# ORIGINAL PAPER

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# Monitoring the abundance of mouflon in South France

**Abstract** Monitoring change in the population size of mouflon (*Ovis gmelini musimon* × *Ovis* sp.) in rugged areas is an important yet difficult task for wildlife ecologists. To assess population change of mouflon inhabiting the Caroux-Espinouse massif, France, we compared a pedestrian and helicopter survey, using counts of animals as indices of abundance. Environmental factors such as date of survey and temperature affected the detection of mouflons from the ground and the air. Both indices were sensitive to observed changes in population size. A decrease in the pedestrian index was recorded in 1994, the year following an epizootic of keratoconjunctivitis, which markedly reduced the survival rate of mouflon. Variations in pedestrian index accounted for variations in harvests when excluding epizootic events. Both surveys detected a decrease in population size, which accounted for the recent increase of harvest. Helicopter and pedestrian surveys are reliable tools to monitor annually mouflons in mountainous areas. Simulations indicated that helicopter surveys should be preferred by managers because they provide the best trade-off between cost and precision.

**Keywords** Caroux-Espinouse massif · Helicopter survey · Monitoring costs · *Ovis gmelini musimon* × *Ovis* sp. · Pedestrian survey
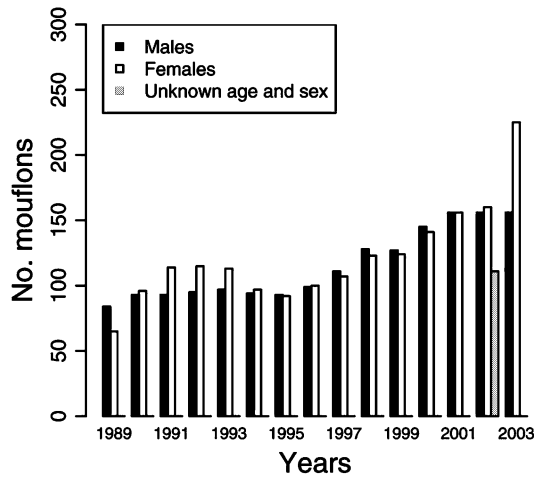
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## Introduction

Assessing population abundance or density is essential for studying population dynamics and for efficient wildlife management (Wilson et al. 1996; Schwarz and Seber 1999; Williams et al. 2002). However, monitoring changes in the size of wild populations remains difficult for wildlife ecologists (Link and Sauer 1997; Pollock et al. 2002). Despite a long history of refinements in design and development of census methods (Caughley 1977; Seber 1982; Eberhardt and Simmons 1987; Lancia et al. 1994; Buckland et al. 2000; Pollock et al. 2002), few attempts have provided satisfactory results except for capture–mark–recapture methods (Schwarz and Seber 1999) and distance sampling (Buckland et al. 2004). However, for most species, mark–recapture or mark–resight techniques are costly and time-consuming (Link and Sauer 1997). Moreover, distance sampling is not well suited to 3D areas such as mountains. Approaches using count statistics have thus been developed as alternatives to census methods.

Count statistics are well adapted when cost and effort to estimate total population size are prohibitive and only the relative differences in abundance are required (Eberhardt and Simmons 1987; Pollock et al. 2002; Williams et al. 2002). Count statistics include numerous methods, such as number of birds seen and heard at a point-count location, number of ungulates seen while walking a transect, or number of small mammals caught on a trapping grid (Nichols et al. 2000). The relationship between a count statistic and the population abundance can be written as $C_I = N_I P_I$, where $C_I$ denotes the count, $N_I$ the true abundance, and $P_I$ the detection probability, all associated with time and location $I$ (Lancia et al. 1994). If a standardized method is used to obtain the count statistic, and the detection probabilities are similar across time and locations sampled (i.e. that $P_I = P$ for all $I$ in the comparison), then the count statistics provide reliable index of abundance (Nichols et al. 2000; Williams et al. 2002).

