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Research Article

Factors affecting home range size of male Alpine ibex (*Capra ibex ibex*) in the Marmolada massif

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The study was performed in compliance with current Italian laws.

Abstract

In this study we investigated on the effects of different land cover types, meteorological conditions and age on the seasonal home range size of male Alpine ibex (*Capra ibex ibex*). The study was conducted in the Marmolada massif (Eastern Italian Alps). From September 2003 to the end of August 2009, 28 different male ibexes were regularly located by sightings and VHF radiotracking. We first analysed habitat selection performing a compositional analysis of log ratios and found that males positively selected grasslands all year long, likely for forage availability. We then estimated the cluster seasonal home ranges and modelled the logarithmic home range size with mixed linear models. We tested the effects of the individual and research year as random variables, season and age class as classification variables, and different combinations of percentage of grassland in the home ranges, slope, elevation and aspect as covariates. Model selection was based on the Akaike criterion. Inter-individual variability, research year and age class had no significant effects. The percentage of grassland within the home range and the slope of grasslands within the home range were the main determinants of home range size, explaining also the differences between seasons. Home range size in winter and spring was inversely correlated with the amount of snow depth. These results suggest that in winter spatial behaviour of male Alpine ibex is mostly influenced by snow while in the other seasons it is linked to resource exploitation: when forage is easily available ibexes did not need to seek out it by moving important distances.

Introduction

Understanding the organization of animal in space and time is a fundamental issue in ecological studies. In general, animals tend to confine space use to a restricted area, the home range, classically defined as the area traversed by an individual in its normal activities of food gathering, mating and caring for young (Burt, 1943; Powell, 2000). Home range size is affected by several different factors, such as body weight and phylogeny (Mysterud et al., 2001; Ottaviani et al., 2006), energy requirement (McNab, 1963), sex (Clutton-Brock, 1989; McLoughlin and Ferguson, 2000; Dahle and Swenson, 2003), age (Cederlund and Sand, 1994) and reproductive status (Dahle and Swenson, 2003; Saïd et al., 2005) of individuals, and, in social species, social factors such as group size and

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composition (Loveridge et al., 2009). In addition, several extrinsic factors linked to the species ecological needs may act as important determinants of home range extension: population density (Massei et al., 1997; Kjellander et al., 2004), forage abundance and availability (Larter and Gates, 1994; McLoughlin and Ferguson, 2000; Nilsen et al., 2005; Schradin et al., 2010; van Beest et al., 2011), landscape structure (Tufto et al., 1996; Anderson et al., 2005; Saïd and Servanty, 2005; Lamberti et al., 2006), climate variability (Börger et al., 2006), seasonality (McLoughlin et al., 2000), predator pressure (Creel et al., 2005) and human disturbance, as hunting (Vercauteren and Hyngstrom, 1998; Scillitani et al., 2010). Therefore, understanding variation in spatial behaviour and identifying which factors shape this variation is crucial for a better knowledge of the species biology (Morales et al., 2010) and for improving management and conservation actions (Sutherland, 1998; Apollonio et al., 2003). At a population and individual level, availability of resources is most likely one of the major determinant of home range size (McLoughlin and Ferguson, 2000). At this purpose, important knowledge on the causes of intra-specific variations can be gained by the acquisition of information on different populations of the same species because, due to diverse geographical and – as a result – ecological constraints, availability and acquisition of resource may vary in different areas and time periods. The majority of studies on the effects of habitat structure on home range size in large herbivores focused on deer species (roe deer *Capreolus capreolus*: Börger et al. 2006; Lamberti et al. 2006; Saïd and Servanty 2005; Tufto et al. 1996; mule deer *Odocoileus hemionus colombianus*: Kie et al. 2002; elk *Cervus elaphus*: Anderson et al. 2005), while lesser attention has been paid to mountain dwelling ungulates, which often live in extreme habitats where resources availability and seasonal climatic fluctuations are expected to strongly influence the spatial behaviour. Alpine ibex (*Capra ibex ibex* L., 1758) is a gregarious species characteristic of the Alps (Shackleton, 1997). The species typically inhabit open habitats at high altitudes, above the tree line, where it uses rocky environments characterized by steep slopes, which are actively selected by both sexes particularly in winter (Nievergelt, 1966; Girard, 2000; Tosi and Pedrotti, 2003). Spatial behaviour patterns of ibexes is still poorly studied. Parrini et al. (2003) found in the Italian Western Alps that the home range size of male ibex tended to decrease with age, and was larger in summer and autumn. A similar pattern was described in the French Alps (Girard, 2000). Other studies refer to translocated animals (Michallet, 1994; Pedrotti, 1995), which however behave differently from native individuals (Scillitani et al., 2012).

