bailey 1985, Wakelyn 1987). The reduction of controlled burning during the last century has caused forest and shrubs to invade wild sheep ranges (e.g., Wakelyn 1987), causing a decrease in resource availability and quality that is likely to have detrimental effects on individual performance, and hence on population dynamics.

Here, we explore the long-term changes in phenotypic traits of a wild population of mouflon (*Ovis gmelini musimon* × *Ovis* sp.) that experienced unrestricted selective hunting from 1973 onward, and that has faced habitat loss since its introduction in 1956. We used monitoring spanning 28 years in the Caroux-Espinouse population (southern France). We studied two zones (Fig. 1): the wildlife reserve (WR), situated in the central part of the massif, where hunting was prohibited, and the surrounding harvesting area (HA) where large-horned rams were selectively targeted. In both areas, habitat closure began late in the 19th century with the reduction of pastoral activity and controlled burning (Bousquel 1999). Consequently open areas (Appendix A) markedly decreased, from 4830 ha (67.2%) in 1955 to 2378 ha (33.1%) in 1992, mainly because of increasing invasion by dense broom moorlands, as well as various woody species (Bousquel 1999).

We tested three hypotheses. First, we expected a general decrease in body size, horn size, and body mass due to both a decrease in habitat quality (WR and HA) and unrestricted selective harvesting of large-horned males (HA only). Second, we expected that body mass should vary positively with the proportion of open area in the WR in the absence of direct selective hunting. Finally, we expected that horn shape should change over the study period because selective harvesting (HA) focused on animals with horn characteristics resembling the original Corsican mouflon (*Ovis gmelini musimon* var. *corsicana*; Cugnasse 1994), i.e., animals with widely flaring horns (Fig. 2). We thus predicted that horn breadth should become narrower over time for a given horn length.

STUDY AREA

Population characteristics

We studied mouflon in the Caroux-Espinouse massif (43°38′ N, 2°58′ E, 150–1124 m above sea level) situated on the southern border of the Massif Central, in southern France (17 000 ha, Fig. 1). Environmental characteristics of this site have been presented elsewhere (Garel et al. 2005*a*, see also Appendix A on vegetation types).

The population has been monitored by the Office National de la Chasse et de la Faune Sauvage since 1974. This population grew from 19 individuals (nine males and 10 females) released between 1956 and 1960 in the WR (1704 ha), situated in the central part of the massif (Fig. 1). Mouflon released in 1956 ($n = 4$) and 1959 ($n = 4$) originated from native Corsican mouflon, whereas those released in 1960 ($n = 11$) came from continental populations which have a mixed origin (see Garel et al. 2005*a* for more information about mouflon releases and life history consequences of a mixed origin).

Hunting practice

Except in the protected areas (WR and three 318-ha adjacent areas, Fig. 1), hunting occurred from 1 September to the end of February from 1973. Hunting was based on quotas. A total of 5879 mouflon (2838 males, 2882 females, and 159 mouflon of unknown sex) were harvested from 1973 to 2003. Hunters harvested the same number of females as males in order to control population size. In addition, 786 mouflon (417 males and 369 females) chosen at random were removed from the WR during spring from 1974 to 1999 through scientific culls and live exportation of trapped animals.

Stalking is the most common hunting practice in our population. Hunters are accompanied by a guide, generally spending two days in the field. A hunter may observe more than five large-horned males during a single hunting day. There is no limitation on the number and the quality of mouflon harvested, although a given hunter never shoots more than three mouflon per trip. Hunters preferentially target the largest-horned males observed. Only the trophy fee, which increases with trophy size, might be a limiting factor. However, in our population, trophy fees are low compared to other populations of ovids in Europe and North America (see *Management implications*). These hunting conditions are thus likely to promote the selective effect of hunting.