**Fig. 1** Total number of male and female mouflons removed annually through hunting from 1988 to 2003. Because hunting occurred from September to February, year reported corresponds to the end of hunting season (i.e. 1989 corresponds to 1988/1989 hunting season)

The wild population of mouflon (*Ovis gmelini musimon × Ovis* sp.) of the Caroux-Espinouse massif (south of France) has been monitored since 1989 (Santosa 1990) through a pedestrian survey derived from bird surveys based on point estimates (Blondel et al. 1970). Additionally, helicopter surveys have been conducted yearly since 1994. We aim to test the relevance of such census techniques to track trends in population sizes. During our study, population size varied according to an epizootic of keratoconjunctivitis in autumn 1993 (Cugnasse 1997), which reduced the

survival probability of all age and sex classes (Cransac et al. 1997). Moreover, hunting occurs annually and quotas have recently increased in response to increase in damage caused by mouflon (Fig. 1). To assess the accuracy of the methods, we tested whether the pedestrian survey was sensitive to the decrease of population size after the keratoconjunctivitis die-off. We also expected that both surveys would detect the same trend in population size and track variation in yearly harvest. Further, we used simulations to optimize the monitoring protocol used to calculate indices and we compared the cost of each type of survey to identify the method providing the best trade-off between cost and precision.

## Materials and methods

### Study area

The study area was situated on the south-western border of the Massif Central, in southern France (Fig. 2). Elevations ranged from 300 m to 1,124 m. Mouflons occupy Caroux-Espinouse massif (43°40′N, 3°0′E), which covers approximately 17,000 ha. This population grew from 19 individuals introduced between 1956 and 1960 in the wildlife reserve of Caroux-Espinouse (1,708 ha), situated in the central part of the massif (Cugnasse and Houssin 1993). No other introduction occurred in nearby mountain massifs. Hunting (Fig. 1), by stalking and beating, was based on quotas and occurred from September to February. Quotas are completely harvested each year. A mean number of 107 (±34) males



**Fig. 2** Location of the study area in southern France. Transects (and observation points) sampled during pedestrian surveys (for the sake of clarity only the sunset transects were reported) and route sampled during helicopter surveys were reported

and 110 ($\pm45$) females were removed annually between 1973 and 2003. The population is monitored by the Office National de la Chasse et de la Faune Sauvage since 1974 (Cugnasse and Houssin 1993).

Climatic conditions consisted of dry summers (Garel et al. 2004) and dominant south–southeast winds, wet autumns and fairly cold winters associated with dominant north–northwest winds (Thiebaut 1971). The vegetation includes an irregular mosaic of beech (*Fagus silvatica*), chestnut (*Castanea sativa*) and evergreen oak (*Quercus ilex*) forest in a north–south gradient. The high plateaus have been replanted with coniferous woodland (*Pinus sylvestris*, *P. nigra*, *Picea abies*). The vegetation in open areas is dominated by moorlands of heather (*Calluna vulgaris, Erica cinerea*) and broom moorlands (*Cytisus purgans, C. scorparius*) frequently mixed with grasses (e.g. *Festuca paniculata*, *F. ovina*, *Agrostis capillaris*) and whortleberry (*Vaccinium myrtillus*). Between 1955 and 1992, the decrease in pastoral activity and fire suppression has allowed encroachment of mouflon range by dense broomland and forests (V. Bousquel, Syndicat Interchambre Montagne Elevage, unpublished data). During this period, the area of open moorland decreased by 49% (from 4,830 ha to 2,378 ha).

## Survey procedures

### Pedestrian survey

We estimated population trends between 1989 and 2003 from punctual abundance index (PAI) estimated from a pedestrian survey (Santosa 1990). The PAI was calculated from days of intensive large-scale systematic census during the spring, following lambing period when large groups occur in open areas (Bon et al. 1990). Twelve transects were defined across the entire massif in open areas and were surveyed during the period of maximal activity of mouflon (Santosa 1990; Bon et al. 1991). Six were simultaneously surveyed within 2 h after sunrise, while the other six were simultaneously surveyed during the 2 h before sunset (e.g. Fig. 2). About three to four observation points were distributed along each transect. Each transect was surveyed by one observer, in the same way to prevent observation problems related to sunlight. From the 40 observation points ($n=21$ for sunrise transects and $n=19$ for sunset transect and), each observer searched and located mouflon for 15 min with binoculars (10×42 mm). Each sample area was independent from each other. The procedure was repeated over consecutive days between three and nine times (median = 6) depending on weather conditions encountered each spring. In 1992 and 1999 no data were collected due to adverse weather conditions that obscured observation (wind, rain and fog). Since 1998, the surveys have been based on sunset transects alone to reduce the effort spent in the field. For each day, PAI was calculated per transect as the sum of the number of individuals observed on all points.