The aim of this study was to improve the understanding of factors that might shape the variation in the home range size of male alpine ibex. We assumed that home range size should be linked to the extent of the preferred habitat resource. Based on the available literature (Grignolio et al., 2003; Lembke, 2005), we expected that the preferred resource should be alpine grassland, and we hyphotesized that seasonal home range size should be inversely related to this habitat feature, especially in winter and early spring, when snow cover prevents free access to resources. As other studies suggested (Parrini et al., 2003) we also expected an age effect. Finally, we expected to find a negative relationship between the home range size and snow depth, since deep snowpack may hamper ibex movements preventing them free access to all study area.

Materials and Methods

Study area

The study area was the Marmolada massif group, in the Eastern Italian Alps (Dolomites - 46°26' 13" N, 11°51' 54" E, Fig. 1). It encompasses about 150 km^2 and lies between 1200 and 3343 m a.s.l. The group is characterized by steep mountains with a high ridges complexity. The main ridge axis orientation is east-west. Over 1600 m the vegetation is represented by woodland of Norway spruce (*Picea abies*) and larch (*Larix decidua*). Above the timberline (1900 m) vegetation is mainly represented by alpine grasslands and bushes as mountain pine (*Pinus mugus*), hairy alpen rose (*Rhododendrum hirsutum*), willows (*Salix* sp.), and green alder (*Alnus viridis*). The characteristic dolomitic limestone rock tend to form screes and vertical cliffs that interrupt the continuity of grassland.

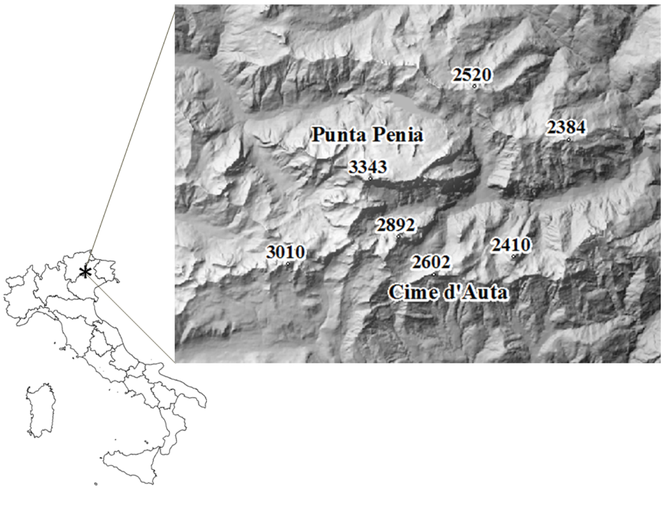

Figure 1 – Map of the study area and its location in Italy.

Data collection

Free-ranging ibexes were sedated by tele-injection of xylazine (Rompun ®, Gauthier 1993). Captures were performed during late spring-summer of each year from 2001 to 2009, and a total of 95 males of different ages (range 1-15 years old) were captured. All animals were aged by dentition and horn annuli, measured, examined for health status and ear-tagged with a unique colour and number combination. A VHF radiocollar (Televilt TXH3, Telonics CMM-320) was fitted to 31 males.

Table 1 – Results of compositional analysis of ibex locations versus random locations within the study area (second-order selection). "⋙" indicates a significant positive selection of one class, while ">" indicates non-significant selection.

