A general approach of using hair-tubes to monitor the European red squirrel: a method applicable at regional and national scales

Running title: A general approach to monitor red squirrels with hair-tubes

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Content of the manuscript: original investigations

Abstract

Monitoring constitutes a key element in the management and conservation of many mammal species. We describe a technique to obtain population indices for red squirrels (*Sciurus vulgaris*) using hair-tubes and compare these indices to population estimates obtained by live trapping. Data were collected in seven study areas in the Western and Central Alps in Italy and compared with data previously collected in 11 sites in northern England. The aim was to test if hair-tube census could be used to derive a general predictive model allowing accurate predictions of squirrel numbers in different years, habitats and geographic regions. We used model equations developed from the proportion of hair-tubes visited to predict densities obtained from live-trapping. Hair-tube data gathered in the Central Alps correctly predicted squirrel densities in the Western Alps. A combined data set pooling the sites of these two regions based on the first three years successfully predicted the two successive years. In addition, a combined model derived from areas monitored for five years had a high predictive value locally (89%) and internationally (73%) when applied to the English data set. We therefore believe that the predictive model developed in this study could be of general value and be used to monitor squirrel populations in European low density conifer habitats (0.1-0.5 squirrels/ha). The approach may also be suitable for many tree squirrel populations in North America and other arboreal rodents that occur at similar densities.

Key words: Sciuridae; hair-tubes; monitoring; mountain forests; census techniques

Introduction

The implementation of wildlife management and conservation measures requires knowledge of species distribution and abundance. Effective population estimates are usually labor intensive and for small and medium-size mammals often require the capture and handling of animals. For this reason, many population indices obtained with direct and indirect methods have been proposed (Lancia et al. 2005). These indices can be used to address questions regarding differences in density through time and space, and are widely used instead of total counts (Eberhardt and Simmons 1987; Conroy 1996). An index is a sort of count of animals or their signs that is presumed related to density, although rarely is the true relationship known (Eberhardt 1978; Eberhardt and Simmons 1987). To be effective, an index should be validated against known population sizes obtained with other, more precise methods (Davis and Winstead 1987).

Tree squirrel populations are monitored with a number of methods that require the capture of animals or collection of signs of presence. Gurnell et al. (2004a) recently reviewed direct and indirect methods to monitor the European red squirrel (*Sciurus vulgaris*) and the Eastern grey squirrel (*S. carolinensis*). Live trapping and marking squirrels is the most accurate technique used to collect information on population abundance (Wauters and Lens 1995; Gurnell 1996; Gurnell et al. 2004b; Wauters et al. 2004, 2008). Capturing and handling squirrels is time consuming, costly, requires expertise, and usually also a license. On the other hand, handling live animals allows researchers to collect much more information on life history characteristics, such as breeding activity and body condition, and to collect samples for genetic or parasitological research. In many studies, however, data on the presence/absence of the species and on population densities and trends would be sufficient. For these reasons, indirect methods that do not require trapping have been developed. Gurnell et al. (2004a) analyzed five methods for squirrels, that involve the use of feeding stations, hair-tubes, feeding transects, or the count of nests or animals by visual census. Methods, such as nest surveys or visual transects, are unsuitable in conifer habitats where visibility of the crowns is low and squirrels are rarely seen. Hence, using hair-tubes in conifer sites is less labor intensive than other methods and allows to distinguish between different species of squirrels. Hair tubes were used for the first time by Suckling (1978) to detect the presence of arboreal mammals and were then employed by several authors with different species of small mammals (Dickman 1986; Scott and Craig 1988; Lindenmayer et al. 1994). Since then, hair-tubes have been used in many studies due to their low cost, limited effort in terms of man-hours, the possibility to cover large areas, and many sites in replicate studies (Capizzi et al. 2002; Sanecki and Green 2005).

Hair-tubes have been previously used to monitor squirrel populations (Finnegan et al. 2007; Mortelliti and Boitani 2008). One of the advantages of this technique is that the squirrel that enters the tubes can be identified to species by characteristics of the hairs (Teerink 1991; Dagnall et al. 1995). Thus, in Europe, it is possible to distinguish the native red squirrel from the introduced Eastern grey squirrel. For this reason, hair-tubes have been chosen among other techniques to record the presence of the two species in Great Britain, Ireland and Italy. (Gurnell et al. 2004a ; Finnegan et al. 2007). Garson and Lurz (1998) reported a relationship between the number of tubes used by red squirrels in each of 11 sites in large conifer plantation forests in England and the number of individuals trapped. Gurnell et al. (2004a) concluded that this relationship may be used to estimate squirrel abundance with moderate accuracy and that hair-tubes can be used to monitor relative trends in population indices over time.