### Helicopter survey

We conducted helicopter surveys of the open areas of the entire massif between 1994 and 2003 (Fig. 2), ensuring visual independence between observations. Each mouflon was recorded during the flight (between 23 min and 60 min, median = 32 min) to estimate an aerial abundance index (AAI). The 5.0 km route was surveyed 2 h before sunset when mouflons were most active. The speed (30–50 km/h) and altitude (20–30 m) were maintained constant in all flights, allowing us to assume high and equal detectability of age and sex classes (LeResche and Rauch 1974) and to prevent double counts (mouflons join vegetal cover during the passage of the helicopter and remain below). To limit disturbance, no stops were performed. Helicopter doors were removed to improve observation. The helicopter survey took place each spring immediately after pedestrian surveys and was repeated over consecutive days between three and nine times (median = 5.5). The same observer performed all aerial counts. For each census day, the AAI was calculated as the sum of the number of individuals observed.

## Statistical analysis

### Model adjustment

Analyses of changes in population size can be biased when factors related to the acquisition of data are not adequately controlled (Link and Sauer 1997). We therefore fitted models with the following factors of variation in the detection of mouflons: date of survey (PAI and AAI), temperature (PAI and AAI), transects (PAI) and duration of the flight (AAI). Temperature (daily mean) and the date of surveys ranged from 6.3°C to 20.3°C and from 13 May to 14 June, respectively, for the pedestrian surveys, and from 11.0°C to 23.0°C and from 5 June to 12 July, respectively, for the helicopter surveys. The date of survey and the temperature are expected to influence counts because these variables influence the use of open areas by mouflons and the intensity of spatial and sexual segregation (Bon et al. 1990; Santosa et al. 1990; Cransac and Hewison 1997; Cransac et al. 1998). We also accounted for differences in PAI and in temperature according to transects due to differences in space use of mouflons and physical characteristics of the sample areas (e.g. orientation, slope, vegetal cover). We discarded censuses ($n=14$) done during conditions that obstructed observation (e.g. wind, rain and fog, Santosa et al. 1990).

### Analysis procedure

We first tested for an epizootic effect on PAI for which data were available both before and after the epizootic event. We then performed analyses by excluding the epizootic year to test whether PAI accounted for varia-

tion in yearly harvest and whether both surveys detected the same trend in population size. To compare both surveys, we performed the analysis on a common period (1995–2003) during which the harvest increased (Fig. 1). We believe that hunting quotas settled throughout the study period most likely have a significant effect on the population dynamics. Indeed, a simple Leslie matrix model (Caswell 2000), with optimistic demographic values, no stochasticity and including harvests, predicted a maximum population size of 2,450 mouflons in 1989 when the pedestrian survey started (M. Garel, unpublished data).

Pedestrian survey analysis was based on 751 PAI sampled on 12 transects between 1989 and 2003. During the 1989–1998 survey period, there was no difference in PAI between sunrise transects and sunset transects for the same day of sampling ($F_{1,\ 454} = 0.04$, $P = 0.83$). Therefore, the two data sets were pooled. Data were log-transformed (after adding one individual to each count because some counts were equal to zero) to ensure a homogeneous variance across treatments (Fligner–Killeen test (Conover et al. 1981) for the homogeneity of variance throughout years: $Fk_{11} = 20.93$, $P = 0.06$; and across transects: $Fk_{11} = 12.44$, $P = 0.33$). We then examined the annual variations of PAI by using linear models. The observer effect was ignored because the number of observers in PAI was large ($n = 60$). The bias associated with differences among observers is indeed likely to be offset by gains in precision obtained when ignoring observer effect (James et al. 1996).

Comparison between pedestrian and helicopter surveys was based on 415 PAI and 43 AAI sampled between 1995 and 2003 (excluding 1999 because poor weather conditions occurred for PAI). We applied the same procedures as used for the analysis of the pedestrian surveys and compared the model selected in both cases.

### Model selection

Model selection was based on Akaike Information Criterion (AIC) with second order adjustment (AICc) to correct for small-sample bias (Burnham and Anderson 1998). This criterion is based on the principle of parsimony and is well adapted when performing multiple comparisons between non-nested models. The most parsimonious model (i.e. lowest AICc) was selected as the best model. We followed Burnham and Anderson (1998) to conclude that the models were different when the difference in AICc was >2. When the difference was <2, we kept the simplest model. We also computed Akaike weights (AICc weight) to compare the relative performance of the models rather than only their absolute AICc value. Weights can be interpreted as the probability that a model is the best model given the data and the set of candidate models (Burnham and Anderson 2001). Thus, the strength of evidence in favour of one model over the other is obtained by dividing their Akaike weights.