Period	d.f.	Wilk's Λ	*p*	Landcover types ranking
Overall	6	0.001	< 0.001	Grassland mixed with rocks and screes > Grassland ⋙ Scree ⋙ Rocks ⋙ Woods > Shrubland ⋙ Glacier & Anthropic features
Summer	6	0.001	< 0.001	Grassland > Grassland mixed with rocks and screes ⋙ Scree ⋙ Rocks ⋙ Woods > Glacier & Anthropic features ⋙ Shrubland
Autumn	6	0.005	< 0.001	Grassland > Grassland mixed with rocks and screes ⋙ Scree ⋙ Rocks > Woods ⋙ Shrubland > Glacier & Anthropic features
Winter	6	0.147	< 0.001	Grassland mixed with rocks and screes > Grassland ⋙ Shrubland > Scree > Woods > Rocks > Glacier & Anthropic features
Spring	6	0.001	< 0.001	Grassland ⋙ Scree ⋙ Grassland mixed with rocks and screes > Shrubland > Woods ⋙ Glacier & Anthropic features > Rocks

Field work was conducted from September 2003 to the end of August 2009. Radio-tagged ibexes were located mostly by sightings, and – during 2003-2006 – also by triangulation with a portable receiver and a hand-held Yagi antenna. For individual identification we used a 60x magnifier telescope (Swarovski CT85). Sightings were georeferenced in ArcView 3.2 (ESRI ®) and stored in a Access (Microsoft ®) database.

Temperature and precipitation data from the nearest weather stations to our study area were provided by the Avalanche Centre of Arabba (Regional Agency for Environment Protection of Veneto Region, ARPAV).

Data analysis

All statistical analyses were conducted with the statistical software SAS 9.1 ® (SAS 2006), and spatial analysis were performed in ArcGIS 9.3 (ESRI ®).

We defined four seasons, on the basis of climatic characteristics and ibex biology: "Summer": June-August; "Autumn": September-November; "rutting season and Winter": December-February; "Spring": March-May. For all the analyses we employed a total of 28 different radio-collared male ibexes located at least 10 times per season, after checking with the incremental analysis in Ranges VI (Kenward et al., 2003), that home range stabilized at 10 locations. In order to understand which environmental factors were most likely to affect home range size and therefore should be used as covariate when modelling home range size, we firstly performed an exploratory habitat selection analysis. We compiled a 1:5000 land-use cover map by refining the forest cover maps produced by the Veneto Region and by the province of Trento using the orthophoto of the study area. We reclassified landcover data into eight habitat types most likely to influence ibex: "Grassland", "Grassland interspersed with rocks and scree", "Rocks", "Scree", "Shrubland", "Woods", "Glaciers", "Anthropic features". We assigned to each ibex location the correspondent habitat type and computed the percentage of use of every habitat type by each individual ibex. We estimated habitat availability by generating random locations which equalled the total number of ibex locations at a seasonal level and for the overall study period using the random point generation function of the Hawth's Analysis Tool extension for ArcGIS 9.3 (Beyer, 2004). We analysed habitat selection performing a compositional analysis of log ratios (Aebischer et al., 1993) with the Compos analysis software (Smith, 2005). We obtained elevation (m), slope (degree) and aspect of the study area from a Digital Elevation Model (DEM), a raster map with a pixel size of 25 × 25 m, developed by the Veneto Region and the Trento Province.

Finally, we computed the average slope, elevation and aspect of the preferred habitat type within each home range, and we then tested for the presence of correlation between these different habitat variables in order to select the variables to be included into the subsequent analysis of home range. We transformed the circular variable aspect (0–360°) into a linear north-south gradient (northness) and an east-west gradient (eastness) by performing cosine and sine transformations, respectively.We estimated seasonal home range size with cluster estimators (Kenward, 2001; Kernohan et al., 2001) by using the software Ranges VI (Kenward et al., 2003). Cluster estimators are built using nearest-neighbour distances between locations: locations are linked in clusters that minimize the mean joining distance (Kenward, 2001). This estimator can be useful to describe the space use by ibexes, which generally use small areas connected by corridors (Pedrotti et al., 1995). Home range size (in hectares, ha) was log-transformed to meet a normality assumption. We modelled the logarithmic home range size with mixed linear models (Proc Mixed, SAS) in which we considered the individual as a random effect to take into account the intra-individual variance and pseudo-replication due to repeated observations on the same individual. Also the research year was used as a random effect to reduce the effects of stochastic unexplained variability.