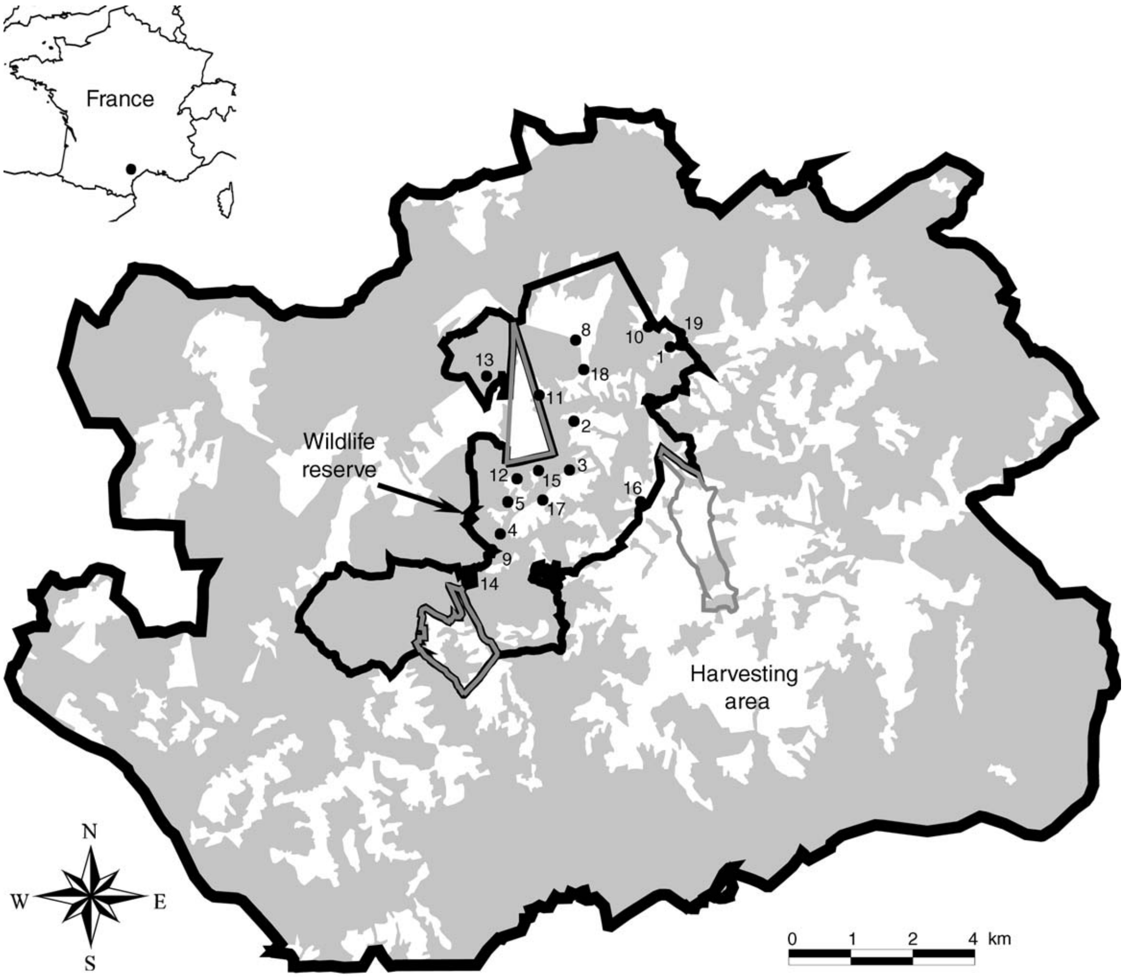

FIG. 1. Location of the study area in southern France and population range recorded in 2000. Open and closed habitats (see Appendix A) recorded in 1992 are represented in white and gray, respectively. Plots (black circles) correspond to traps located in the wildlife reserve (WR, outlined in black), labeled with their identification number. Polygons outlined in gray ($n = 3$) correspond to 318-ha areas adjacent to the WR with no hunting.

METHODS

Data collection

Body mass.—In the HA, eviscerated body mass was recorded from males and females harvested during the hunting seasons of 1977–1984 and 2000–2002. In the WR, males and females were trapped during spring–summer from 1976 onward (from 29 April to 27 September) and weighed. Mouflon were trapped in 17 traps distributed across the WR and its periphery (Fig. 1). Body mass was measured to the nearest 0.5 kg with a spring scale.

Morphological characteristics.—Official measurements for trophy point evaluation (see International Council for Game and Wildlife Conservation 1977), including horn length, horn circumference and horn breadth (Fig. 3A), were available for the hunting seasons of 1977–1984 and 1996–2002 in the HA. Horn curve diameter of males (Fig. 3B) and shoulder height of both sexes (along the perpendicular line from the middle of the hoof to the withers) were also recorded during the hunting seasons of 1977–1984. Six people performed most of the measurements over the course of the study. No specific protocol was implemented to account for observer effects, but these effects should be limited because horns are easy to measure, and because horn measurements determine trophy value. The measurements were taken with a flexible steel tape (to the nearest 0.5 cm for horn length and circumference, and to the nearest 1 cm for shoulder height) or vernier calipers (to the nearest 0.5 cm for horn breadth and to the nearest 1 cm for curve diameter). The mean values of the circumference, curve diameter, and length of the left and right horns were used.

Tooth eruption and replacement were the only reliable criteria available to estimate the age of females (Piegert

FIG. 2. Difference in horn configuration between two males of the Caroux-Espinouse population (France): the male on the right has a trophy with wide horn breadth and curve diameter very similar to the "Corsican" horn type in comparison to the male on the left. Photo © P. Arnaud; used by permission.

and Uloth 2005). Age determination of males was based on counts of horn growth annuli (Geist 1966).

Habitat characteristics.—Vegetation maps were available for 1955, 1971, 1982, and 1992, respectively, covering the population range (7182 ha) recorded in 1982 (the map available in 1992 also covered the population range in 2000; see Fig. 1). Maps were stored in a geographical information system. We used vegetation cover of three groups of species to define open and closed habitats (Appendix A). This classification took into account the presence of escape terrain, habitat visibility, food availability and quality based on observed diet in the population (Faliu et al. 1990, Cransac et al. 1997) known to be important factors in determining habitat suitability for wild sheep (Risenhoover and Bailey 1985, Wakelyn 1987, Cransac and Hewison 1997).

Statistical analyses

Changes in mouflon phenotypic traits over time.—We used a linear model to describe changes in body mass of lambs trapped within WR from 1976 to 2003. We used the mass recorded at first capture because few recaptures occurred (17%). We fitted models including capture date as a covariable to account for mass gain during the capture season. We also looked for between-sex (i.e., interaction between date and sex) and among-year (i.e., interaction between date and year) differences in growth, and between-sex differences in body mass changes over years (i.e., interaction between sex and year).