### Simulation procedure to optimize the protocol surveys

We explored how the PAI and AAI estimates depended on the number of repetitions. We chose years with a large number of repetitions (1994, 1996, 1997 for pedestrian surveys and 1997, 1998, 1999 for helicopter surveys). We performed Monte-Carlo simulations, to estimate values of PAI and AAI that would have been obtained for different numbers of repetitions of the surveys. For each year with a total of $R$ repetitions of the surveys, we randomly chose $r$ values ($1 < r \leq R$) among the $R$ possible values of total number of mouflons seen per survey. For each value of $r$, we performed 1,000 samplings of $r$ values among the $R$ possible values. For each sampling, we then estimated the mean number of mouflons seen over $r$ repetitions of the survey. For each $r$ value, we therefore obtained 1,000 values of PAI and AAI. Based on these values, we estimated the coefficient of variation (CV) of the PAI and AAI. The CV of PAI and AAI was used as a measure of the repeatability of the result and was expected to decrease with increasing $r$.

The cost of each survey was calculated as a function including a constant cost (staff training and organization) and a cost generated by each additional repetition (cost of realization of the survey). For pedestrian survey, we used only sunset transects in the simulation procedure and cost estimate to account for reduction in the time spent in the field since 1998. All analyses and resampling procedures were performed using R 1.8.0 (Ihaka and Gentleman 1996).

## Results

Pedestrian surveys (1989–2003 period)

The model with the lowest AICc included an effect of the interaction between temperature and transects, and additive effects of date and year (Table 1). This model was 13 times more supported than the second best model without year effect (AIC weights ratio: 0.928/0.072 = 12.889). The PAI decreased with the date of observation (slope $= -0.018 \pm 0.004$ (SE), $P < 0.001$). Between 13 May and 14 June, PAI decreased from $24.68 \pm 1.77$ (SE) to $13.61 \pm 1.13$. The PAI decreased with temperature (slope $= -0.050 \pm 0.011$, $P < 0.001$) but not in the same way for all transects sampled (Table 1). As expected, the decrease of PAI following the epizootic (autumn 1993) was the most important ever recorded: PAI was significantly less in 1994 than in any other year (Fig. 3).

The variation in harvest best accounted for the variation from year to year in PAI (slope $= -0.00093 \pm 0.00044$, $P = 0.03$) after excluding 1994 (Table 1). This model was over three times more supported than the second best model without a harvest effect (AIC weights ratio: 0.781/0.214 = 3.650). When the harvest increased from 149 to 427 animals, the PAI predicted from the selected model decreased from an

**Table 1** Set of models fitted to investigate the variation of the punctual abundance index (PAI) recorded in a mouflon population in the Caroux-Espinouse massif, France, 1989–2003

| Models[a] | AICc | ΔAICc | AICc weight |
|---|---|---|---|
| Control factors | | | |
| Null | 1,800.8 | 318.1 | 0.000 |
| Date | 1,785.3 | 302.6 | 0.000 |
| Date + temperature | 1,772.9 | 290.2 | 0.000 |
| Date + temperature + transects | 1,507.7 | 25.0 | 0.000 |
| Date + temperature + transects + temperature × transects | 1,487.8 | 5.1 | 0.072 |
| Epizootic effect | | | |
| Date + temperature + transects + temperature × transects + years + years × transects | 1,599.0 | 116.3 | 0.000 |
| **Date + temperature + transects + temperature × transects + years** | **1,482.7** | **0.0** | **0.928** |
| Harvest effect (excluding epizootic year) | | | |
| Date + temperature + transects + temperature × transects + years + years × transects | 1,301.6 | 102.9 | 0.000 |
| Date + temperature + transects + temperature × transects + years | 1,211.4 | 12.7 | 0.001 |
| Date + temperature + transects + temperature × transects + harvests + harvests × transects | 1,209.9 | 11.2 | 0.003 |
| Date + temperature + transects + temperature × transects | 1,201.3 | 2.6 | 0.214 |
| **Date + temperature + transects + temperature × transects + harvests** | **1,198.7** | **0.0** | **0.781** |