The aim of our study was to describe a technique to obtain red squirrel population indices using hair-tubes and to compare these indices with precise population estimates from live trapping. We also investigated whether this index, derived from a subset of data over a limited number of years, or areas, could be applied generally as an accurate predictor of squirrel numbers and/or densities in different years, habitats and regions.

Material and methods

Study areas

Seven study areas were chosen within mature, secondary montane and subalpine mixed conifer forests of the Italian Alps, with elevations ranging from 1100 to 2100 m a.s.l. (the upper tree-line). These areas are distributed over two geographic regions: Cogne (COG) and Rhemes (RHE), are located in the Cogne and Rhemes Valleys of the Gran Paradiso National Park, in the Western Alps, while Cedrasco (CED), Oga (OGA), Valfurva (VAL), S. Antonio (SAN) and Bormio (BOR), are in the Valtellina Valley in Fig. 1
the Central Alps (Fig. 1). RHE, SAN, and VAL are dominated by Norway spruce (*Picea abies*), OGA by Scots pine (*Pinus sylvestris*), and BOR by Arolla pine (*Pinus cembra*). COG is spruce-larch (*Larix decidua*) forest and at CED the forest is mainly composed of silver fir (*Abies alba*) and spruce with small proportions of larch, Scots pine and some beech (*Fagus sylvatica*) at lower elevations (Tab. 1a). Tab. 1

Trapping and handling techniques

In each study area, squirrels were live-trapped bimonthly from April to October 2000-2004, using ground-placed Tomahawk 'squirrel' traps (Tomahawk Live Trap Co., Wisconsin, USA). Traps were set in a grid (n = 20-30 in every area, spaced 100 m) for eight to twelve days, until no new, unmarked squirrels were trapped for at least two consecutive days. Traps, partly covered by dark plastic to give shelter from rain or cold, were checked two or three times a day. Each trapped squirrel was flushed into a light cotton handling bag with velcro-type fasteners or with a zipper (Koprowski 2002), or into a wire-mesh ‘handling cone’ to minimize stress during handling. All animals were individually marked using numbered metal ear-tags (type 1003 S, 10 by 2 mm, National Band and Tag Co, Newport, Kentucky, USA*)*. Sex, age, weight, and reproductive condition were recorded as described elsewhere (Wauters and Dhondt 1989, 1993; Wauters and Lens 1995). Trapping and marking was authorized under the licence of the Gran Paradiso national Park Authority and the Region of Lombardy.

Hair-tubes

In each study area a survey using hair-tubes was carried out before a population estimate was made by live trapping. The hair-tubes (length 300 mm, inner diameter 60 mm) were cut from PVC drainage pipe. A hair-tube was attached to a tree in correspondence of each trap. At the beginning of the study the tubes were tied around the trunk using metal wire, or on horizontal branches with packaging adhesive tape (Fig. 2) and remained permanently in the field. One month before each trapping session (see Table 1) the hair-tubes were activated. On both ends of the tube, a wooden tablet was placed and covered by double sided sticky tape (Fig. 2), and the tube was baited with a mixture of hazelnuts and sunflower seeds to attract the squirrels. Hair-tubes were checked twice, after two and four weeks. Trapping was initiated one to three days after the end of the hair-tube monitoring, in order to reduce changes in population size. Hair-tubes monitoring and live trapping were not simultaneous to avoid interference between the two methods (e.g. squirrels entering the traps and running away after release

Fig. 2

avoiding the hair-tubes). At every check, tapes were retrieved and replaced with new ones. The hairs contained on the tapes were identified in the laboratory. Hairs were observed directly at a binocular microscope or taken off the adhesive layer using xylene before identification. Identification was conducted using a reference collection and with the help of the figures reported in Teerink (1991). Staining was not carried out since only red squirrels occurred in our study areas.

Statistical analyses

We used the proportion of hair-tubes visited after four weeks (HT4) as an index of population abundance. Since HT4 is a proportion, it was arcsine squareroot (ARCS) transformed to meet assumptions of normality (Shapiro-Wilk's test $W = 0.974$, $P > 0.22$) and then used as independent variables in multivariate parametric models (Sokal and Rohlf 1995; SAS 1999). In each study area and survey period ($N_{TOT} = 60$, Table 1b), population estimates were based on minimum number alive (MNA) calculated from the number of different squirrels trapped and those known to be alive by radio-tracking or subsequent recaptures. MNA was preferred for comparison with previous studies on population dynamics of tree squirrels (Wauters and Lens 1995; Gurnell 1996; Kenward et al. 1998; Lurz et al. 2000; Wauters et al. 2001, 2004, 2005), so that the development of an equation that correlates the use of hair-tubes to density values obtained from MNA will allow broad-scale comparisons of squirrel densities. Red squirrels are easy to trap and animals that enter a trap once are recaptured regularly in consecutive trapping sessions, showing they do not become trap-shy. The ratios between the number of animals trapped in every session and the number of animals known to be present in the study areas from a calendar of captures were always > 80%. Finally, MNA estimates where highly correlated with density-estimates using a POPAN model (Arnason and

Schwarz 1999) in MARK ($r = 0.91$, $n = 54$, $p < 0.0001$, Wauters et al. 2008). We thus feel confident that MNA realistically represent red squirrel population size.