In HA, we also used linear models for analyzing both changes in dressed mass and morphological characteristics. To assess mass changes between the two periods (i.e., hunting seasons of 1977–1984 and 2000–2002) for males and females, we pooled mouflon of $\geq$3.5 years of age due to the low sample size for some years and age classes. We used log-transformed dressed mass to make mass changes comparable between males and females. We looked for changes in horn length, circumference, and breadth of males harvested during the two periods of study (1977–1984 and 1996–2002). We also tested for a decrease in horn curve diameter of males and in the

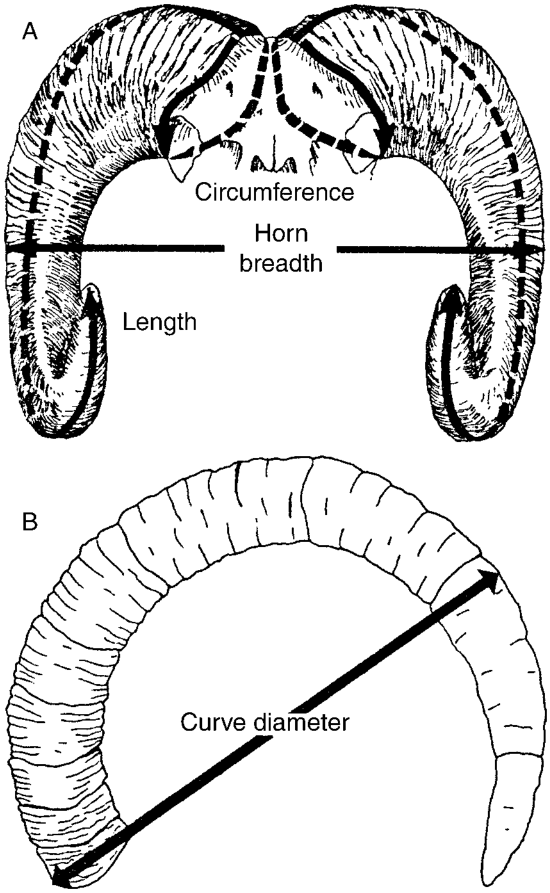

FIG. 3. Measurements of trophy characteristics recorded for mouflon harvested in the Caroux-Espinouse population (France), during hunting seasons 1977–1984 and 1996–2002. (A) Horn length was measured from the base to the tip of the horn, along the external side; horn circumference was measured at the base of the horn; horn breadth corresponds to the widest distance between external horn sides, horn tips included. (B) Horn curve diameter corresponds to the distance between the anterior side of the horn base and the diametrically opposed external side.

height at shoulder of both sexes from data recorded during the hunting seasons of 1977–1984. Models for dressed mass included the date of shooting as a covariable to account for a decrease of mass during the rut and winter. No such correction for date was necessary for morphological measurements for which there is no growth during the harvesting/rutting and winter periods (Hoefs 1982). Models of morphological characteristics included age class and year of birth, except for females for which exact age was unknown beyond 2.5 years of age (in this case we included year of shooting and tooth eruption classes).

Spatiotemporal variation in body mass of mouflon trapped in the WR.—We assessed more specifically the impact of habitat loss on phenotypic traits by looking for spatial differences in body mass among population units within the WR where there was no direct selective harvesting. Previous studies have shown that females and lambs form population units (Martins et al. 2002). Because body mass of lambs should depend on the quality of the habitat used by them with their mother (e.g., on moose *Alces alces* Sæther and Heim 1993), we looked for variation in lamb body mass among spatial units in relation to habitat openness. We also tested whether temporal variation in habitat closure among spatial units could explain temporal variation in body mass.

We first identified trap groups for which trapped adult females ($n = 19$) and lambs (male or female, $n = 42$) shared a similar home range by (1) computing for each trap the arithmetic center of the radio locations ($n = 4$ 775) of animals caught in that trap from 1988 to 1998 (see Martins et al. [2002] for further details) and (2) performing a hierarchical cluster analysis based on the dissimilarities among arithmetic centers to identify relevant trap clusters. We used the unweighted pair group method of aggregation, using the average linkage as a measure of distance between arithmetic centers. The distance between nodes of the dendrogram was used to identify four trap clusters (see Martins et al. 2002). To compute trap clusters, we only used those traps with >30 locations of radio-tagged mouflon. For each cluster, we then estimated a "home range" (kernel method, 95%; Kenward 1987) by using radio-locations of trapped females and lambs. Then, we computed the level of habitat openness for the two periods for which data on body mass were available. We used the 1982 and the 1992 maps for the 1976–1984 period and the 1995–2003 period, respectively. The change in habitat openness between periods for a given spatial unit was then related to the temporal variation in body mass of lambs trapped in that unit.

Changes in horn shape of males harvested in HA.—We regressed the horn breadth on the horn length (after log-transformation) of a given animal to look for changes in the allometric relationship between these two horn characteristics. We expected that, for a given horn length, horn breadth should be narrower during 1996–2002 than during 1977–1984 as a result of selective harvesting. We removed age classes with less than 20 data points for each study period (1977–1984 and 1996–2002) or for which data were not available each year within a given period from these morphological analyses.