[a] In model notation, " + " corresponds to additive effects and "×" to interaction between two factors. The selected model (lowest AICc) occurs in bold type
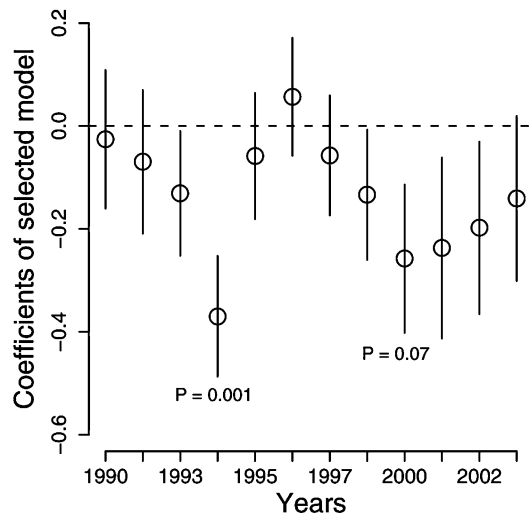
average of $24.2 \pm 3.4$ to $18.5 \pm 2.5$ per transect for a survey that would occur at the median date of survey (27 May) and median temperature (12.5°C).

Comparison between pedestrian and helicopter surveys (1995–2003 period)

For pedestrian surveys, the model with the lowest AICc included an effect of the interaction between temperature and transects, and additive effects of date and harvest (Table 2). This model was three times more



**Fig. 3** Temporal variation in the punctual abundance index (PAI) predicted from the selected model (see Table 1, model including epizootic effect) in the mouflon population of the Caroux-Espinouse massif, France. Coefficients of the year effect were reported to show the year to year variations in PAI (1989 corresponds to reference year, i.e. null value). In 1992 and 1999 no data were collected due to adverse climatic conditions (wind, rain and fog)

supported than the second best model without a harvest effect (AIC weights ratio: 0.746/0.249 = 3.000). The PAI tended to decrease when the harvest increased (slope = $-0.00095 \pm 0.00053$, $P = 0.07$). When the harvest increased from 185 to 427 animals, the PAI predicted from the selected model decreased from an average of $24.0 \pm 3.6$ to $19.4 \pm 2.9$ per transect for a survey that would occur at the median date (24 May) and median temperature (13.3°C).

For helicopter surveys, the model with the lowest AICc included additive effects of date, temperature, duration and harvest (Table 2). This model was over 13 times more supported than the second best model without a harvest effect (AIC weights ratio: 0.909/ 0.068 = 13.368). The AAI decreased with the date of survey (slope = $-0.03 \pm 0.009$, $P = 0.001$), temperature (slope = $-0.16 \pm 0.03$, $P < 0.001$) and tended to increase with the duration of survey (slope = $0.032 \pm 0.01$, $P = 0.08$). As for the pedestrian surveys, the AAI decreased when the harvest increased (slope = $-0.0032 \pm 0.0011$, $P = 0.008$). When the harvest increased from 185 to 427 animals, the AAI predicted from the selected model decreased from an average of $116.2 \pm 1.1$ to $54.5 \pm 1.2$ for a survey that would occur at the median date (16 June), median temperature (16.0°C) and median duration (31 min).

Simulation procedure to optimize the surveys

The curves linking the CV to the number of repetitions $r$ were similar for all years (Fig. 4a, b). The CV tended to be less variable for AAI than PAI. The simulations for PAI and AAI indicated that increasing the number of surveys decreased the variation in the mean number of animals seen from one random sample to another. Assuming that the same number of repetitions is needed

**Table 2** Set of models fitted to compare the variation of the PAI and of the aerial abundance index (AAI) recorded in a mouflon population in the Caroux-Espinouse massif, France, 1995–2003 (excluding epizootic year)

| Survey | Models[a] | AICc | ΔAICc | AICc weight |
|---|---|---|---|---|
| Pedestrian | | | | |
| | Control factors | | | |
| | Null | 950.4 | 168.1 | 0.000 |
| | Date | 947.9 | 165.6 | 0.000 |
| | Date + temperature | 943.0 | 160.7 | 0.000 |
| | Date + temperature + transects | 792.5 | 10.2 | 0.005 |
| | Date + temperature + transects + temperature × transects | 784.5 | 2.2 | 0.249 |
| | Harvest effects | | | |
| | Date + temperature + transects + temperature × transects + harvests + harvests × transects | 798.4 | 16.1 | 0.000 |
| | **Date + temperature + transects + temperature × transects + harvests** | **782.3** | **0.0** | **0.746** |
| Helicopter | | | | |
| | Control factors | | | |
| | Null | 93.5 | 32.8 | 0.000 |
| | Date | 84.1 | 23.4 | 0.000 |
| | Date + temperature | 68.1 | 7.4 | 0.023 |
| | Date + temperature + duration | 65.9 | 5.2 | 0.068 |
| | Harvest effects | | | |
| | **Date + temperature + duration + harvests** | **60.7** | **0.0** | **0.909** |