Density from live trapping (D_{LT}) was obtained by dividing MNA by study area size (Table 1). The latter was calculated by adding a boundary strip of 200 m to the area covered by the traps where the forest was contiguous. The extension of the boundary strip was based on average home range size of females determined by radio tracking (Wauters et al. 2001, 2005). The relationship between HT4 in each site and the density or the number of individual squirrels trapped was investigated using General Linear Modelling (GLM) with the stepwise backward procedure. The density or the number of individual squirrels in the different sites was used as the dependent response variable and the ARCS of HT4 as independent variable. Study area was added as a factor and models tested for a study area by ARCS HT4 interaction (SAS 1999). We used linear regression models to evaluate relationship between hair-tube indices and squirrel number or density. Equations where use of hair-tubes was used to predict densities had higher determination coefficients (R^2) than those obtained from the relation between hair-tubes and number of animals. Therefore, we report here only the former.

To explore the predictive value and the stability of the hair-tube/density relationship (HT4-D_{LT}) we used data collected during the first three years of the study in each site to produce equations that were then used to predict density for the following years. We also evaluated whether locally developed equations (obtained in one region or the whole Alps) could be used to predict density in other areas (another region or another country).

In a first step we evaluated if the use of hair-tube may be useful to predict the density at a regional level. We thus developed a simple linear regression equation with data of the period 2000-2002 from Gran Paradiso (RHE + COG) and used this equation to predict the density in the period 2003-2004 and did the same with data from Valtellina (CED +

OGA + SAN + BOR + VAL). Subsequently, we used all data (2000-2005) from one region to predict densities in the other region.

In a second step we pooled data from the two regions to produce a single database with all seven alpine study areas. Regression equations for the Alps were developed: (i) considering the whole data set (7 areas); (ii) excluding OGA (6 areas); and (iii) considering only those areas where the surveys were conducted for the entire period of 5 years (4 areas: CED, OGA, RHE, COG, Table 1b). OGA is a Scots pine dominated forest where the highest densities were recorded and where annual fluctuations in density were less pronounced than in the other areas. These reduced between year differences in density were related to low variation in tree seed production and differentiate OGA from the other areas where the fluctuations in seed crops and squirrel density were stronger (Wauters et al. 2005, 2008). For this reason we conducted analysis removing OGA from the data set.

The third predictive analysis was conducted considering only the areas that were studied for five years. The use of hair-tubes by squirrels may be influenced by the density but also by other factors, such as changes in space use patterns and social organization that are related to changes in seed crops (Wauters et al. 2005). Only a monitoring program that is conducted for a medium or long period may include years with low and high seed production, and thus test the relationship between squirrel presence and hair-tube detection under different ecological conditions. Data from areas monitored for few years may bias results due to a low or high seed crop and influence the relationship between density and use of hair-tube by squirrels. In all cases, regression equations were developed from 2000-2002 and used to predict densities in 2003-2004.

The predictive value of the equations was evaluated considering the proportion of densities from live-trapping (D_{LT}) in year 2003-2004 that fell in the range predicted by density (D_{HT}) ± 1 SE obtained from regression equations calculated with data from 2000-2002 for a single region and for all alpine sites. Population densities in successive years are obviously correlated, however using data from a period to make prediction for a successive period is a common way to test the prediction ability of a model (Jacobson et al. 2004).

The regression lines were not constrained through the origin because at low squirrel density it is possible that either proportion of hair-tube visited, or squirrels trapped is zero while the other is not. We further compared D_{HT} to D_{LT} using the percent deviation between the density estimated and that recorded during trapping, calculated as $[(D_{HT} - D_{LT}) / D_{LT} * 100]$, and omitting cases where $D_{LT} = 0$. For each region or the entire Alps we calculated the mean percent deviation (%dev) between monitoring periods as a measure of the accuracy of predictions.

We calculated local regression equations over the entire study period (2000-2004) to evaluate if the equations can predict local densities. We then applied these equations to other areas and used the results from a similar project conducted in northern England, where red squirrels were trapped in a total of 11 different sites selected in three English forests (Lurz, unpubl. data). All sites were of cone bearing age and consisted of single species blocks of Sitka spruce (*Picea sitchensis*), Norway spruce (*P. abies*) and lodgepole pine (*Pinus contorta*), or self-thinning mixtures of Sitka spruce with lodgepole pine or Japanese larch (*Larix leptolepis*). In each site a survey using hair-tubes was carried out and a population estimate was made by live trapping and tagging of individuals.