Controlling for possible confounding effects of population density and climate.—Although no measure of population abundance was available for the first 15 years of the study, available evidence indicates that the mouflon population size was quite constant over time, at least between 1989 and the end of the study period (Garel et al. 2005*b*).

Likewise data on temperature were only available from 1987 onward. Therefore, it was not possible to take these effects into account in our analyses. Rainfall data were available from 1976 onward. We thus compared average rainfall in April–May (important for vegetation and animal growth [Albon et al. 1987]) and in June–July (when summer drought may occur [Garel et al. 2004]) between study periods (e.g., 1976–1985 vs. 1995–2003). We did not find any significant difference (mean ± SE rainfall) between the two periods (April–May, 241.9 ± 6.5 mm vs. 247.5 ± 12.3 mm, $P = 0.90$; June–July, 116.1 ± 8.1 mm vs. 114.7 ± 7.4 mm, $P = 0.97$).

Model selection.—Model selection was based on the Akaike Information Criterion (AIC) with second order adjustment ($\mathrm{AIC_c}$) to correct for small-sample bias (Burnham and Anderson 1998). The most parsimonious model (i.e., lowest $\mathrm{AIC_c}$) was selected as the best model. We followed Burnham and Anderson (1998) in concluding that models were different when the difference in $\mathrm{AIC_c}$ was >2. When the difference was ≤ 2, we selected among competing models in relation to their biological significance. All statistical analyses were performed using R 2.4.0 (R Development Core Team 2004). Spatial analyses were performed using ArcView 3.2 (ESRI, Redlands, California, USA), with the spatial analyst and the animal movement extensions (Hooge and Eichenlaub 2000).

RESULTS

Changes in mouflon phenotypic traits over time

The body mass of lambs trapped in the WR in the periods 1976–1984 and 1995–2003 increased with trap date (74.4 ± 14.1 g/d), but not significantly in all years (e.g., in 1982 from 10 May to 8 September, $r = 0.69$, $P < 0.001$; whereas in 1997 from 4 June to 25 August, $r = 0.19$, $P = 0.21$; Table 1). Between-sex differences in lamb mass at the start of the trapping season were 624.4 ± 461.1 g and increased over time (13.0 ± 7.3 g/d). The effect of year on lamb body mass was best modeled as a categorical variable rather than as a continuous one (difference in $\mathrm{AIC_c} = 22.5$, Table 1). Body mass variation from year to year was similar for lambs of both sexes. Over years (Appendix B), body mass decreased (model with linear(year): slope of -0.106 ± 0.012, $P < 0.001$). From the model including the two

TABLE 1. Effects of date, sex, and time (year or period of study) on body mass of lambs trapped in the Wildlife Reserve (WR) during the periods 1976–1984 (105 females, 117 males) and 1995–2003 (139 females, 167 males) in the Caroux-Espinouse massif (France).

Biological hypotheses	Models	AIC$_c$
No effect	null	2742.6
Spring–summer growth	date	2514.3
Sexual dimorphism	date + sex	2477.7
Differences in growth pattern between sexes	date + sex + date × sex	2475.9
Period (1976–1984 vs. 1995–2003) effects	date + sex + date × sex + periods	2424.5
Linear changes from 1976 to 2003	date + sex + date × sex + linear(year)	2404.3
Annual effect (year as factor)	date + sex + date × sex + year	2381.8
Difference between years in annual growth pattern	**date + sex + date × sex + year + date × year**	**2359.7**
Sex effect in annual changes	date + sex + date × sex + year + date × year + sex × year	2378.0

Notes: Additive effects are denoted by +, and an interaction between factors is denoted by ×. The selected model (lowest AIC$_c$) is in bold type.

periods of study, lambs were 1.6 kg lighter in the second period as compared to the first one (males, 12.3 ± 0.2 kg vs. 10.7 ± 0.2 kg, −12.8%; females, 11.0 ± 0.2 kg vs. 9.4 ± 0.2 kg, −14.3%) at the median trapping date (24 June).

In HA, the model including an effect of date on adult dressed body mass did not out-perform the null model (Table 2). Dressed body mass of both sexes decreased similarly (males, −17.8%; females, −18.3%) between the harvesting periods 1977–1984 and 2000–2002 (males, from 37.0 ± 0.3 kg to 30.4 ± 0.5 kg; females, from 22.3 ± 0.5 kg to 18.3 ± 0.5 kg), despite the increase reported in the average age of harvested adults (see *Changes in horn shape and selective hunting in HA*).

Over the 28-year study period, all horn measurements recorded on males harvested decreased with increasing year of birth (Table 3). Horn length decreased by 14.8 cm (18.3–20.1%, percentage based on prediction of the selected model for each age class; see also Appendix C) and horn breadth by 5.0 cm (10.7%) for all age classes. The decrease in horn circumference (3.6 cm, 13.6–14.1%) was similar for five- and six-year-old animals (difference of slope, 0.004 ± 0.024; $P = 0.87$), and lower for seven-year-olds (difference of slope, 0.063 ± 0.022; $P = 0.005$;–7.4%) and eight-year-olds (difference of slope, 0.101 ± 0.024; $P < 0.001$; −3.4%). A decrease of 19.1 cm (33.8–38.3%) in the horn curve diameter of males born between 1972 and 1982 was also recorded. Similarly, height at shoulder decreased by 10.8 cm (12.1–12.5%) for males born between 1972 and 1983, and by 10.3 cm (12.1–13.6%) for females harvested between 1977 and 1984.