[a]See Table 1 for model notations

to obtain the same precision for AAI and PAI estimates (Fig. 4a, b), AAI was more cost effective than PAI (difference of 34.1% between PAI and AAI costs, Table 3). Pedestrian surveys were more complex than helicopter surveys and involved at least six observers. Therefore, difference in cost between the two methods came from the additional cost of organization, training and implementation of pedestrian surveys (Table 3).

## Discussion

### Validation of the surveys and changes in mouflon abundance

To use pedestrian and helicopter surveys as reliable indices of population abundance, we assumed that such indices are directly proportional to the population size. Therefore, it is necessary to assume that the probability of detection was constant across locations and years which rarely occur in practice (Lancia et al. 1994; Nichols et al. 2000; Pollock et al. 2002; Williams et al. 2002). The increasing closure and degree of fragmentation of habitat likely modified the distribution of resources by reducing food availability for mouflons, which in turn could changed social and spatial organization of the animals. Alternatively, the detection probability of mouflons might have been reduced with increasing habitat closure. There are basically multiple approaches to deal with failure of the detectability assumptions (Nichols et al. 2000; Farnsworth et al. 2001; Pollock et al. 2002). We chose to adjust our models with date of sampling, temperature and transects to make detectability constant across locations and years. For example,



**Fig. 4** Relationship between the number of repetitions of the survey for 3 years (1994, 1996 and 1997 for PAI, and 1997, 1998, and 1999 for AAI), the cost of repetition and the CV of the PAI (**a**) or the CV of the AAI (**b**).The CV was estimated from 1,000 values of a random sample of $r$ values of the index (PAI or AAI) among the possible observed values of the index for a given year (see text for details). For the cost of the survey, see Table 3
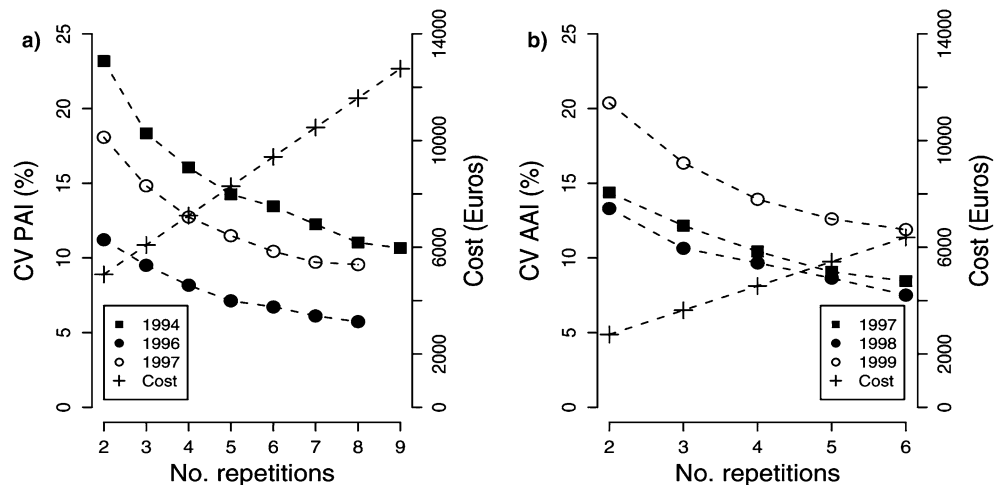
**Table 3** Global costs of pedestrian and helicopter surveys

