Demographic characteristics, seasonal range and habitat topography of Balkan chamois population in its southernmost limit of its distribution (Giona mountain, Greece)

Haritakis Papaioannou, Stefanos Sgardelis, Basilios Chondropoulos, Dimitrios Vassilakis, Vassiliki Kati and Panayotis Dimopoulos

Department of Environmental and Natural Resources Management, University of Patras, Agrinio, Greece; School of Biology, Aristotle University of Thessaloniki, Thessaloniki, Greece; Department of Biology, University of Patras, Patras, Greece

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The annual range of Balkan chamois (Rupicapra rupicapra balcanica) in Giona mountain was found to be 5502 ha, with a low population density (2 individuals/100 ha). Seasonal range patterns varied significantly, with a minimum extent in summer and a maximum in winter (30% and 79% of the annual range, respectively). Summer stress and the rutting period might be associated with the observed aggregated distributions during the summer and autumn (core areas of 28% and 22% of seasonal ranges, respectively, defined after the Fixed Kernel Density Estimator). Chamois were found to use significantly lower altitude habitats in winter (1212 m) than in summer (2223 m), and significantly steeper slopes in winter (35°); aspect was not found to have a significant effect on habitat use. Population structure consisted of kids (21%), yearlings (8%), females (35%) and males (36%). Conservation management for the species should consider poaching, livestock competition and global warming.

Keywords: conservation; habitat use; Rupicapra; range; topography

Introduction

The genus Rupicapra includes two species: the southern chamois (Rupicapra pyrenaica) with three subspecies in southwestern Europe and the northern chamois (Rupicapra rupicapra) with seven subspecies in the rest of Europe and in the Near East (Corlatti et al. 2011). Chamois is the most abundant native mountain-dwelling ungulate in Europe and the Near East, with a population size of 36,000 individuals for the southern chamois and a larger population size of about 250,000–350,000 individuals for the northern chamois (Giacometti et al. 1997; Corlatti et al. 2011). Furthermore, some 18,500 individuals of the northern chamois are encountered in New Zealand (Forsyth 2005) as a result of an artificial introduction at the beginning of the twentieth century (Banwell 2013).

The ideal chamois habitat at lower and medium altitudes includes forests adjoining cliffs and rocky slopes, while at higher altitudes the habitat includes screes, steep peaks, couloirs and elongated ledges with herbaceous vegetation, as well as alpine pastures or otherwise sub-alpine grassy or semi-grassy areas in proximity with steep rocky slopes (Knaus and Schroeder 1975; Schaller 1977; Elsner-Schack 1985; Lovari

*Corresponding author. Email: haritakis1000@hotmail.com
and Cosentino 1986; Adamakopoulos and Matsoukas 1991; Pepin and N’Da 1992; Papaioannou 2005; Papaioannou and Kati 2007).

Balkan chamois (Rupicapra rupicapra balcanica) is probably one of the most poorly studied subspecies of the Rupicapra genus. Its geographical distribution extends across nine countries forming usually small and often isolated populations with varying conservation and management status (Corlatti et al. 2011). The total population size of the Balkan chamois is estimated to be around 17,000 individuals, based on the 1997 census (Adamakopoulos et al. 1997; Giacometti et al. 1997; Gjiknuri 1997; Krystufek et al. 1997; Spiridonov and Genov 1997). The Balkan chamois is listed in the Lower Risk category (Least Concern) of the IUCN Red List of Threatened Animals (Aulagnier et al. 2008). In addition, it is included in Annexes II and IV of the Directive 92/43/EEC “on the conservation of natural habitats and of wild flora and fauna”, (Annex II comprises species of Community importance whose conservation requires the designation of Special Conservation Areas and Annex IV comprises species of Community Importance in need of particularly strict protection). The conservation status and population trends of Balkan chamois vary along its geographical distribution according to the different national wildlife policies and the degree of local communities’ interest in the conservation of the species (Adamakopoulos et al. 1997; Gjiknuri 1997; Krystufek et al. 1997; Spiridonov and Genov 1997; Papaioannou and Kati 2007; Papaioannou 2010; Paunovic et al. 2010; Stojanov et al. 2010). However, it is reported that several populations of this subspecies currently exhibit a declining trend (Aulagnier et al. 2008; Corlatti et al. 2011).