We used our regression equations from the Alps to test if we could predict population density using proportion of hair-tube visited by squirrels in the English areas. The predictive value of the equation from the Alps was evaluated considering the proportion of English densities obtained from live-trapping (D_{LT}) that fell in the range predicted with density (D_{HT}) ± 1 SE.

Results

The proportion of hair-tubes visited after four weeks (HT4) varied between 0.11 and 0.97, while squirrel density ranged between 0.08 and 0.45 animals/ha.

Regions

Using the entire Alpine data set (N_{TOT} = 60), the region effect and the region by ARCS HT4 interaction were not significant (GLM with the 2 regions: region x ARCS HT4 $F_{1, 56}$ = 3.11, P = 0.084; region $F_{2, 56}$ = 2.32, P = 0.13; ARCS HT4 $F_{1, 56}$ = 10.80, P = 0.002; R^2 = 0.24). Thus, the tendency for the two regions to have different slopes for the ARCS HT4 – density relationship (see also Table 3) was weak and not significant. In contrast, when using study area instead of region, squirrel density was significantly affected by both ARCS HT4 and study area (area $F_{6, 52}$ = 4.23, P = 0.0015; ARCS HT4 $F_{1, 52}$ = 8.29, P = 0.0058; area x ARCS HT4 $F_{6, 46}$ = 0.67, P = 0.68; R^2 = 0.45). The slope of the regression line of one study area in Valtellina (VAL) was greater than those of the Gran Tab. 2
Paradiso study areas (Table 2).

In a next step, we explored what would be the result if we had developed our model in only one region. Using the equation obtained in Valtellina with data from 2000-2002 to predict D_{LT} in successive years [D_{HT} = -0.004 (± 0.080) + 0.275 (± 0.093) * ARCS HT4; $F_{1, 18}$ = 8.74, P = 0.0084, R^2 = 0.33], 11 out of 12 (92%) density values fell in the range predicted by density (D_{HT}) ± 1 SE, with a 6.2 % deviance. A linear regression with all data from Valtellina [period 2000-2004: D_{HT} = -0.022 (± 0.075) + 0.305 (±

0.081) * ARCS HT4; $F_{1, 30}$ = 14.01, P = 0.0008, R^2 = 0.32] predicted correctly 27 out of 28 (96.4 %) D_{LT} values from Gran Paradiso. However, regression models with data from Gran Paradiso of the periods 2000-2002 [D_{HT} = 0.113 (± 0.119) + 0.142 (± 0.114) * ARCS HT4; $F_{1, 14}$ = 1.56, P = 0.23, R^2 = 0.10] and 2000-2004 [D_{HT} = 0.166 (± 0.090) + 0.092 (± 0.084) * ARCS HT4; $F_{1, 26}$ = 1.21, P = 0.28, R^2 = 0.04] were not significant.

Alps

The results of different GLM models and linear regression models are reported in Table 3. When all study areas and all areas without OGA were considered, density varied with study area but the study area x ARCS HT4 interaction was not significant. In contrast, the GLM model which used only areas with five years data did not have a significant area effect. Linear regression models produced with data from 2000-2002 predicted correctly 83.3-90.5% of the D_{LT} of the successive years (Table 3), with an accuracy of 0.9-8.1 % deviance. The three models failed to predict some of the extreme densities that were < 0.15 or > 0.4 squirrels/ha.

Tab. 3

England

To further test the general validity of predicting red squirrel densities from hair-tube indices, we used regression equations produced using the entire alpine data set from Italy to predict the D_{LT} obtained in the areas monitored in England (Table 3). Our models predicted correctly 7-8 out of 11 (64-73 %) D_{LT} values. The best predictive power was obtained using the model with the four areas monitored for five years. Two of the three values that were not predicted correctly corresponded to situations where only one animal and no animals were trapped, while, respectively, 25% and 9% of hair-tubes were visited. The mean percent deviation ranged between 24-29 %.

The model built with the data from four areas monitored for five years had the best predictive value, with 88.9% of correct prediction in the same area (data 2003-2004 predicted from data 2000-2002) and 72.7% in areas from England. Also the model with all areas except OGA had a good predictive value. We propose the regression model of density recorded in the four alpine areas monitored over five years on ARCS HT4 (Fig. 3) as a general model that can be used to predict red squirrel densities in conifer forests from hair-tube surveys. Fig. 3

Discussion

To monitor fluctuations in population size or density using an indirect population index, the relationship between this index and true density must be known. One way to explore index – density relationships is to look for simple model equations between the index and actual population density based on estimates derived from accurate methods (Finnegan et al. 2007). In this paper, we compared results from a hair-tube monitoring program with red squirrel densities obtained with live-trapping. Trapping success in tree squirrel studies is generally very high and the capture and recapture method has been widely used to obtain reliable density values (Wauters and Lens 1995; Gurnell 1996; Lurz et al. 1997; Wauters et al. 2001, 2004, 2008; Gurnell et al. 2004b).

