ECOLOGICAL SIGNIFICANCE OF A SPECIES-AREA RELATIONSHIP IN HELMINTH COMMUNITIES OF THE ALPINE CHAMOIS
(RUPICAPRA R. RUPICAPRA LINNÉ, 1758)

Thierry DURAND*

RÉSUMÉ


SUMMARY

From 1994 to 1996, an actual and retrospective inquest on pastoral practices and Alpine Chamois (Rupicapra r. rupicapra) home ranges was performed in Vanoise National Park, Écrins National Park and in the Bauges Game Reserve (France), to investigate the patterns of inter specific cohabitation between livestock and wild ungulates. Statistical treatments performed on a sanitary data base, recording the results of parasitological examinations performed on 307 Chamois, permitted an estimation of parasite diversity in ten groups of chamois populations. Looking for the influence of environmental factors on diversity indices, we revealed significant species-area relationships. Whereas no correlation was found between diversity indices and the total surface of Chamois home range, H’ (Shannon & Weaver) and N_1 (Hill) were significantly correlated with the surface of spring home ranges of Chamois and with the surface grazed by livestock within spring preferential ranges. Moreover, a significant correlation between species richness (S) and the surface grazed by livestock in chamois

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summer preferential home ranges is noted. These results suggest an influence of cattle breeding on diversity fluctuations in helminth communities of Rupicaprinae.

INTRODUCTION

Whereas, in the past, studies on wildlife mainly focused on the assumed role of wild animals as reservoirs of infectious and parasitic diseases for livestock (Thorton et al., 1973; Joubert, 1977; Allonby, 1980), recent reports insist on the consequences of livestock breeding on the sanitary status of wild ungulates (Genchi et al., 1984 a-b; Rossi et al., 1985; Gauthier et al., 1991; Durand & Gauthier, 1996; Durand 1997a).

Surprisingly, few authors really take into account overall environmental factors such as pastoral pressure, climate and interspecific spatial competition, in the context of transversal actual and retrospective epidemiologic studies.

The aim of this paper is to describe, on a regional scale, interspecific spatial behaviour of mountain wild ungulates and transhumant cattle, in French alpine mountains, holding ten groups of chamois populations, which may form several metapopulations.

We try to understand the assumed influence of cattle breeding on the sanitary status of wildlife, focusing on the chamois helminth fauna. Considering the insularity of mountain ecosystems (Durand & Gauthier, 1996), we look for species-area relationships in chamois helminth communities, and for the sanitary consequences of cattle intrusions within the preferential home ranges of Rupicaprinae.

MATERIALS AND METHODS

CARTOGRAPHIC ANALYSIS

Chamois home range

An exhaustive cartography of Chamois home ranges was performed, according to seasonal patterns, in both Vanoise National Park (V.N.P.) and the Lautaret district of Écrins National Park (É.N.P.), as well as in the Bauges Game Reserve (B.G.R.).

As V.N.P. was supposed to be inhabited by distinct chamois populations, functioning as metapopulation(s), a complementary investigation¹ was necessary to determine the geographic limits and surface of corresponding home ranges of the eight groups of populations identified there.

Then, a total of ten districts, characterized by their contrasted biogeography (Table I) and their respective population dynamics (Durand, 1997a), were submitted to the same research protocols.

¹ Pastoral activities and wildlife, I: research program of the Vanoise National Park.
TABLE I

Some basic biogeographic data on population home ranges.