The total population size for Balkan chamois in Greece is estimated to be between 480 and 750 individuals (Papaioannou and Kati 2007). It is characterized by a fragmented distribution pattern, forming six major population blocks in six geographical regions. A total of up to 18 distinct populations exist in the above geographical regions, with probably six more populations of very low population size, remnants of its larger distribution of the recent past (Hatzirvassanis 1991; Papaioannou 1991, 2005, 2010; Adamakopoulos et al. 1997; Papaioannou and Kati 2007) (Appendix 1, Figure 1). The Balkan chamois in Greece is under a strict conservation status, and hunting has been totally forbidden since 1969. However, the greatest threat for the survival of this species in Greece is well-documented to be poaching and the construction of forest and mountain roads, which provide poachers with access to its habitats (Papaioannou 1991, 2005, 2010; Karandinos and Paraschi 1992; Adamakopoulos et al. 1997; Papaioannou and Kati 2007).

The aim of the present study was to investigate the distribution pattern, demographic characteristics and the effect of season on the ranges and habitat topography of Balkan chamois on Giona mountain (Giona Mt). As our target population is located in the southernmost limit of the Balkan chamois distribution, we set as a null hypothesis that the warm summer period is a stress factor that impels an aggregated distribution towards the few adequate cool microhabitats with sufficient feeding resources. Furthermore, we discuss the synergistic effect of poaching, road construction, competition with livestock and global warming on the long-term survival of the population. We set in particular five distinct objectives: (a) to delineate the annual range and core area of the species on Giona Mt in a Natura 2000 site, (b) to investigate the pattern of seasonal differentiation of the species range and respective core areas, (c) to estimate its population size and demographic
characteristics, (d) to investigate the effect of season on the chamois habitat selection in terms of elevation, inclination and aspect, and (e) to interpret our findings in a conservation context.

Material and methods

Study area

Our research was conducted on Giona Mt. The study area covers a surface area of 21,880 ha (73% of the whole mountain) and includes the Natura 2000 site GR
Giona Mt is the southernmost limit of the Balkan chamois’ natural geographic distribution in Europe (Papaioannou and Kati 2007; Papaioannou 2010). Available meteorological data concerning the study area (Meteorological Station of Mavrolithari, 1220 m altitude 2009–2012), show an annual precipitation of 1191.03 mm with a high in winter (454.1 mm) and a low in summer (95.07 mm), whereas precipitation in spring and autumn is 277.65 and 364.2 mm, respectively. Mean temperature ranges between 0.05°C (in February) and 18.53°C (in July). The lowest temperature during winter is in February (−13.40°C) and during summer in June (3.75°C), whereas the highest during winter is in December (15.05°C) and in summer in July (33.65°C). The geological bedrock is primarily limestone. Elevation ranges from 600 to 2510 m above sea level; most (80%) falls within an elevation zone ranging from 1000 to 2000 m and the highest elevation zone (>2000 m) is restricted to 11% of the total area. The tree-line altitude varies between 1600 and 1800 m above sea level. The dominant vegetation type is fir forest (Abies cephalonica) (46%), followed by subalpine (mountain and oro-Mediterranean) grassland (20%) and juniper scrubland (17%). Rocky areas without trees and screes cover 4% of the study area. Pastures, including both grasslands and juniper scrublands, represent about 37% of the total area. They are located more or less in the centre of the study area in the mid-upper altitude zones (1600–2200 m).