Spatiotemporal variation in body mass of mouflon trapped in the WR

From the hierarchical cluster analysis on the 10 arithmetic centers of radio-locations (10 traps), four distinct clusters of branches were identified (three groups of two traps and one group of four traps, Appendix D). The proportion of closed habitat among the four clusters ranged from 38.4% to 76.5% (Fig. 4). We found a significant interaction between the proportion of closed habitat and the study period (Table 4). The decrease in lamb body mass in relation to habitat closure was not significant during the first study period when the proportion of closed habitat ranged from 38.4% to 59.8% (slope, −1.42 ± 1.82; $P = 0.44$). However, during the second period, lamb body mass was significantly lower when the proportion of closed habitat was higher (between-period difference in slope [interaction term] = −4.86 ± 2.30, $P = 0.04$). For a similar level of closed habitat (e.g., unit 4 for the first period and unit 1 for the second period), the body mass of lambs was lower during the second period compared to the first one (Fig. 4). The magnitude of mass loss was related to the proportion of closed habitat: in unit 2, with 51% of closed habitat (during the second period), mass loss was less marked than in unit 4 with 77% of closed habitat (Fig. 4). The effect of habitat closure was similar for both sexes.

Changes in horn shape and selective hunting in HA

Horn breadth increased with horn length ($F_{1,249} = 47.65$, $P < 0.001$; Fig. 5) and this relationship did not

TABLE 2. Effects of date, sex, and period of study on the logarithm of adult dressed body mass of males and females harvested during the hunting seasons of 1977–1984 (49 females, 205 males) and 2000–2002 (47 females, 82 males) in the Caroux-Espinouse massif (France).

Biological hypotheses	Models	AIC$_c$
No effect	null	166.6
Decrease of dressed mass over hunting seasons	date	167.0
Sexual dimorphism	sex	−222.0
Period (1977–1984 vs. 2000–2002) effects	**sex + period**	**−351.2**
Difference in period effects between sexes	sex + period + sex × period	−349.2

Notes: Additive effects are denoted by +, and an interaction between factors is denoted by ×. The selected model (lowest AIC$_c$) is in bold type.

TABLE 3. Effects of age and cohort on horn measurements and physical characteristics of mouflon harvested in the Caroux-Espinouse massif (France).

Cohort, age, sex, and parameter	Sample size	Mean value ± SE (cm)	Models	AIC_c	Slope of cohort effect ± SE
1970–1997, 5–8-yr-old males					
Horn length	321	66.34 ± 0.42	null	2211.2	
			cohort	2093.3	
			age	2201.6	
			cohort + age	**2044.1**	**−0.53 ± 0.04**
			cohort (factor) + age	2055.5	
			cohort + age + age × cohort	2046.1	
Horn circumference	321	23.20 ± 0.09	null	1189.3	
			cohort	1092.5	
			age	1189.6	
			cohort + age	1098.3	
			cohort (factor) + age	1114.8	
			cohort + age + age × cohort	**1080.0**	**−0.13 ± 0.02** (for 5-yr-old)
Horn breadth	252	47.05 ± 0.21	null	1388.7	
			cohort	**1346.8**	**−0.18 ± 0.03**
			age	1391.7	
			cohort + age	1348.9	
			cohort (factor) + age	1370.0	
			cohort + age + age × cohort	1350.3	
1972–1982, 1–9-yr-old males					
Horn curve diameter	246	41.23 ± 0.41	null	1618.5	
			cohort	1515.2	
			age	1587.6	
			cohort + age	**1507.4**	**−1.74 ± 0.18**
			cohort (factor) + age	1511.7	
			cohort + age + age × cohort	1521.1	
1972–1983, lambs to 9-yr-old males					
Height at shoulder	329	74.60 ± 0.31	null	2073.3	
			cohort	1928.0	
			age	1881.5	
			cohort + age	**1823.0**	**−0.90 ± 0.11**
			cohort (factor) + age	1840.8	
			cohort + age + age × cohort	1837.9	
1977–1984†, 1–3- and 5-yr-old females‡					
Height at shoulder	159	66.95 ± 0.52	null	1052.5	
			season	1020.6	
			age	1014.4	
			season + age	**958.6**	**−1.29 ± 0.16§**
			season (factor) + age	968.2	
			season + age + age × season	964.3	

Notes: Additive effects are denoted by +, and an interaction between factors is denoted by ×. The selected model (lowest AIC_c) is in bold type.

† We used harvest season instead of year of birth since exact age was not available beyond 2.5 years old for females. The year reported corresponds to the start of the hunting season (i.e., 1977 corresponds to the 1977/1978 hunting season).

‡ Tooth eruption class (see *Methods*).

§ Slope of season effect.

TABLE 4. Effects of habitat closure on body mass of lambs trapped in the WR in the 1976–1984 and 1995–2003 periods (for sample sizes, see Fig. 4) in the Caroux-Espinouse massif (France).

