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Altitudinal Distribution of Alpine Marmot (*Marmota marmota*) in the Pyrenees, Spain/France

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Abstract

The alpine marmot occupies areas ranging in altitude from 1300 to 2800 m in the Pyrenees, although 67% of the colonies are found between 1800 and 2400 m. Greatest colony density and greater areal use than expected were found between these last limits. The lower edge of the altitudinal range normally coincides with current forest limit and the upper edge seems to be related to the availability of sufficient food as to accomplish its minimum annual cycle (maintenance, reproduction, and fat storage). There is a positive correlation between the number of colonies and the duration of the available food period above 1800 m. In a broad sense, the altitude range of the alpine marmot in the Pyrenees is similar to that in the Alps. Because the natural forest limit seems to be higher in the Pyrenees than in the Alps, the success of the introduction of the alpine marmot in the Pyrenees could be probably due to the existence of a wide supraforestal open area artificially created for pastoral use.

Introduction

The alpine marmot (*Marmota marmota*) inhabited the Pyrenees during the Pleistocene and many fossil sites have been found on both the Spanish and the French sides of the range (Besson, 1971). Marmots probably became extinct because of the climatic changes during the Holocene, with warmer climatic conditions, just as in the Eastern Alps (Bauer, 1991) or in the Apennines (Ferri et al., 1988). Since the first release of marmots in 1948 (Couturier, 1955), there have been numerous introductions of the species onto the French slope of the Pyrenees and today it is widely distributed throughout the Pyrenees (Jean, 1979; Garcia-Gonzalez et al., 1985; Herrero et al., 1987, 1992). We ask the question, Why has the alpine marmot colonized the Pyrenean range so successfully?

The success of introductions normally depends on the availability of suitable habitats where marmots can become established. In the case of the alpine marmot this means (1) open areas with good visibility and sufficient food (Bibikov, 1968); (2) existence of soils with burrowing possibilities (Bibikov, 1968); (3) thermal conditions that allow marmots to avoid thermoregulatory constraints (Turk and Arnold, 1988). These conditions seem to occur in mountains high enough to have an important alpine belt, or in those with lower altitude but with large deforested areas and appropriate thermal characteristics.

Although the Pyrenees are usually included in the Eurosiberian region and form a part of the Alpine mountains, they also present climatic and vegetation characteristics of Mediterranean mountains, especially in the southern slope (Vigo and Ninot, 1987). On the other hand, their altitude is not so high (maximum height, 3404 m) as to have an extensive alpine zone (Ozenda and Borel, 1991). Nevertheless, introduced marmots have spread extensively over the mountain range and have been successful in establishing themselves. In this work we examine the altitudinal distribution and altitudinal preference of alpine marmots in the Pyrenees, with the aim of ascertaining the basis of their widespread occupation, in accordance with their habitat preferences.

Material and Methods

The data referring to the altitude of the colonies were taken from (1) an extensive exploration of the territory (Herrero et al., 1987; Herrero and García-Serrano, 1989); (2) interviews with rangers of various wildlife services; and (3) bibliographic data, particularly those referring to the French and Catalonian areas (Jean, 1979; Canut et al., 1989; González et al., 1989). Only verified data of marmot settlement (i.e. presence of animals and burrows) were taken into account. We have used the term colony in the sense utilized by Huber (1978): an area occupied by one or more families.

Colony data were distributed in 200-m altitudinal intervals. To test the null hypothesis that marmot distribution was proportional to surface availability, we took the planimetric area of each of the 200-m altitudinal intervals above 1200 m in the whole Pyrenean range from adequate maps (Martínez-Rica and Reiné-Viñales, 1988).

To evaluate the degree of utilization of a given altitudinal zone by marmots, we followed the statistical technique of Neu et al. (1974), later described by Byers et al. (1984). The method uses a chi-square goodness-of-fit analysis to test whether observations of habitat use follow the expected pattern of occurrence based on habitat availability (in this case areal availability). When the chi-square test detects a significant difference in usage versus availability, a Bonferroni z-statistic is used to determine which altitudinal interval is used more or less frequently than expected. Altitudinal zones without marmots (below 1200 m and above 2800 m) were not considered.

In order to explain upper altitudinal limits of marmot distribution, we have estimated the extent of the Available Food Period. This period is defined as the number of days between the beginning of the vegetative period (conventionally when the mean air temperature is equal or above 7°C) and the end of the freeze-thaw autumn period, when mean air temperature is equal or below 0°C and most of the precipitation falls as snow. We derived the values of Available Food Period from the regression models established by Del Barrio et al. (1990) for the Pyrenean

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TABLE 1

Descriptive statistics of the altitude occupied by the alpine marmot on both sides of the Pyrenees

	Spain	France	Pooled data
Number of colonies	268	375	643
Mean altitude (m)	2007	2020	2015
Standard deviation	275	286	282
Median	1985	2025	2000
Maximum	2800	2700	2800
Minimum	1400	1300	1300

high mountain belt and used the mid-point of each altitudinal interval. These models relate thermal and seasonal variables with altitude and were elaborated from data from the meteorological stations distributed throughout the Pyrenees.