| Cost type | Survey | |
|---|---|---|
| | Pedestrian | Helicopter |
| Training | | |
| Number of man-days | 1 | 1/2 |
| Number of observers | 6 | 1 |
| Man cost | 238€×6×1 | 238€×1×1/2 |
| Helicopter cost (for one fly of 1 h) | – | 570€ |
| Number of kilometers (car) needed to reach first observation point[a]/airport | 45 | 160 |
| Kilometer cost | 1.38€×45×6 | 1.38€×160×1 |
| Total | 1,800.6€ | 909.8€ |
| Realization | | |
| Number of man-half-days | 5 | 5 |
| Number of observers | 6 | 1 |
| Man cost | 119€×6×5 | 119€×1×5 |
| Helicopter cost (for five flies of 1 h) | – | 2,850€ |
| Number of kilometers (car) needed to reach first observation point[a]/airport | 45 | 160 |
| Kilometer cost | 1.38€×45×6×5 | 1.38€×160×1×5 |
| Total | 5,433€ | 4,549€ |
| Organization[b] | | |
| Number of gathering (one half-day) | 1 | 0 |
| Number of observer include in organization | 6 | – |
| Man cost | 119€×6×1 | – |
| Average number of kilometers needed for organization | 32 | – |
| Kilometer cost | 1.38€×32×6 | – |
| Time of duty[c] by day | 1 h | 0 |
| Duty time cost by hour (e.g. phone, man-time) | 15€×1×5 | – |
| Total | 1,054€ | 0€ |
| Total cost | 8,287.6€ | 5,458.8€ |

Prices were established in 2003. For pedestrian surveys, the cost estimate was based only on the survey of sunset transects

[a] Based on average distance between study station and first observation point of transect

[b] Organization cost of helicopter survey was null because only one person is involved (see text for details)

[c] Pedestrian survey requires duty of one person to organize possible annulations of survey because of adverse climatic conditions

animals reduce their activity and stay in dense cover when temperature increases (Santosa et al. 1990) causing the detection probability to decrease (as supported by the negative relationship we reported between temperature and the two indices). In addition, other factors may have been involved, such as human disturbance, or repartition of resources (Santosa et al. 1990; Rubin et al. 1998), and not all covariates can be measured, modelled or even perceived. In this context, some authors have suggested to develop a monitoring design, which includes an estimation of detection probability (e.g. Nichols et al. 2000; Farnsworth et al. 2001; Pollock et al. 2002). This was however not feasible in our study.

The precision of indices is also often difficult to check due to a lack of reference estimates on "true" population sizes, for example those obtained by capture–mark–recapture methods (e.g. Vincent et al. 1991). Nevertheless, one can use independent information about variations in population size to check whether the indices used track known variations. Both abundance indices were sensitive to observed changes in population size resulting from an epizootic (Cugnasse 1997) and from changes in harvest. Hunting affect population abundance directly by animal removal and possibly indirectly by influencing reproduction and survival (Festa-Bianchet 2003). Indeed, most (>90%) harvested mouflons were trophy males and females >3 years of age (M. Garel et al., unpublished data); increasing hunting pressure reduced the probability of adult survival and could thus have affected population growth (Gaillard et al. 2000). Moreover, even if there is a lack of information on the impact of trophy hunting on population dynamics (Harris et al. 2002; Festa-Bianchet 2003), some evidence suggests that it affects ungulate reproduction (e.g., Solberg et al. 2002; Sæther et al. 2003) and thus growth rate of the population (Festa-Bianchet 2003).

Management implications

To date, comparative tests of helicopter and ground surveys are rare for ungulates and mainly concern gender and age composition data (Tsukamoto 1977; Bender et al. 2003). We suggest that helicopter surveys provide a better alternative to census mouflon populations than pedestrian surveys because:

1. The AAI detected similar trends in population abundance as PAI and strongly accounted for yearly changes in harvest.
2. Only one observer is involved in AAI, so the observer bias is limited compared to the PAI.
3. The AAI provided the best trade-off between cost and precision. It required fewer man-days of sampling, and therefore, were much more cost-effective (Table 3) for assessing mouflon abundance over a large area with an equal number of repetitions for AAI and PAI (Fig. 4a, b). Moreover, training is limited to the first year for AAI, whereas for PAI, it is difficult to work annually with the same observers (60 different observers were used during 1989–2003 vs. 2 for helicopter surveys during 1994–2003). Therefore, the difference in cost between surveys in favour of AAI tends to increase after the first year.
4. The AAI allows one to reduce technical/security problems related to the access to observation points (arrival before the sunrise and back after the sunset) in large, mountainous areas.

Finally, previous comparative studies of data obtained from helicopter and ground surveys reported that helicopter counts were both more representative than ground counts and corroborated by demographic studies (Bender et al. 2003 on elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*)).

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