To be effective, i.e. useful for a large scale and long term monitoring program, the predictive value and the stability of the index should be validated (Finnegan et al. 2007; Mortelliti and Boitani 2008). Our validation of the hair-tube index was conducted at two levels. First, we used data obtained in our alpine study areas during the first three years to produce regression equations that were used to predict squirrel density for the following years. Second, we used locally developed equations, using part or all of the alpine sites, to predict squirrel densities obtained with similar methods, but in another country.

The regression equation obtained with data recorded during three years at a regional level in Valtellina predicted correctly the density values of successive years in the same region and also the values from another alpine region. On the other hand, the regressions obtained in Gran Paradiso, with three or five year data, were not significant. There are two possible explanations for the lack of significance in Gran Paradiso: (i) only two study areas were used, limiting sample size; and (ii) even in a year with low densities after a cone-crop failure (2001) high mobility of squirrels and extremely large home ranges (Wauters et al. 2005), resulted in a high proportion of hair-tubes visited even at low squirrel density. Hence, the different response of the models generated in the two regions is probably related to diverse population dynamics and space use patterns of red squirrels in forests with different tree species composition. This means that equations developed at a local level during live-trapping programs combined with hair-tube surveys have to be validated before they can be used to predict squirrel densities in wide-scale monitoring studies.

Considering that live-trapping is costly and labor intensive, the availability of a simple regression equation for hair-tubes used by squirrels that has a general value and can therefore be used in areas with similar habitat characteristics, in our case conifer-dominated forests, is of great interest.

Pooling together the data from Gran Paradiso and Valtellina increased the variability of the ecological situation that was monitored. In this case the predictive value of the regression equation that we generated was tested both locally, using data from the first three years to predict density in the two successive years, and more generally predicting densities in conifer plantations in England. Removing OGA from the areas monitored increased the power to predict local values with respect to all areas. However, only 64% of the English values were predicted correctly. The regression equation based on data collected in our four areas that were monitored over 5 years, had a high predictive value both locally (89% of corrected values, with a mean percentage of deviation from the real density of only 1%) and in areas in England (73% of corrected values and a mean percentage of deviation from real density of 29%). Since changes in space use patterns and social organization, related to distribution and fluctuations in the abundance of seed crops (Lurz et al. 1997, 2000; Wauters et al. 2001, 2005) may influence the use of hair-tubes, a regression derived from study areas with different forest composition intensively monitored over at least 4-5 years, seemed to be the best choice to derive a general predictive model. We believe that this equation can be used to monitor red squirrel populations efficiently in European conifer forests where the species is present at relatively low densities (0.1 to 0.5 animals/ha during this study).

It must be noted that with our protocol of hair-tube collocation and subsequent control, when the density reaches 0.5 squirrels/ha the tubes are saturated (100% visited) and a potential further increase in density would be impossible to detect. Densities < 0.5/ha are common in conifer forests throughout the red squirrel range (see review in Lurz et al. 1995, Wauters et al. 2004, 2008), while in broadleaf and mixed forests the density is usually higher (up to 0.7-1.3 animals/ha, Kenward et al. 1998; Wauters et al. 2001, 2004). Many tree squirrel populations in North-America also occur at densities below 0.5 animals/ha in suboptimal and poor-quality habitats (e.g. Nash and Seaman 1977; Koprowski 1994a, b). In these circumstances hair-tube surveys might provide a fast and efficient method to monitor changes in distribution and/or population density (size) of rare and endangered subspecies or populations. However, the possibility to use hair-tubes in habitats with higher densities has to be tested in future studies considering different tube spacing and timing of tube control.

We did not estimate variation in detection probability among sites and/or periods (MacKenzie et al. 2006; Mortelliti and Boitani 2008). Biases in detectability can be a problem in landscapes with woodland fragments where, in some sites, small numbers of hair tubes are used to detect presence/absence (MacKenzie et al. 2006; Morteletti and Boitani 2008). However, we believe this is not a relevant problem in our study for the following reasons: (i) we used a large number of tubes in contiguous forests, covering areas larger than the average size of a squirrel's home range (Wauters et al. 2001, 2005; Di Pierro et al. 2008); (ii) in all sessions, more than 10% of tubes were occupied and there was strong spatio-temporal variation in occupation rates which was correlated with fluctuations in squirrel density; and (iii) tubes were located at the same position as traps and trapping probability of squirrels, and most likely also the probability to visit tubes, was similar in most study areas (Wauters et al. 2008).