Models tested the effects of the different combinations of the following explanatory variables on home range size: season and individual's age as class effects, percentage of the preferred habitat type, average slope, average elevation, and average aspect (expressed as: "Northness" and "Eastness") of the preferred habitat type within the home range as covariates. Model selection among the list of candidate models was performed using the Akaike Information Criterion (AIC, Burnham and Anderson 2002). When the difference between AIC values of two models was below 2 we selected the most parsimonious one (Burnham and Anderson, 2002). A multiple comparison post-hoc test was performed with the Tukey-Kramer adjustement.

Finally, we assessed the effects of climatic variables on home range size by testing the presence of a correlation between winter and spring home range size and the average air temperature and snow depth.

Table 2 – List of candidate models used to explain home range size in adult male alpine ibex and relative AIC values. Individual and research year were tested as random factors. In bold the best model according to AIC criterion and parsimony.

Model formulation	AIC
$\log(HRsize) = \beta_0 + \beta_1 Season$	423.2
$\log(HRsize) = \beta_0 + \beta_1 Season + \beta_2 Age$	424.2
$\log(HRsize) = \beta_0 + \beta_1 Season + \beta_2 \% Grassland$	376.8
$\log(HRsize) = \beta_0 + \beta_1 Season + \beta_2 \% Grassland + \beta_3 Age$	381.4
$\log(HRsize) = \beta_0 + \beta_1 Season + \beta_2 \% Grassland + \beta_3 Age + \beta_4 SlopeGrassland$	360.0
$\log(HRsize) = \beta_0 + \beta_1 Season + \beta_2 \% Grassland + \beta_3 SlopeGrassland$	355.1
$\log(HRsize) = \beta_0 + \beta_1 Season + \beta_2 \% Grassland(season)$	369.2
$\log(HRsize) = \beta_0 + \beta_1 Season + \beta_2 SlopeGrassland(season)$	398.7
$\boldsymbol{\log(HRsize) = \beta_0 + \beta_1 Season + \beta_2 \% Grassland(season) + \beta_3 SlopeGrassland}$	**345.4**
$\log(HRsize) = \beta_0 + \beta_1 Season + \beta_2 \% Grassland(season) + \beta_3 SlopeGrassland(season)$	345.0
$\log(HRsize) = \beta_0 + \beta_1 Season + \beta_2 \% Grassland + \beta_3 NorthnessGrassland + \beta_4 EastnessGrassland$	382.6
$\log(HRsize) = \beta_0 + \beta_1 Season + \beta_2 \% Grassland + \beta_3 SlopeGrassland + \beta_4 NorthnessGrassland + \beta_5 \% EastnessGrassland$	361.1
$\log(HRsize) = \beta_0 + \beta_1 Season + \beta_2 \% Grassland + \beta_3 ElevGrassland$	376.0
$\log(HRsize) = \beta_0 + \beta_1 Season + \beta_2 \% Grassland + \beta_3 SlopeGrassland + \beta_4 ElevGrassland$	351.9
$\log(HRsize) = \beta_0 + \beta_1 Season + \beta_2 \% Grassland(season) + \beta_3 SlopeGrassland + \beta_4 NorthnessGrassland + \beta_5 EastnessGrassland + \beta_6 ElevGrassland$	345.6

Results

The compositional analysis revealed a significant difference from random use (Wilk's $\Lambda = 0.001$, $p < 0.001$), in the overall period and in all seasons. The habitat types preferred by male ibex were: "Grassland interspersed with rocks and scree" and "Grassland" (Tab. 1), followed by "Scree" and "Rocks". Therefore we proceeded by computing the percentage of grassland (merging both the types of grassland together) within each home range, and we estimated the average elevation, slope and aspect of grassland. The percentage of grassland was not correlated with slope ($r_{pearson} = 0.136$, $p = 0.08$), elevation ($r_{pearson} = 0.063$, $p = 0.416$), Northness ($r_{pearson} = 0.068$, $p = 0.373$) and Eastness ($r_{pearson} = 0.009$, $p = 0.906$). Slope of grassland was correlated both to elevation ($r_{pearson} = -0.395$, $p < 0.001$) and Northness ($r_{pearson} = 0.167$, $p = 0.0285$).