The main human activities include permanent and transhumant livestock breeding (sheep, goats and fewer cattle) in medium and high altitudes, respectively, as well as bauxite mining and hunting. Transhumant livestock use the mid and high altitude zones of the study area (about 1500–2300 m) from early June till September, whereas the permanent livestock use mainly the lower altitude zones around the villages. However, in certain parts of the study area hunting is either totally forbidden (Game Reserves) or under a special control status (Fokida Hunting Reserve); these areas represent 15% and 12%, respectively, of the total study area. Natural predators of chamois in Giona Mt include the wolf (Canis lupus), the fox (Vulpes vulpes) and the golden eagle (Aquila chrysaetos).

Sampling

Chamois

For the purposes of this investigation a set of predetermined transects was used; in conjunction, visual scanning was carried out from a set of vantage points along them, offering favourable views of the chamois habitat (Hussin et al. 1994). A variety of transects was chosen covering forested as well as treeless areas and involving human trails, paved roads, ridges, goat paths or cross-country sections. Overall, 35 transects were distributed in the whole study area, totalling a length of 130 km. All of them were repeated in all four seasons. A total of 150 observation days were conducted during the years 2006 and 2007, which were evenly distributed throughout four seasons. Seasons were defined on the basis of the annual biological cycle of the species (Pepin et al. 1992) as following: spring was related to parturition (10/3–9/6), summer was the warm period (10/6–9/9), autumn was related to the rutting period (10/9–9/12) and winter was the cold period (10/12–9/3).

Our dataset consisted of 1008 observations, geo-referenced with GPS and a 1:50,000 map. We considered as direct the observation of either one individual or a
group of animals. A group was defined as any animal aggregation occupying the same parcel of land, having sensorial contact and being more or less coordinated in its movements (Schaller 1977). Each group was distinguished from a neighbouring one when the distance between them was greater than the average inter-individual distance within the group (Clutton-Brock et al. 1982). We also collected indirect observations, to confirm species presence or absence in areas of low visibility, such as dense forests. Indirect observations were chamois tracks and/or droppings within a 1-m diameter circle. Of our observations, 32% were direct (individuals or groups) and the remaining 68% were indirect records, i.e. droppings (52%) and tracks (16%). Direct observations were made mostly in summer (128) and autumn (89) and indirect were made during spring (Table 1).

The area’s total chamois population size was estimated in October 2007 (during the rutting season), using the “pointage flash method” (Hussin et al. 1994). Three groups of researchers simultaneously scanned the whole area for five successive days, noting the date, time, group size and composition and the exact location of each direct observation, so as to combine data after the end of the survey by rejecting duplications. Every individual, either single or in a group was assigned to one of four sex/age classes: kids (<1 year), yearlings (between 1 and 2 years), females (>2 years) and males (>2 years) (Catusse et al. 1996).

**Topographic variables**

Three parameters were considered to describe the topography of the localities where the species was recorded (directly or indirectly): elevation (metres), inclination (degrees) and aspect (degrees from north). We extracted the above topographic variables from a digital terrain elevation model covering our study area, with a 20 × 20-m pixel resolution and vector files with digitized contour isoclines at 20-m intervals.

**Data analysis**

We determined chamois seasonal ranges using the 95% Fixed Kernel density estimator, implying a probability of species occurrence in its range greater than 95% (Worton 1989), using Arcview Version 3.2 (ESRI Inc 1994) with the extension “Animal Movement” (Hooge and Eichenlaub 1997) and ArcGIS (ESRI 2011).