Compared to live-trapping, the use of hair-tubes is less labor-intensive and less expensive. During our research, 8-12 days of trapping employing 20-30 traps were necessary to get a density value in an area. In contrast, the monitoring with hair-tubes required only 3 periods (activation and two controls) of 2-3 hours of field work and few hours of laboratory analysis. Hair-tubes can be used to monitor red squirrel populations, and other species of arboreal rodents, over space and time. In this kind of studies, comparisons between areas and the detection of changes in population trends are more important than a single accurate density estimation. We suggest that for these purposes, our regression equation can be used in regions and/or habitats where the expected red squirrel density is less than 0.5 animals/ha.

Acknowledgements - we wish to thank M. Adamo, G. Airoldi, S. Caffo, M. Zaninetti, for assistance with fieldwork. The study was part of the ASPER (Alpine Squirrel Population Ecology Research) project, carried out by the University of Insubria, Varese, the University of Turin and Istituto Oikos NGO, Milan. Financial support was provided by the Wildlife Service of the Province of Sondrio, the Parco Regionale Orobie Valtellinesi, and grants awarded to S.B. and L.W. from the Gran Paradiso National Park, Italy (DGE 25-2000), and the Committee for Research and Exploration of the National Geographic Society, Washington DC, USA (grant no. 6997-01). Additional financial support was obtained from MIUR (Ministero dell'Istruzione, dell'Università della Ricerca, project COFIN 2003, number 2003053710-006) to Insubria University, and logistic support was provided by the Stelvio National Park. This is paper n. 15 of ASPER (Alpine Squirrel Population Ecology Research) Project.

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Table 1. (a) Tree species composition, study area size (ha) including boundary strip and minimum and maximum elevation (m a.s.l.) of seven study areas in Valtellina (Sites 1-5, Central-Italian Alps) and Gran Paradiso (Sites 6-7, Western-Italian Alps); (b) Period of hair-tube surveys conducted in each area and year, followed by live trapping (N_{TOT} = 60).

	Valtellina					Gran Paradiso	
(a)	1. CED	2. OGA	3. SAN	4. BOR	5. VAL	6. RHE	7. COG
Tree species	% (n=359)	% (n=612)	% (n=387)	% (n=400)	% (n=371)	% (n=928)	% (n=1073)
Picea abies	23.4	8.8	83.2	8.0	88.9	85.0	45.0
Abies alba	58.2	0	0	0	0	0	0
Larix decidua	2.2	2.5	9.8	17.8	1.9	11.0	54.0
Pinus sylvestris	4.7	88.7	0	0	0	0	0
Pinus cembra	0	0	0	73.2	6.2	0	0
Fagus sylvaticus	6.9	0	0	0	0	0	0
dead trees	4.7	0	7.0	1.0	3.0	4.0	1.0
Trees/ha	449 ± 163	765 ± 251	484 ± 323	496 ± 92	464 ± 93	773 ± 333	895 ± 460
Study area size	76 ha	46 ha	49 ha	93 ha	78 ha	69 ha	56 ha
Elevation (min-max)	1100-1600	1250-1450	1620-1770	1950-2130	1650–1870	1740-1890	1600-1800
Coordinates	46°07’N 9°48’E	46°28’N 10°22’E	46°07’N 10°12’E	46°27’N 10°30’E	46°27’N 10°31’E	45°39'N 7°10'E	45°36N 7°21’E
(b)							
2000	Apr, Sep	Apr, Sep	Apr, Sep			Jun, Sep	Jun, Sep
2001	Apr, Sep	Apr, Sep	Apr, Sep			Apr, Jun, Sep	Apr, Jun, Sep
2002	Apr, Sep	Apr, Sep		Apr, Sep	Apr, Sep	Apr, Jun, Sep	Apr, Jun, Sep

2003	Apr, Sep	Apr, Sep		Apr, Sep	Apr, Sep	Apr, Jun, Sep	Apr, Jun, Sep
2004	Apr	Apr		Apr	Apr	Apr, Jun, Sep	Apr, Jun, Sep

Table 2. Comparison of slope in the regression model for each area with respect to COG. RHE and COG are in the region Gran Paradiso, all other areas are in the Valtellina region.

Parameter	Estimate	SE	t value	P
Intercept	0.100 x B	0.060	1.66	0.10
CED	-0.045 x B	0.036	-2.14	0.22
OGA	0.043 x B	0.034	1.26	0.21
SAN	-0.017 x B	0.045	-0.37	0.71
BOR	-0.065 x B	0.042	-1.56	0.13
VAL	0.144 x B	0.041	3.52	0.0009
RHE	-0.009 x B	0.030	-0.29	0.77
COG	B			
ARCS HT4	0.159	0.055	2.88	0.0058

Table 3. Prediction of densities (D) or number of animals trapped (N) applying different linear regression models. The validity of the models was tested in the Alps using data from 2000-2002 to predict period 2003-2004, and more generally using data from Alps (2000-2004) to predict data from areas in England. ARCS HT4 was used as independent variable. %dev = mean percent deviation for that period and area.