Mean seasonal home range size was 194.0 ha (N = 171, SD: 215.1 ha; range: 11.9-1612.0 ha). The list of candidate models is reported in Tab. 2. The best model according to the AIC criterion and parsimony was the one with the following explanatory variables: season, percentage of grassland nested within season, slope of grassland (AIC = 345.4). The effect of season was close to statistical significance ($F_{3,129} = 2.26$; $p = 0.084$), while percentage of grassland nested within season ($F_{4,129} = 13.25$; $p < 0.001$) and slope of grassland ($F_{4,129} = 35.38$; $p < 0.001$) showed highly significant effects. Inter-individual variability and year accounted for only 1% of total variability. The β-estimates obtained for the covariates are given in Tab. 3.

The percentage of grassland within the home range affected negatively home range size in all seasons, and also slope was inversely related to home range size (Tab. 3). Home range size in winter and spring was inversely correlated with the amount of snow depth ($r_{pearson} = -0.21$, $p = 0.05$). We found no correlation between home range size and temperature ($r_{pearson} = 0.08$, $p = 0.45$).

Discussion

Our results indicate the tendency of a stable space use pattern by male Alpine ibex throughout different years, as testified by the low amount of variability explained by the year. Estimated seasonal home range sizes were similar to those reported for other alpine ibex populations (Girard, 2000; Parrini et al., 2003), and, as expected, were smaller than those reported in studies on relocated ibexes, which usually tend to occupy larger areas as a consequence of their exploratory movement in the new environment (Michallet, 1994; Pedrotti, 1995; Scillitani et al., 2012). As expected, Alpine grasslands, which are actively selected during active phase because they provide forage (Grignolio et al., 2003; Lembke, 2005), were the preferred habitat for adult male ibex.

Table 3 – List of the β-estimates obtained for the covariates in the best model.

Covariate name	β	SE	t value	p
Grassland percentage in Summer	-1.46	0.47	-3.11	0.002
Grassland percentage in Autumn	-2.80	0.55	-5.10	< 0.001
Grassland percentage in Winter	-1.30	0.53	-2.44	0.016
Grassland percentage in Spring	-2.73	0.71	-3.85	< 0.001
Slope	-0.11	0.02	-5.95	< 0.001

Accordingly to our hypothesis, the change in percentage of grassland significantly explained variation in home range size in all seasons. This result is in agreement with an analysis conducted on male ibex in the Gran Paradiso National park (Grignolio et al., 2003), which reported a negative correlation between home range size and grassland. Habitat characteristics are important determinants of home range size in large herbivores (Börger et al., 2006; Kie et al., 2002; Saïd and Servanty, 2005; Lamberti et al., 2006). The inverse relationship between grassland percentage and home range size found in this study copes with the resource exploitation hypothesis suggested by several authors (Larter and Gates, 1994; McLoughlin and Ferguson, 2000; Anderson et al., 2005): when forage is easily available ibexes do not need to seek out it by moving important distances. Our results indicate also a negative relation between grassland slope and home range extension. First of all, this result can be linked to a simple geometry rule: an increase in slope corresponds to a decrease in the projected surface. However, there might be also a biological explanation: in fact the importance of slope in ibex habitat selection has been described by several authors (Couturier, 1962; Wiersema, 1983; Pedrotti, 1995; Girard, 2000). This is particularly true for winter and the beginning of spring when ibexes concentrated on south facing mountainside, in grasslands characterized by steep slope, which are more frequently free of snow in relation to other areas.

In this study, the best model did not detect significant effects of season on home range size, which was surprising on the basis of previous studies (Parrini et al., 2003; Grignolio et al., 2004). However, this finding can be interpreted by examining the results of simpler candidate models. In fact the model, testing only the effect of season detected significant differences between seasons ($F_{3,134} = 9.44$, $p < 0.001$), with home range size larger in Summer and Autumn than in Winter and Spring (Fig. 2), in agreement with the expected pattern. This differences diminished greatly when habitat covariates were included in the model, especially as a results of the addition of slope. In fact slope varied significantly over different seasons ($F_{3,134} = 45.54$, $p < 0.001$), and in Winter and Spring the slope of grasslands were significantly steeper than in Summer and Autumn (estimated average slope values: Summer = 30.0°SE = 0.4; Autumn = 32.4°SE = 0.4; Winter = 36.5°SE = 0.6; Spring = 35.7°SE = 0.5).