The annual range was extracted after merging the seasonal ranges. We considered the methodology of Powell (2000) to delineate the core area, defined as the area that is used more heavily excluding any random effect, using a diagram that plots the area of animal range (%) with the probability of area use (%) (see Figure 2). The

| Observation type | Winter | Spring | Summer | Autumn | Total |
|------------------|--------|--------|--------|--------|-------|
| Animals          | 53     | 54     | 128    | 89     | 324   |
| Droppings        | 87     | 182    | 133    | 118    | 520   |
| Tracks           | 39     | 49     | 35     | 41     | 164   |
| Total            | 179    | 285    | 296    | 248    | 1008  |

Table 1. Number of direct (animals) and indirect (droppings and tracks) observations throughout the four seasons.
The straight line reflects a random use of space, while the curve that sags below the straight line reflects a clumped use of space. The point where the curve’s tangent becomes parallel to the line of random use is the threshold to define the core area. We calculated the seasonal core areas as above and we merged them to calculate the annual core area. Finally, we calculated the overlap of seasonal ranges and seasonal core areas, using ArcGIS.

We estimated the chamois population density in the species annual and seasonal ranges by dividing the estimated population size (October 2007) with the respective ranges. Elevation and inclination did not show a normal distribution (Kolmogorov–Smirnov test; \( p > 0.05 \)), so we investigated whether the elevation and inclination vary significantly throughout the four seasons using non-parametric statistics (Kruskal–Wallis \( H \)-test). We compared the pairs of successive seasons in terms of the above three parameters (Man–Whitney \( U \)-tests), using a Bonferroni correction \( (p = 0.0083) \). Each observation was attributed one out of four aspects (north, east, south, west), and chi-squared tests were performed to examine the significance of seasonal aspect variation. Data analysis was performed using SPSS 16 (SPSS Inc 2007). Violin Plots (Hintze and Nelson 1998) were created using statistical software R (R Development Core Team 2010).
Results

Annual and seasonal ranges

The annual range of the Balkan chamois consisted of two nuclei and covered an area of 5502 ha, covering 25% of the area of the Natura 2000 site, whereas a tiny fraction of less than 1% of it falls outside the Natura 2000 site. The annual core area accrued from the overlapping of the seasonal core areas. It consisted of two large nuclei and one very small nucleus and covered an area of 2967 ha (54% of the annual range) (Figure 3, Table 2).

Figure 4 demonstrates the seasonal change in chamois ranges and their respective core areas. The probability of species detection in the seasonal core areas during winter and summer was 85% and during spring and autumn was 70%. The seasonal pattern differed substantially: the species was encountered in three distinct nuclei with two core areas during winter, in two nuclei with two core areas during spring and autumn, and in four – mostly smaller – nuclei with two core areas during summer (Figure 4). The surface area of its range was very different in relation to the seasons, with a maximum during the spring (79% of annual range) and a minimum during the summer (30% of annual range) (Table 2). The spatial distribution of the species in terms of core areas was more aggregated during the autumn (22% of seasonal range) and summer (28%), whereas in spring and winter the core areas occupied larger ratios (41% and 55%) of their respective seasonal ranges.

The overlap of winter and summer ranges, as well as of winter and autumn ranges, was impressively low, especially when considering the respective core area overlap (1% in both cases), manifesting the species’ spatial dynamism in Giona Mt. In contrast, the species did not seem to change its range greatly between winter and spring, as demonstrated by the substantial overlap of its respective ranges and core areas (56% and 44%, respectively) (Table 2).

Habitat use

The results have shown elevation of used chamois habitat to significantly vary throughout the seasons (\(H = 226,852, p < 0.001\)). Considering median values, chamois were found to move to significantly higher altitudes in spring (1484 m) and summer (2223 m) and back down to significantly lower altitudes in autumn (1900 m) and winter (1212 m) (\(U = 16640, U = 20370, U = 23945, U = 6714\) respectively with \(p < 0.0083\)) (Figure 5). Inclination also varied significantly throughout the seasons (\(H = 28,421, p < 0.001\)), as the species used steeper slopes in winter (35°) than in the other seasons (30°) (Figure 5). Aspect was found not to be significantly different among seasons (Pearson \(\chi^2 = 12, p > 0.05\)). Considering only direct observations, the animals were observed mostly on south-facing slopes in winter (34%), west-facing slopes in spring (41%) and east-facing slopes in summer and autumn (34% and 46%, respectively).