<table>
<thead>
<tr>
<th>Weather station</th>
<th>Altitude of the weather station</th>
<th>Reference period (years)</th>
<th>Snow-cover duration (in days)</th>
<th>Precipitation (mm)</th>
<th>Temperature below 0 °C (number of days)</th>
<th>Corresponding populations</th>
<th>Altitude gradient of the unit</th>
<th>Biogeographic area</th>
</tr>
</thead>
<tbody>
<tr>
<td>B.G.R.</td>
<td>Ecole en Bauges</td>
<td>732 m</td>
<td>1977-1995</td>
<td>65</td>
<td>1,500</td>
<td>131</td>
<td>B.G.R.-9</td>
<td>800 m to 2,217 m</td>
</tr>
<tr>
<td></td>
<td>La Grave Le Monêtier (1)</td>
<td>2,000 m</td>
<td>1960-1995</td>
<td>87</td>
<td>900</td>
<td>175</td>
<td>E.N.P.-10</td>
<td>1,400 m to 3,893 m</td>
</tr>
<tr>
<td></td>
<td>Pralongnan la Vanoise</td>
<td>1,420 m</td>
<td>1977-1995</td>
<td>143</td>
<td>1,190</td>
<td>154</td>
<td>V.N.P.-8</td>
<td>900 m to 3,850 m</td>
</tr>
<tr>
<td></td>
<td>Termignon la Vanoise</td>
<td>1,280 m</td>
<td>1977-1995</td>
<td>82</td>
<td>740</td>
<td>157</td>
<td>V.N.P.-2/4</td>
<td>1,400 m to 3,890 m</td>
</tr>
<tr>
<td></td>
<td>Bessans</td>
<td>1,715 m</td>
<td>1984-1995</td>
<td>166</td>
<td>930</td>
<td>200</td>
<td>V.N.P.-2/3 (3)</td>
<td>1,300 m to 3,750 m</td>
</tr>
<tr>
<td>V. N. P.</td>
<td>Tignes Val d’Isère</td>
<td>1,840 m</td>
<td>1984-1995</td>
<td>140</td>
<td>1,200</td>
<td>194</td>
<td>V.N.P.-7</td>
<td>1,400 m to 3,747 m</td>
</tr>
<tr>
<td></td>
<td>Aussois</td>
<td>1,490 m</td>
<td>1985-1995</td>
<td>79</td>
<td>730</td>
<td>128</td>
<td>V.N.P.-4</td>
<td>900 m to 3,850 m</td>
</tr>
<tr>
<td></td>
<td>St-Martin de B®site</td>
<td>1,500 m</td>
<td>1977-1995</td>
<td>70</td>
<td>970</td>
<td>143</td>
<td>V.N.P.-5</td>
<td>640 m to 3,470 m</td>
</tr>
<tr>
<td></td>
<td>Peisey-Nancroix</td>
<td>1,350 m</td>
<td>1977-1995</td>
<td>102</td>
<td>1,040</td>
<td>207</td>
<td>V.N.P.-6</td>
<td>630 m to 3,779</td>
</tr>
<tr>
<td>Intermediate values, between the data recorded for V.N.P.-7 and V.N.P.-2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>V.N.P.-1</td>
<td>1,800 m to 3,850 m</td>
</tr>
</tbody>
</table>

(1): Mean values between Le Monêtier and La Grave weather stations; (2): population unit; (3): for the Mont-Cenis massif, the Val-Cenis weather station gives more precise values.

Cartography of pastoral units

From 1994 to 1996, through an actual and retrospective pastoral inquest, livestock breeding activities were described according to administrative data, controlled and validated by park staffs and O.N.C. agents. We defined pastoral

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units as delimited pastures, holding domestic ruminants at a given time and likely to be grazed by several successive livestocks during the transhumance period.

For each pastoral unit (342 in V.N.P., 26 in the B.G.R., 45 in the Lautaret district of É.N.P.), limits and descriptive variables were recorded. The main factors which were taken into account were the pastoral pressure (number of animals × duration of the grazing period in days), the duration of the grazing period, cattle management modalities (presence/absence of a shepherd, of sheepdogs, of paddocks) and the cohabitation modalities between livestock and wildlife (permanent overlapping of home ranges with frequent contacts, daily or seasonal alternance on pastures, long distance cohabitation).

Computer cartography was then performed thanks to a Geographic Information System (G.I.S.) using "Arc-Info" software and estimations of grazing surfaces and descriptive parameters including grazing pastures and chamois home range overlapping were thereby available.

**WILDLIFE SURVEYS**

During the fifteen past years, 307 samples (V.N.P.: unit 1 = 16 samples (s.), unit 2 = 46 s., unit 3 = 10 s., unit 4 = 29 s., unit 5 = 41 s., unit 6 = 17 s., unit 7 = 22 s., unit 8 = 13 s.; B.G.R.: 88 s.; É.N.P.: 25 s.) were collected thanks to a sanitary surveillance network coordinated by the Savoie Veterinary Laboratory. Samples were obtained on game during hunting periods, and on dying animals found in the context of mortality inquests performed in national parks and in the B.G.R. Few of them came from the SAGIR network, coordinated by O.N.C. The sampling according to age and sex was almost equilibrated, except in É.N.P., where the unbalanced distribution was related to particular sampling modalities (almost entirely during the hunting period).

At hunting, just after killing, the digestive tracts were collected, put into waterproof bags and forwarded to the Savoie Veterinary Laboratory (Chambéry, France), sometimes after an intermediate deep-freezer storage made by park staffs or hunters.

**PARASITOLOGICAL INVESTIGATIONS**

*Strongyle worm counts*

After defreezing at the laboratory, digestive tracts were divided in abomasum, large and small intestines and their mucosae washed under water pressure. Then, their respective washings and digestive contents were filtrated on adequate sieves (20 µm, 40 µm and 100 µm respectively). Worms were extracted, counted and identified according to Euzéby (1961, 1963, 1966), Biocca *et al.* (1976, 1982), Rossi (1983), Demolin (1984), Durette-Desset (1989) and Khalil *et al.* (1994). A close collaboration with the Veterinary School of Lyon (Pr Gevrey) and the Veterinary University of Turin (Pr Rossi), was vouching for the accuracy of parasite identification.