Biological hypotheses	Models	AIC_c
Best model including a period effect and without spatial structure (see Table 1)	date + sex + date × sex + period + date × period	2027.9
Difference in lamb body mass in relation to the proportion of habitat closure	date + sex + date × sex + period + date × period + closure	2014.1
Difference in habitat effect on lamb body mass between periods	**date + sex + date × sex + period + date × period + closure + closure × period**	**2011.6**
Difference in habitat effect on lamb body mass between sexes	date + sex + date × sex + period + date × period + closure + closure × period + closure × sex	2013.7

Notes: Additive effects are denoted by +, and an interaction between factors is denoted by ×. The selected model (lowest AIC_c) is in bold type.

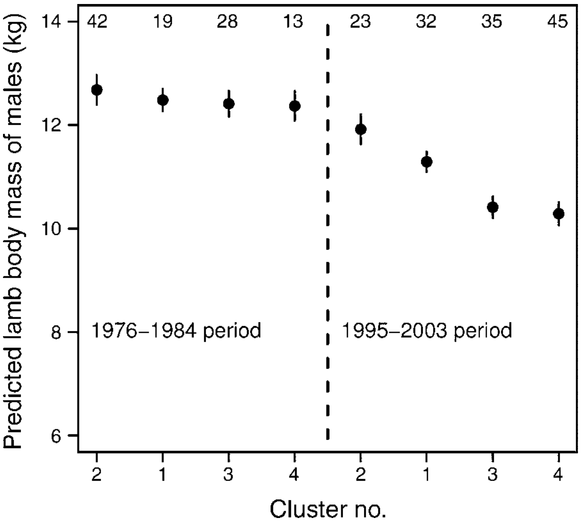

FIG. 4. Variations in mean (±SE) body mass of male lambs predicted from the selected model (see Table 4) for the median date of capture (26 June), the two periods of study (1976–1984 and 1995–2003), and in relation to trap cluster (Appendix D) as a function of the proportion of closed habitat (1976–1984, cluster 2 = 38%, cluster 1 = 52%, cluster 3 = 57%, cluster 4 = 60%; 1995–2003, cluster 2 = 51%, cluster 1 = 61%, cluster 3 = 75%, cluster 4 = 77%). Because the effect of sex was additive, we do not provide values for females for the sake of clarity. The sample size is given above the corresponding point.

depend on male age (age class 5–8 years, additive effect of age, $F_{3,246} = 0.84$, $P = 0.48$; interaction between age and horn length, $F_{3,243} = 0.29$, $P = 0.83$). While the slope of the allometric relationship did not differ between the two periods of study ($F_{1,247} = 0.23$, $P = 0.63$), the intercept was significantly higher during the first period than during the second one ($F_{1,248} = 14.50$, $P < 0.001$; see equation in Fig. 5 legend). Thus, for the average horn length (66 cm), horn breadth decreased by 1.85 cm (95% CI = 1.73, 1.97 cm) (back-transformed values) between the two study periods.

Both the number of males culled (slope = 4.09 ± 0.38, $P < 0.001$) and the proportion of largest-horned males harvested (defined as trophies > 184 points [see International Council for Game and Wildlife Conservation 1977, 1981]; slope (logit scale) = 0.08 ± 0.01, $P < 0.001$) increased over time. This increase resulted from an increase in commercial hunting (G. Dalery, *personal communication*). In particular, the notoriety of the population for hunting, as well as the hunting organization, much improved over the study period, allowing hunters to cull more and more large-horned males. At the same time, the age of males shot increased strongly (28.6% [$n = 426$] of males older than five years of age during the 1977–1984 period vs. 81.1% [$n = 350$] during the 1996–2002 period, $\chi^2 = 210.2$, df = 1, $P < 0.001$), as did the average age of the largest-horned males harvested (6.6 years, $n = 142$, in 1977–1984 vs. 10.2 years, $n = 289$, in 1996–2002 $t = -19.16$, $P < 0.001$). Likewise, the age of harvested females increased (average tooth eruption class of 3.0 [$n = 148$] and 4.5 [$n = 77$] in the periods 1977–1984 and 2000–2002, respectively; $\chi^2 = 50.8$, df = 4, $P < 0.001$). Given that there are no reliable age criteria for hunters to distinguish among adult females (Garel et al. 2005*c*), this increase is probably due to the cessation of culling young females, particularly lambs (after 1984).

DISCUSSION

Changes in mouflon phenotypic traits over time

Live and dressed body mass of males and females decreased by between 12.8% and 18.3% in all age classes from the 1970s, both in the WR and in the HA. Changes in other phenotypic characteristics were also recorded over the same period, namely a change in horn shape, a decrease in horn size of males and in height at shoulder. We also performed an independent analysis (not reported here) only based on trophies that scored more than 184 points (medal trophies, see International Council for Game and Wildlife Conservation [1977, 1981]) and still found that horn measurements decreased by 3.3% (horn breadth) and 11.4% (horn length) over the 20-year study period. This decrease was similar for all ages (from five to 13 years of age).