Demographic characteristics

The population size of Balkan chamois in Giona Mt was estimated at 110 individuals. Population density was found to be remarkably low, with only 2 individuals (ind.)/100 ha. Population density in winter and spring was 3 ind./100 ha, reached a
Figure 3. Annual range and core area of Balkan chamois in the study area, and overlap with the Natura 2000 site in Giona Mt.
maximum in summer when the most aggregated distribution was observed (7 ind./100 ha) and was 4 ind./100 ha in autumn when the population was more dispersed. As far as population structure was concerned, kids constituted 21% (n = 23), yearlings 8% (n = 9), females 35% (n = 38) and males 36% (n = 40) of the overall population (n = 110). The estimated fecundity rate was 0.60 (kids/females) and the sex ratio 1.05 (males/females).

**Discussion**

**Annual range**

The estimated Balkan chamois annual range was found to cover 25% of the Natura 2000 site. Considering our sampling methodology, species presence was not recorded in the remaining area of Giona Mt, although adequate chamois habitat such as fir forests, subalpine pastures and rocky areas occur throughout the study area. We therefore argue that population isolation in a small part of the mountain is not due to a lack of adequate chamois habitat but to human-related disturbance. Bauxite mining is a well-developed activity mostly in the southern and northeastern parts of the study area, where chamois is absent. It is not clear whether mining activity *per se* constitutes a decisive disturbance factor. Results are contradictory for mountain-dwelling ungulates; it has been suggested that in some cases where steep slopes and rugged terrain are scarce, mining can create such microhabitats and even have a beneficial effect to mountain sheep (Bleich et al. 2009). It is possible that it is the dense road network, associated with mining activities, that is the main detrimental factor concerning the chamois population, as it increases accessibility and direct human disturbance (including poaching) to chamois habitats. The negative impact of road infrastructure to biodiversity erosion is well documented (e.g. Selva et al. 2011), with ungulates showing a clear avoidance pattern related to roads (Bleich et al. 2009; Lian et al. 2012).

**Seasonal movement**

We found a clear seasonal elevation-shifting pattern of over 1000 m, from low-elevation winter habitats (1212 m) up to high-elevation summer habitats (2223 m).

Table 2: Annual and seasonal ranges and respective core areas of Balkan chamois in Giona Mt (ha) and seasonal range overlap (in parenthesis the overlap of seasonal core areas). Range (%) is the proportion seasonal range out of the annual range and core areas (%) is the proportion of seasonal core areas out of the respective seasonal ranges.

| Season  | Range (ha) | Core area (ha) | Range (%) | Core area (%) | Range (%) | Core area (%) | Seasonal range (core area) overlap (%) |
|---------|------------|----------------|-----------|---------------|-----------|---------------|---------------------------------------|
| Winter  | 3496       | 1911           | 64        | 55            | 100       | 56 (44)       | 18 (1) 26 (1)                         |
| Spring  | 4324       | 1772           | 79        | 41            | 100       | 36 (16)       | 53 (19)                              |
| Summer  | 1675       | 467            | 30        | 28            | 100       | 41 (27)       | 100                                   |
| Autumn  | 3000       | 668            | 55        | 22            |           |               | 100                                   |
| Annual  | 5502       | 2967           | 100       | 54            |           |               |                                       |

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Figure 4. Seasonal range generated from a Fixed Kernel Density Estimator (FKDE) (95% probability) and respective core areas of Balkan chamois in Giona Mt for (A) winter, (B) spring, (C) summer and (D) autumn. In the upper right corner the diagram presents the delineation of the probability of species occurrence within the core area.
This elevation-shifting pattern is well-documented in chamois populations throughout Europe and is associated with the seasonal migration pattern, from low-altitude forests in winter to supraforestal subalpine grasslands as the snow recedes (Knaus and Schroeder 1975; Schaller 1977; Elsner-Schack 1985; Hamr 1985; Lovari and Cosentino 1986; Garcia-Gonzalez et al. 1992; Pepin et al. 1992). The above migration pattern, which is inherent to chamois ecology, also explains the partial spatial overlap of ranges in successive seasons and the minimal overlap of the winter range with that of the autumn and summer.