Areas	Use data 2000-2002 to predict 2003-2004			Use data 2000-2004 Alps to predict data from UK	
	Predicted correctly (%)	%dev	linear regression 2000-2002	Predicted correctly (%)	%dev
7 areas	20/24 (83.3)	5.2	R^2 = 0.25, P = 0.0018	7/11 (63.6)	27.5
6 areas without OGA	19/21 (90.5)	8.1	R^2 = 0.26, P = 0.0036	7/11 (63.6)	24.1
4 areas with 5 years data	16/18 (88.9)	0.9	R^2 = 0.27, P = 0.0044	8/11 (72.7)	28.9

Models used to predict squirrel densities using 2000-2004 data

7 areas (CED+OGA+SAN+BOR+VAL+RHE+COG)

General linear model parameters	*Linear regression model*
ARCS HT4 $F_{1, 52}$ = 8.29, P = 0.006	D_{HT} = 0.062 (± 0,055) + 0,201 (± 0.055) * ARCS HT4
Area $F_{6, 52}$ = 4.23, P = 0.0015	R^2 = 0.19, P = 0.0006
Area x ARCS HT4 $F_{6, 46}$ = 0.67, P = 0.68, R^2 =0.45	

6 areas (without OGA)

General linear model parameters	*Linear regression model*
ARCS HT4 $F_{1, 44}$ = 6.84, P = 0.012	D_{HT} = 0.061 (± 0,055) + 0,194 (± 0.055) * ARCS HT4
Area $F_{5, 44}$ = 5.45, P = 0.0005	R^2 = 0.20, P = 0.0009
Area x ARCS HT4 $F_{5, 39}$ = 0.77, P = 0.58, R^2 = 0.51	

4 areas (CED+OGA+RHE+COG)

General linear model parameters

ARCS HT4 $F_{1, 41} = 4.87$, $p = 0.033$

Area $F_{3, 41} = 1.71$, $p = 0.18$

Area x ARCS HT4 $F_{3, 38} = 0.40$, $P = 0.75$, $R^2 = 0.27$

Linear regression model

$D_{HT} = 0.084 (\pm 0.057) + 0.172 (\pm 0.060) * \text{ARCS HT4}$

$R^2 = 0.18$, $P = 0.0037$

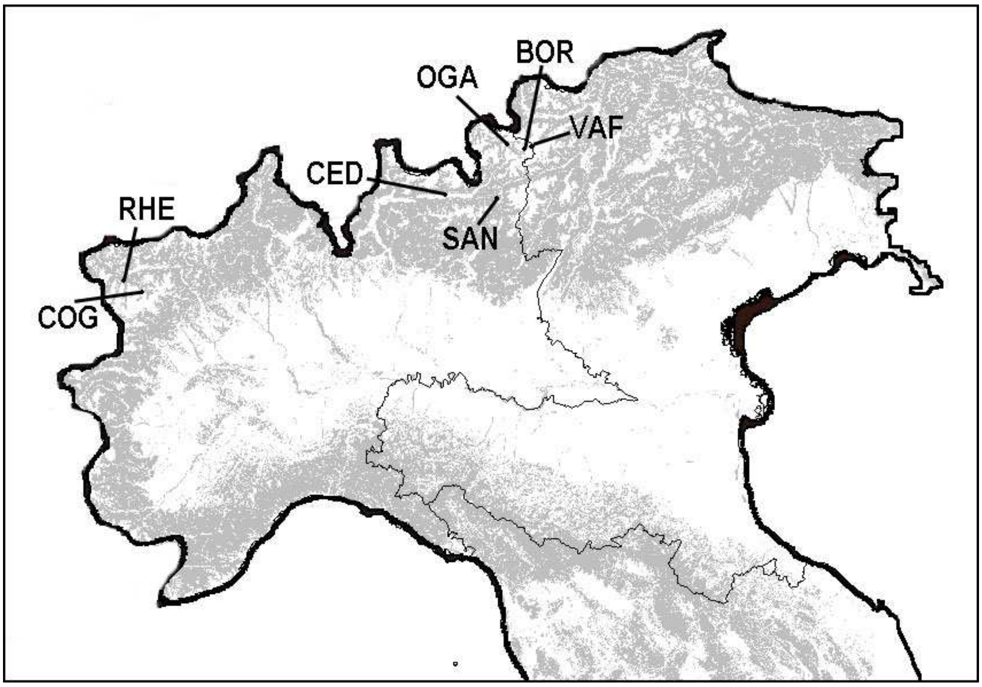

Fig. 1. Location of the seven study sites in the Italian Alps (North Italy). Grey areas represent forests.