Results and Discussion

GENERAL DISTRIBUTION

The mean altitude occupied by marmots on both the French and the Spanish sides of the Pyrenees does not significantly differ ($t = 0.40$, $p = 0.58$, Table 1), thus we pooled data from both slopes to determine the altitudinal distribution. The altitudinal distribution (Table 2) ranges from 1300 to 2800 m, which coincides fairly well with that of the Alps (Couturier, 1964; Huber, 1978; Solari, 1988). Extreme localities on the southern slope coincide with spring dispersals at 900 m and at 3000 m (unpublished data). Distribution over altitude intervals significantly varies from random distribution ($x^2 = 435.1$; $p < 0.001$; d.f. = 7). Bonferroni-intervals test show that marmots use less than expected altitudes below 1600 m and above 2600 m. Marmots use of two altitudinal intervals (1601–1800 m and 2401–2600 m) occurs in proportion to their availability. Altitudes used more than expected range from 1801 to 2400 m, which is where the greatest densities were found (9.2 colonies/100 km^2). At the zones where use was as expected, density was 4.7 colonies/100 km^2 and at the altitudinal extremes, where observed usage was less than expected, use ranged between 0.2 and 2.4 colonies/100 km^2.

The number of colonies in the altitudinal zones where observed use was greater than expected (between 1801 m and 2400 m), comprised 67% of the total, thus placing the marmot at the subalpine level in a broad sense (Vigo and Ninot, 1987). There is good agreement with other areas of the Alps where altitudinal distribution was quantified: 68% of the colonies in Orobie Alps range between 1700 to 2100 m (Panseri, 1992) and in the Canton of Ticino, 69% of the colonies range between 1800 and 2300 m (Solari, 1988).

In the Pyrenees the subalpine level has normally been transformed by anthropic activity, mainly grazing and fire, to livestock pastureland (Chocarro et al., 1990). This process has had a relevant importance from the 12th to 13th century (Montserrat, 1992), as it has in certain parts of the Alps (Kral, 1990) and in the Apennines (Cruise, 1991). Thus the present upper forest limit (normally between 1600 and 1800 m), was lowered in regard to the natural limit, which should be 2300 to 2400 m (Cantegrel, 1987; Del Barrio et al., 1990; Ozenda and Borel, 1991; Vigo and Ninot, 1987) and increased the available grass surface for subalpine herbivores. Also, this deforestation led to a descent of the lower altitudinal limit of the periglacial belt (Höllermann, 1985), causing increased slope instability and favoring the creation of suitable places for marmot settlements (screes and rockfall accumulations).

TABLE 2

Analysis of proportional usage of the different altitudinal zones by the alpine marmot in the Pyrenees and the duration of available food period at each altitude

Altitudinal zone (m)	Available area (km^2)[a]	Expected proportion of usage	Number of observed colonies	Observed proportion of usage	Bonferroni intervals	Available food period (days)[b]
1201–1400	3314.2	0.231	8	0.012	0–0.024*	243
1401–1600	2707.2	0.190	45	0.070	0.042–0.098*	228
1601–1800	2238.2	0.156	106	0.165	0.125–0.205	211
1801–2000	1830.4	0.128	170	0.264	0.217–0.312*	196
2001–2200	1543.0	0.108	164	0.255	0.208–0.302*	181
2201–2400	1297.7	0.091	96	0.149	0.111–0.188*	165
2401–2600	936.6	0.066	44	0.068	0.041–0.096	150
2601–2800	420.4	0.029	10	0.016	0.002–0.029*	135
Total	14287.7	1.0	643	1.0		

[a] From Martinez-Rica and Reiné-Viñales (1988).

[b] Recalculated from Del Barrio et al. (1990).

* Significant difference ($p < 0.05$).

LOWER ALTITUDINAL LIMIT

Studies on thermal tolerance of the alpine marmot pointed out that certain limitations in the thermoregulatory system could impose a physiological (behavioral) altitudinal limit on this species (Turk and Arnold, 1988). An effective environmental temperature over 25°C reduces the available time for above-ground activity of marmots. "Excessive temperatures during summer in low altitudes could be responsible for limiting the alpine marmot vertical distribution below 800 m" (Forter in Turk and Arnold, 1988) and could be the reason why marmots do not establish permanent colonies in forest clearings or deforested areas below this altitude. Also, the precarious situation of certain low-altitude colonies, as those of the Jura Mountains (Neet, 1992), could be related to these thermal restrictions.