**The role of inclination and aspect in habitat use**

Our results indicated that chamois in Giona Mt used slopes between 22° and 38° in spring, summer and autumn. A similar optimal range (25° to 35°) associated with local landscape topography is also reported for Tatra chamois (*Rupicapra rupicapra tatrica*) in central Slovakia (Backor 2010). In Giona Mt the species was found to use steeper slopes in winter (from 28° up to 42°). This could be attributed to the selection of wind-protected steeper slopes and/or the selection of less accessible and more secure microhabitats (Elsner-Schack 1985; Lovari and Cosentino 1986). Although one could expect Balkan chamois to favour the use of southern slopes in winter and northern slopes during the warm period of summer, no such clear pattern of aspect
use was observed. It would seem that aspect is not the primary driver of chamois habitat use and that the species succeeds in overcoming the stress imposed by the warm period, by simply occupying the highest elevation microhabitats. Although our knowledge concerning Balkan chamois habitat use is poor, results of other sub-species remain contradictory with regards to aspect use. In higher latitudes, the alpine chamois (*Rupicapra rupicapra rupicapra*) were found to show a clear preference for north-facing slopes in the pre-Alps, southern-facing slopes in the inner massif of Isère in France during winter (Michallet et al. 1999), and towards south-to-southeast-facing slopes in the western Alps (Nesti et al. 2010). On the other hand, Tatra chamois (*R. rupicapra tatrica*) demonstrated a clear preference towards the northern-facing slopes during the summer and southern-facing slopes during the winter (Backor 2010). Similarly, chamois in northern Tyrol occupied mainly the southern-facing cliffs during the winter (Hamr 1985). Radio-tracking data for Giona Mt would provide a clearer explanation of the role of aspect in chamois habitat selection in the Mediterranean area.

**Mediterranean range pattern under global warming**

According to our results, the species demonstrated a strong aggregation pattern in the summer (minimum range and core area) and a more dispersed distribution in the spring (maximum range) and winter (maximum core area). A home range analysis of alpine chamois in the Alps showed that the animals have greater home ranges in the warm period and more reduced home ranges in the cold period (Nesti et al. 2010). Similarly, chamois in the Pyrenees exhibited an extremely reduced home range in winter areas, whereas in summer the animals used a wider area at higher altitudes (Garcia-Gonzalez et al. 1992). Assuming that small individual home ranges during one season are associated with a small population range for the same period, it seems that our results contradict the corresponding findings concerning chamois seasonal patterns in more continental climates. The results suggest that the stress period for the Balkan chamois in the southermost limit of its distribution is the hot and dry summer season and not so much the winter period, as in the case with chamois populations in northern latitudes. During the summer the species occupies the highest elevation habitats on the summits of Giona Mt, so as to exploit cooler more favourable microhabitats with sufficient food resource availability of high quality such as fresh palatable grass (Elsner-Schack 1985). The search for food is quoted as one of the main factors affecting the spatial distribution of mountain cliff-dwelling ungulates, and food availability plays a crucial role in seasonal movements (Geist 1971; Garcia-Gonzalez et al. 1990). On the other hand, the chamois population on Giona Mt is characterized by a rather large winter range, as individuals disperse in winter fir forest habitats to make the best use of the available food resources, without facing the limiting factor of extreme cold and snow fall that increases mortality in several European chamois populations in Central and Western Europe (Gonzales and Crampe 2001). The Giona Mt chamois have proved their ability to overcome the hot season stress factor through their adaptive behaviour towards aggregation around the highest summits. However, the temperature increase during the spring and summer season has been found to negatively affect body mass of the alpine chamois in the Alps (Rughetti and Festa-Bianchet 2012). Range-restricted species, particularly polar and mountaintop species, have
experienced severe range contractions and have been the first groups in which entire species have gone extinct due to recent climate change (Parmesan 2006). Under this context, it is conceivable that chamois populations in Mediterranean climates, such as the Giona Mt population, will be particularly vulnerable to global warming, as food resources of good quality will be further reduced and degraded, and adequate microhabitats will be lost, leading to decreased animal fitness. A home range analysis, using GPS-collared animals of the Giona Mt population, is needed to further elucidate chamois Mediterranean seasonal range pattern.