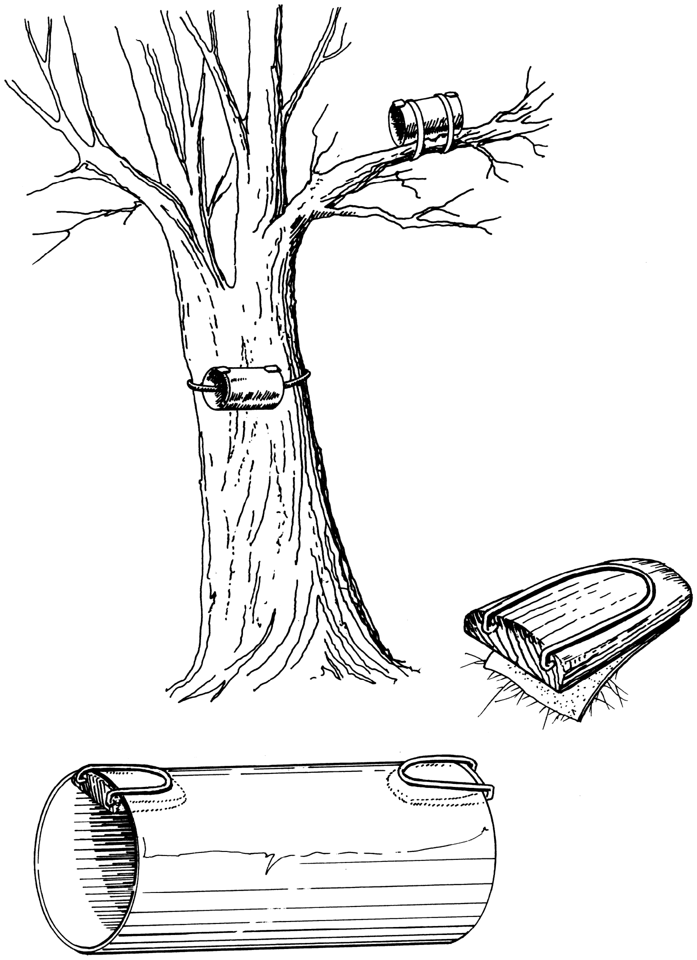

Fig. 2. Hair-tube and its position on the tree. In the smaller drawings how to insert the wooden tablet on the tube and the double sided sticky tape covered by hairs (drawing by M. Venegoni).

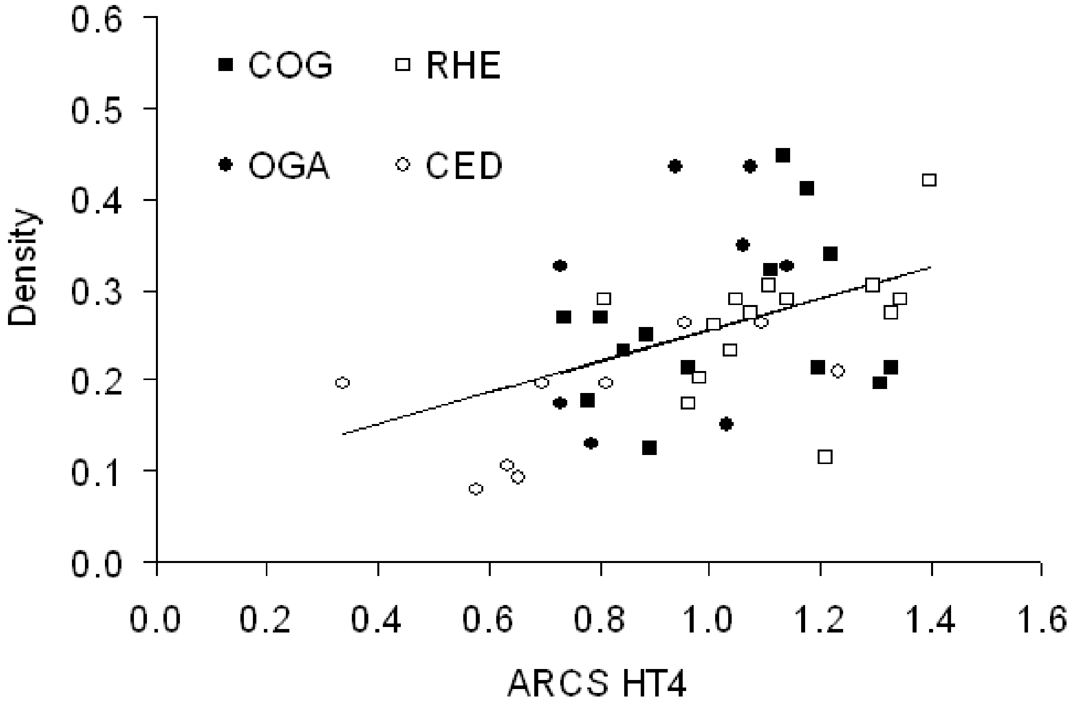

Fig. 3. Linear regression of the density (squirrels/ha) recorded in four areas studied for 5 years on the arcsine square root (ARCS) HT4. See Table 3 for more details on the linear regression model.