All these analyses are very conservative given that, during the study period, hunter selection of medal males increased (see *Changes in horn shape and selective hunting in HA*) and, thereby, the data recorded during the second period came from a much more selective hunting focused on trophy males as compared to the first period of study. As predicted, these long-term changes likely

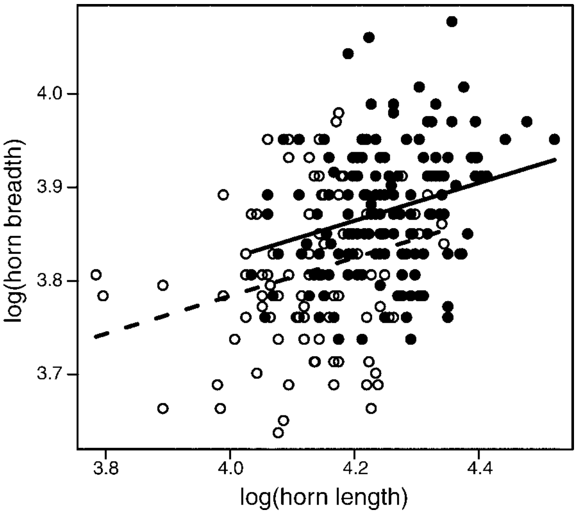

FIG. 5. Change in the allometric relationship between horn breadth and horn length during the two periods of study (1977–1984, solid circles, solid line; 1996–2002, open circles, dashed line). Lines correspond to the predicted values from the equations for the range of horn length measures recorded in each period (coefficients [±SE]): period 1, log(horn breadth) = 3.01 [0.20] + 0.202 [0.046] × log(horn length); period 2, log(horn breadth) = 2.97 [0.19] + 0.202 [0.046] × log(horn length).

occurred due to both selective harvesting and the habitat loss experienced by our population.

Selective hunting effects

The unrestricted selective harvesting in our population likely contributed to the production of small-horned rams (Harris et al. 2002, Coltman et al. 2003, Festa-Bianchet 2003), but also small-sized animals, since there is probably a high genetic correlation between horn and body size (see, e.g., in bighorn sheep, Coltman et al. [2003]). Further, it is quite unlikely that horn shape can be affected by changes in habitat characteristics. The decrease in horn breadth for a given horn length (Fig. 5), as well as other changes recorded in horn configuration (horn curve diameter, see Table 3), support the hypothesis that by selectively targeting males with widely flaring horns (e.g., Fig. 2, animal on the right), corresponding to the Corsican phenotype (see Maudet and Dubray 2002), hunters have increased the frequency of horns with small curve diameter and breadth (e.g., Fig. 2, animal on the left) and thus elicited a decline in the traits that determine trophy quality.

Under these conditions, males with fast-growing horns were at greater risk of being shot young than rams with slow-growing horns. Males attain over 70% of their final horn size by three years of age in our population (Garel et al. 2005*c*), becoming desirable trophies for hunters early. Thus, selective hunting reduces the reproductive contribution of high quality males and provides a selective advantage for males with slow-growing horns (Coltman et al. 2003, Festa-Bianchet et al. 2004). As illustrated by the marked increase in age of males shot over our study period, males then required more time to develop a desirable trophy (6.6 years vs. 10.2 years), indicating that they have slow growing horns compared to males shot in the first study period. Habitat loss is less likely to explain these changes in horn growth pattern since it would need that male compensate for a low early horn growth until almost 10 years of age which seems quite unlikely (e.g., Toïgo et al. [1999] in ibex, *Capra ibex*; Festa-Bianchet et al. [2004] in bighorn). By shooting animals with large horns at an early age during the first study period (1977–1984), the impact of hunting on male phenotype is likely to have been stronger during that time. This could thus account for the marked decrease over this period in horn curve diameter and height at shoulder that we reported here (Table 3).

Such declines in the early part of the study period also provide strong support for the effect of selective harvesting. Indeed, spatial variability in habitat closure within WR (Fig. 4) had almost no effect on body mass before 1985, despite the fact that most morphological characteristics had already decreased (see above and, e.g., for horn length, cohort 1970–1979, best model including additive effects of cohort and age; cohort effect, slope = -0.56 ± 0.26 cm, $P = 0.03$; decrease by 6.5–7%). Moreover, independently of any spatial variation in habitat closure, even lamb body mass tended to decrease over this period (best model including additive effects of date, sex and year; year effect, slope = -0.310 ± 0.170 g, $P = 0.11$).

Effects of habitat closure

The changes in quality and availability of food over the study period also contributed to the decline in phenotypic quality of mouflon. Although the diet of mouflon may include a wide variety of plant species (e.g., 48 species in Heroldova 1996), the bulk of food intake is normally made up of only a few species (less than 15, e.g., Cransac et al. [1997]). Between 1977 and 1979, Faliu et al. (1990) reported that mouflon fed essentially on grasses (56.4%) and supplemented their diet with forbs, shrubs and fruits in approximately equal amounts. Probably linked to the loss of open areas, mouflon have recently changed the composition of their diet (Cransac et al. 1997), feeding on grasses (35.4%) and shrubs in equal proportions, and supplementing their diet with forbs and fruits. This diet shift could have caused the observed decrease in body growth. This might indicate that a threshold at ~50% of closed habitat exists beyond which mouflon cannot compensate for the reduction in forage availability/quality (see Fig. 4). In addition, the reduction of high-visibility habitats might also likely contributed to affect mouflon growth by increasing forage competition and social interactions (Risenhoover and Bailey 1985), as well as the level of stress (McArthur et al. 1979), as animals must spend more time surveying their surroundings.