A second stress factor that is acting synergistically with warm period stress and that further explains the aggregative chamois summer pattern is the upward movement of sheep and goat flocks, which occupy subalpine pastures from July to September in Giona Mt. Chamois populations in Europe (R. rupicapra rupicapra and R. yrenaica) are known to avoid pastures grazed by livestock, by aggregating in higher and steeper habitats (Rebollo et al. 1993), rocky areas (Chirichella et al. 2013), even in low altitudes in the forests (Herrero et al. 1996), in an attempt to avoid disturbance, food competition and disease spread from domesticated animals (Fankhauser et al. 2008).

Finally, no stress factor seems to drive chamois range during spring and autumn in Giona Mt. In spring, the animals move gradually to higher altitudes, following the receding snowline in search of sprouts and fresh palatable grass in accordance with the general pattern of annual habitat use of most European chamois populations (Schaller 1977; Pepin et al. 1992). However, we must take into account that births in the study area take place in May and pregnant females have a tendency to become isolated before parturition (Couturier 1938; Perez-Barberia and Nores 1994). Females therefore might continue to use forested habitats to give birth in safety (Pepin et al. 1997), avoiding the open areas above the tree line. In autumn, the population also exhibits an aggregative pattern, as female harems are formed during the rutting period. Open habitats, above tree line, with higher visibility, represent prime areas for dominant males striving to control harems, as observed in red deer (Clutton-Brock et al. 1982). Besides the dominant ones, more males are attracted by the female groups. Single sub-adult males or small male groups can be observed far away from the places where harems exist, even in lower-altitude forested zones, explaining the great elevation range (>1000 m) used by the chamois in autumn (Figure 4).

Population demography

Giona Mt hosts the second largest population of chamois in Greece after the Tymfi Mt population (130 individuals) in northwestern Greece (Papaioannou and Kati 2007). Even though the Giona Mt population is one of the largest at a national scale, its impressively low density of 2 ind./100 ha is six- to twelve-fold lower than the densities reported for the Pyrenees or the Alps – for instance 12.2 ind./100 ha (Herrero et al. 2012), 13 ind/100 ha (Boschi & Nievrsgelt 2003), 14 ind./100 ha (Berducou and Bousses 1985), 21–23 ind./100 ha (Pepin et al. 1996), 24 ind./100 ha (Hussin et al. 1994)]. Even if we consider the summer population density, which reaches 7 ind./100 ha because of the aggregation, the population status in Giona Mt is poor, falling far below the carrying capacity threshold, compared with other European chamois populations. The fecundity rate of the
population is 0.60, falling in line with the typical range of fecundity reported from the rest of Europe (0.55–0.85) (Salzmann 1977; Garcia-Gonzalez and Hidalgo 1988; Allaine et al. 1990), implying that external factors other than the inherent demographic characteristics affect its population dynamics. We also found that the yearlings occupy an unusually low proportion of 8% of the population, for instance, the respective percentage in an alpine chamois population in Bavaria is 18% (Kramer 1969), implying a higher kid mortality in Giona Mt. Furthermore, we found a sex ratio of 1 : 1 during the autumn survey. Although the sex ratio at birth is usually 1 : 1 in ungulates (Clutton-Brock et al. 1982), in a naturally regulated population females typically outnumber males (Loison et al. 1999; Bocci et al. 2010). The higher male mortality is mainly due to the depletion of fat stores after the rutting period and just before the harsh winter period, as well as being due to trophy hunting (Knaus and Schroeder 1975; Cramp 1986; Wolff 1994). Our results could be explained by the lower male mortality in the milder winter period of Giona Mt, by the limited male trophy hunting culture of Greek poachers, and/or by the easier detection of the female groups by the poachers because of their aggregation in female–kid groups.