Nevertheless, it seems that the effective ecological lower limit could be imposed by the existence of forest. The habitat of the alpine marmot (and almost all the *Marmota* genus) is the open space or the deforested area (Bibikov, 1968). All classical and recent studies on marmot habitat characteristics have pointed out the exceptional presence of permanent colonies in woodland, as in the Alps (Couturier, 1964; Huber, 1978; Grimod et al., 1991; Macchi et al., 1992) or the Pyrenees (Herrero, unpublished data).

The inability of marmots to live in the forest areas is not a resolved question. It is quite likely related to the difficulty of detecting predators (Huber, 1978), limitations of visual communication within the colony (Bibikov, 1968), or difficulties in obtaining a suitable food supply. But it seems to determine the ecological lower altitudinal limit for the alpine marmot. So, for example, the vertical distribution of marmots in the Aosta Valley is quite high, between 2100 to 2500 m, but the forest limit reaches 2000 to 2300 m in this area (Grimod et al., 1991). In the Tuscan-Emilian Apennine ridge, alpine marmots range between 1800 and 1950 m, but the forest limit was lowered to 1600–

1700 m there due to livestock rearing practices (Sala et al., 1992). In the Spanish Pyrenees the forest limit is higher in the mid-eastern part than in the mid-western part (Vigo and Ninot, 1987) and, correspondingly, the lower vertical limit of marmots is higher in Catalonian than in the Aragonese Pyrenees (Herrero et al., 1992).

At present in the Pyrenees, forest limit ranges on average between 1600 to 1800 m, with wide variations depending on human exploitation of the landscape. Above this altitude interval, the area begins to be significantly utilized by the marmots (Table 2).

UPPER ALTITUDINAL LIMIT

The upper edge of the distribution area is determined by food availability and the presence of a suitable substratum for burrowing (Bibikov, 1968; Huber, 1978). In the Pyrenees colony density decreases above 1800 m (Table 2) and there is a positive correlation between the number of colonies and the duration of the Available Food Period over this limit ($r^2 = 0.961$; $p = 0.003$). Marmots probably occupy territories above 2600 m only during the summer, as plant availability is too brief at this height (Table 2). The alpine belt ends at 2800 to 2900 m in the Pyrenees, and above it vegetation is very scarce and sparse (Vigo and Ninot, 1987), reducing substantially the feeding possibilities for marmots, although in certain favorable areas, as in Maladeta Massif, marmots can settle at these altitudes (Herrero et al., 1992).

Available food must assure minimum vital activities for marmots, i.e., reproduction, breeding, and fat storage for the winter, requiring a minimum of 5.5 mo activity (Zelenka, 1965). The maximum altitude in which Available Food Period reaches this value is in the interval of 2200 to 2400 m (Table 2). When the Available Food Period is shorter, marmots probably can occupy high altitudes only for a short period ("summer burrows"; Huber, 1978) and would need to migrate to other lower feeding areas to complete their vital activities. Further research would be advisable in order to ascertain the existence of these seasonal altitudinal migrations of alpine marmots as well as the proportion of the population that takes part in them.

Conclusion

The altitudinal distribution of the alpine marmot in the Pyrenees is similar to that in the Alps and seems to reflect its preference for open habitats, with steppe or alpine tundra vegetation, which is characteristic of almost all the genus (Bibikov, 1968; Barash, 1989). In mountains, dense forest and thermoregulatory constraints determine the marmot's lower spatial limit, whereas the brief Available Food Period and the impossibility of completing its minimum maintenance cycle seem to mark its upper spatial limit. This restriction normally leads marmots to settle between specific altitudinal limits (preferably between 1800 and 2400 m in the Alps and Pyrenees). As the natural forest limit seems to be higher in the Pyrenees (2400 m) than in the Alps (2100 m), due to its southern latitudinal situation (Ozenda and Borel, 1991), at present and in natural conditions (without human landscape modifications), marmots would have had few possibilities of colonizing the Pyrenean range extensively. The success of the introduction of the alpine marmot in the Pyrenees is probably due to the existence of a wide subalpine open area artificially created for pastoral use. This belt furnishes food and suitable habitat during sufficient time throughout the year to allow the species to complete their life-cycle. This phenomenon probably accounts for the colonizing success in other mountains without a large alpine belt, like the Apennines. When the altitude is too low, like in Jura Mountains, colonization is fairly difficult. Those findings should be taken into account in future introductions and reintroductions.

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