Within the WR, our results support the interpretation that habitat modification probably explains a large part of the observed body mass changes. However, we believe that mouflon in the WR could also have been influenced by the selective hunting that occurred outside this area, because about 30.0% of home ranges (26.2% [$n = 1565$] and 34.0% [$n = 1499$] for ≥ 2 year-old females and males, respectively) of mouflon trapped in the WR were located in the HA during the hunting season.

Biological consequences of changes in body mass and horn characteristics

A decrease in mouflon body mass may lead to both short and long-term demographic effects on population dynamics, because most fitness components of large herbivores are closely related to body mass (Gaillard et al. 2000). There might also be unexpected effects on genetically correlated traits that could result in further deterioration (Coltman et al. 2003). For example, in Soay sheep, a significant positive genetic correlation occurs between body mass and parasite resistance (gastrointestinal nematodes) in both sexes (Coltman et al. 2001). A decrease in body mass might also result in lower immunity, increasing the likelihood of epidemic outbreaks (Jorgenson et al. 1997, Coltman et al. 2001) such as the keratoconjunctivitis experienced by our population in autumn 1993 (Cransac et al. 1997).

Changes in horn size and horn configuration could also act negatively on individual fitness (Hartl et al. 2003). First, some authors (Scribner et al. 1989, Fitzsimmons et al. 1995) have suggested that horn size is positively correlated with genetic variability, at least among adult males (>5-year-old bighorn sheep rams in Fitzsimmons et al. [1995]). Second, a change in horn shape may lead to a non-adaptative horn configuration, as shown by the presence in our population of males with wounds in their neck caused by the excessive growth of their horns (Cugnasse 1988), increasing the risk of infection and, thereby, the probability of death.

Management implications

Trophy hunting is a major economic activity in the Caroux-Espinouse massif, as well as in numerous other wild sheep areas (e.g., Lewis and Alpert 1997, Singer and Zeigenfuss 2002, Whitfield 2003), generating large income. However, the fee for a trophy male in our study site (e.g., from 500 € to 1300 € in 2004; G. Dalery, *personal communication*) remains well below fees in other European populations of mouflon (from 153 € to 7740 €; G. Dalery, *personal communication*). Wildlife managers could take advantage of the fact that a large income may be generated from the harvest of a small number of trophy males (Lewis and Alpert 1997, Whitfield 2003) to finance action plans for mouflon range improvements, including clear-cutting and range burning which are known to be effective for restoring wildlife habitat (e.g., Smith et al. 1999). For instance, a split hunting regime which consists of harvesting young (mostly lambs) and old animals, i.e., a mortality pattern close to that of an ungulate population experiencing only non-hunting mortality (Gaillard et al. 2000, Harris et al. 2002), may be a good trade-off between hunter satisfaction, income, and long-term evolutionary concerns (Crête et al. 1981, Thelen 1991).

Indeed, while the consequences of habitat loss are often immediate and easily recognized (Hanski 1999), selective harvesting could have long-term evolutionary consequences which could be extremely difficult to reverse (Coltman et al. 2003). By provoking an evolution towards smaller-trophy males, and by reducing the frequency of the desired horns type (e.g., "Corsican" horns in our case), selective harvests may limit future opportunities for trophy hunting and thus lead to an unsustainable situation. More generally, by altering allele frequency, selective hunting may have a detrimental effect on population performance since targeted alleles may be linked to life history traits (e.g., Hartl et al. 2003, Coltman et al. 2005).

Research on the genetic consequences of selective hunting has been much less common than research on demographic and behavioral consequences of hunting in ungulate populations. However, to assess long-term consequences of hunting, the effects of selective hunting on population genetics need to be quantified (Harris et al. 2002, Festa-Bianchet 2003). For this task, long-term studies are badly needed. We have shown that long-term information on horn measurements collected from hunter associations may be used to assess the effects of selective harvest. We encourage wildlife managers to use this kind of data, given that they can be easily obtained from culled animals. Such data could allow us to better understand the population dynamics of Corsican mouflon, a species classified as vulnerable, which is poorly studied and for which the Caroux-Espinouse population is probably one of the closest populations, both genetically (Montgelard et al. 1994) and phenotypically (our study; Garel et al. 2005*a*). Finally experimentation may also be of use (Festa-Bianchet 2003): in our population, a test of the hypothesis that decreases in body and horn size were due to selective hunting would be to lower population density through greater culling of adult females.

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APPENDIX A

A table showing classification of open and closed habitats in the Caroux-Espinouse massif in relation to the cover of three species groups and the corresponding habitat types (*Ecological Archives* A017-068-A1).

APPENDIX B

A figure showing annual variations in lamb body mass of males predicted from the selected model for the median date of capture (*Ecological Archives* A017-068-A2).

APPENDIX C

A figure showing decrease in horn length among cohorts born in the 1970–1997 period and in relation to age at harvesting (*Ecological Archives* A017-068-A3).

APPENDIX D

A figure showing hierarchical cluster analysis to distinguish four clusters of traps used to analyze the effect of habitat closure on lamb body mass within the wildlife reserve (*Ecological Archives* A017-068-A4).