**Conservation implications**

The Balkan chamois population in its southernmost limit of its distribution exhibits a particular Mediterranean pattern, as the population aggregates around the highest available summits, to overcome the stress imposed by the warm summer period. Global warming might well be a very realistic threat for the long-term survival of the population, since Giona Mt sets a fixed upper limit, or “ceiling” of 2510 m, preventing further upslope movement for animals struggling to overcome a future temperature increase.

Chamois population density in Giona Mt is remarkably low in relation to other European chamois populations. Although one could hypothesize that this low population density is due to the scarcity of suitable habitats being at the limit of chamois distribution, Giona Mt hosts one of the largest chamois populations, when compared with other Greek mountains. Low density therefore should not so much be attributed to biogeography, but rather to serious and direct threats such as poaching. During our 2-year survey, we found six carefully excoriated abandoned chamois skulls (5% of the total population), providing evidence for the magnitude of the problem. Livestock breeding and the competitive pressure on chamois habitats is also another stress-factor during the hot and early rutting period. The synergistic effect of poaching, road construction following mining, livestock breeding in the short term and global warming in the long term could prove to be detrimental for the maintenance of the Giona Mt chamois population. Urgent conservation measures are needed to guarantee Giona Mt chamois population survival. These involve poaching abatement, an efficient guarding system of well-trained rangers to safeguard the natural growth of the population, control of road use towards chamois habitats through barriers, and the implementation of a sustainable grazing scheme both for livestock and for chamois populations. Finally, further research is needed, using GPS-collared individuals, to focus on home range patterns and population trend monitoring on an annual basis.
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Appendix 1

Balkan chamois populations in Greece, modified from Papaioannou and Kati 2007 (see Figure 1).

| Area                              | Balkan chamois population | Remnant of Balkan chamois population |
|-----------------------------------|---------------------------|-------------------------------------|
| 1 Grammos Mt                      | x                         |                                     |
| 2 Smolikas Mt                     | x                         |                                     |
| 3 Trapezitsa Mt                   | x                         |                                     |
| 4 Tymphi Mt                       | x                         |                                     |
| 5 Ligos–Tsouka Rossa Mts          | x                         |                                     |
| 6 Vassilitsa Mt                   | x                         |                                     |
| 7 Kleftes–Flabouro Mts            | x                         |                                     |
| 8 Central Zagori                  | x                         |                                     |
| 9 Nemertsika Mt                   | x                         |                                     |
| 10 Peristeri–Kakarditsa–Stefani Mts | x     |                                     |
| 11 Tzoumerka–Pahtouri Mts         | x                         |                                     |
| 12 Kokkinolakka Mt                | x                         |                                     |
| 13 Trigia Mt                      | x                         |                                     |
| 14 Avgo Mt                        | x                         |                                     |
| 15 Hatzi Mt                       | x                         |                                     |
| 16 Vardoussia Mt                  | x                         |                                     |
| 17 Giona Mt                       | x                         |                                     |
| 18 Iti Mt                         | x                         |                                     |
| 19 Olympus Mt                     | x                         |                                     |
| 20 Fracto forest                  | x                         |                                     |
| 21 Gyftocastro-Haidou             | x                         |                                     |
| 22 Falakro Mt                     | x                         |                                     |
| 23 Tzena–Pinovo Mts               | x                         |                                     |
| 24 Varnountas Mt                  | x                         |                                     |