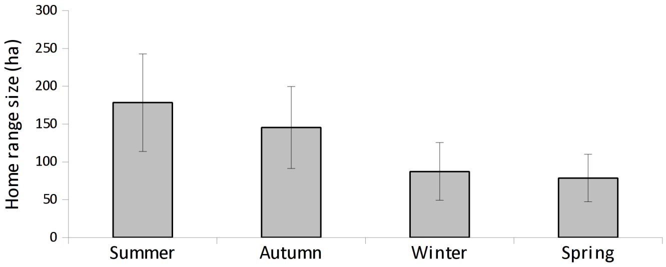

Figure 2 – Seasonal home range size (least square means) of adult male ibex in the Marmolada massif. Error bars represent standard errors.

For most species inhabiting Northern or alpine environments, the availability of resources, in terms of quantity and quality, is reduced during winter and the beginning of spring, since they are covered by snow (Festa-Bianchet, 1988; Collins and Smith, 1991; Nordengren et al., 2003). Alpine ibex are well adapted to climb in rocky environments with steep slopes (Geist, 1987), but their movements are hampered by the presence of a high snow depth (Raye, 1994; Tosi and Pedrotti, 2003). The extent and depth of snow cover affect cost of locomotion (Dailey and Hobbs, 1989), and limiting movement to confined patches free from snow permits to save energy (Rivrud et al., 2010). In this study we observed a tendency to a negative trade-off between the snow depth and the extension of home range, and this negative correlation might partially explain the small home range size we observed in winter and spring. The tendency of male alpine ibex to reduce ranging behaviour in winter has been reported for other populations (Terrier et al., 1994; Pedrotti, 1995; Girard, 2000; Parrini et al., 2003).

We found no effects of temperature on home range size, but the pre-defined seasonal scale could hide the effects of climate variability (Börger et al., 2006; Rivrud et al., 2010) and, also, direct and indirect effects of climate are often difficult to separate (Mysterud et al., 2008). In fact, the relationship between local weather variables such as temperature and home range size is probably partially mediated by the effects of climate on forage availability in terms of plant productivity and quality (Pettorelli et al., 2005) and secondarily through the interaction between climatic variability and population density (Hallett et al., 2004; Moen et al., 2006), which in turn affects herbivores space use patterns (Owen-Smith, 2002).

In contrast with the findings of other studies that highlighted the importance of different personalities when studying spatial ecology (Morales and Ellner, 2002; Réale et al., 2007), individual variability did not explain a substantial amount of variance in observed home range size. This result is probably linked to the gregarious nature of male alpine ibexes that in most part of the year live in large herds. Herding behaviour might partially reduce differences in individual behaviour, in terms of settlement and ranging behaviour, by influencing habitat selection (Fortin et al., 2009) and foraging decisions (Fortin and Fortin, 2009).

Another explanation lies into the morphology of the study area and the habitat preferences of male ibexes in geographical terms. In fact, in the Marmolada massif males tended to occupy the same mountainsides throughout the year. This high site fidelity and the gregariousness shown by males might explain the observed flattened differences between individuals, and the lack of differences in ranging behaviour between males of different ages. We expected to find differences in space use pattern of younger males in comparison to adult and old ones, because of conspicuous differences in body size, and therefore in energy requirement, and because studies on segregation indicated that younger males tend to associate more with females (Ruckstuhl and Neuhaus, 2001; Villaret and Bon, 1995). However, this was true especially for yearlings and two years old males, while males older than 3-4 years did not differ that much from older males with respect to patterns of inter-individual associations (Villaret and Bon, 1995). For this analysis we had only two individuals younger than four years at the first capture and this can probably explain why we did not find any effect of age on home range, as described in other studies that used adult individuals (Parrini et al., 2003).

In conclusion, this study demonstrated that seasonal home range size of male alpine ibex in the Marmolada massif is mostly influenced by grassland extent and steepness. A further step in the analysis of the link between grassland and home range size might be considering the structure of vegetation (in terms of species composition and richness, biomass and interspersion) within the grasslands in different mountainsides, in order to test whether plant diversity affects home range size and geographic location of male ibexes. In fact, as suggested by McLoughlin and Ferguson (2000), at the individual level forage abundance and quality are likely to be the most important factor affecting home range size.

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