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1 “Observatoire en écopathologie de la faune sauvage de montagne”. Coordination: Dr Gauthier (LDAV of Savoie, France) and Pr Rossi (Univ. di Torino, Dipartimento di produzioni animali, epidemiologia ed ecologia).
**Diversity indices**

For each Chamois group of population, diversity indices, chosen according to Baev & Penev (1993), were calculated. We selected species richness (S), Shannon & Weaver (1949) index (H'), mainly influenced by common species and Hill diversity index (Hill, 1973; Daget, 1980), which better takes into account rare species than the Shannon & Weaver index does. Correlations between diversity indices and environmental factors were tested, using power function (Arrhenius, 1921) and exponential function (Gleason, 1922), as recommended by Connor & McCoy (1979).

**RESULTS**

**PASTORAL AND WILDLIFE INVESTIGATIONS**

**Chamois home range**

Table II summarizes the results of our field investigations on Chamois home range in Vanoise National Park. Besides the total surface of seasonal home ranges, we focussed particularly on preferential home ranges (refuges and places where wild ungulates spend most of their time), and overlapping with pastoral units. As an illustration, figure 1 gives the distribution of the preferential and occasional ranges of the chamois populations in Vanoise National Park and figure 2 gives the limits of the eight groups of populations identified there. Cohabitation modalities were previously described by Durand & Gauthier (1996).

**Pastoral data**

In Vanoise and Écrins National Parks, the entire available lawn surfaces are grazed by livestock, which results in a considerable overlapping between wildlife refuges and grazing pastures (Fig. 3). In B.G.R., because of a previous management policy, few domestic cattle were authorized to feed inside the reserve. Nevertheless, chamois home range spreads over the administrative limits and close cohabitation between Rupicapra, goats, milk and beef-cattle is likely to occur in the surroundings.

Taking into account the patterns of interspecific cohabitation and duration of the grazing period, we give an estimation of the pastoral pressure within the respective home ranges of the ten groups of populations (Table III).

The whole pastoral pressure (U.G.B. \( \times D \) = duration of the grazing period) calculated in table III, approximates the combined impacts of cows, sheep and goats.

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1 These data were validated by park staffs and also by further investigations on interspecific spatial behaviour of chamois and domestic ungulates, performed on five restricted areas, in Vanoise National Park (research program "pastoral activities and wildlife, II").

2 U.G.B.: French unit corresponding to a 500 kg cow-equivalent ruminant. It permits a rough estimate of the pastoral pressure, which results from simultaneous feeding of cows, sheep and goats.
TABLE II

Surfaces (in km$^2$) of the respective home ranges of the eight groups of populations of Vanoise National Park.

<table>
<thead>
<tr>
<th>Population unit</th>
<th>Total surface (km$^2$)</th>
<th>Surface of the spring preferential home range</th>
<th>Surface grazed by livestock in spring preferential home range</th>
<th>Surface of the summer preferential home range</th>
<th>Surface grazed by livestock in summer preferential home range</th>
</tr>
</thead>
<tbody>
<tr>
<td>VNP-1</td>
<td>57.47</td>
<td>3.74</td>
<td>0.68</td>
<td>20.03</td>
<td>5.74</td>
</tr>
<tr>
<td>VNP-2</td>
<td>63.46</td>
<td>7.53</td>
<td>3.46</td>
<td>24.97</td>
<td>10.63</td>
</tr>
<tr>
<td>VNP-3</td>
<td>60.38</td>
<td>23.94</td>
<td>5.45</td>
<td>4.55</td>
<td>1.77</td>
</tr>
<tr>
<td>VNP-4</td>
<td>80.18</td>
<td>17.33</td>
<td>8.07</td>
<td>20.95</td>
<td>8.60</td>
</tr>
<tr>
<td>VNP-5</td>
<td>78.17</td>
<td>2.51</td>
<td>0.03</td>
<td>11.11</td>
<td>3.29</td>
</tr>
<tr>
<td>VNP-6</td>
<td>116.52</td>
<td>9.8</td>
<td>2.81</td>
<td>27.93</td>
<td>6.57</td>
</tr>
<tr>
<td>VNP-7</td>
<td>29.93</td>
<td>13.19</td>
<td>5.61</td>
<td>17.55</td>
<td>3.87</td>
</tr>
<tr>
<td>VNP-8</td>
<td>26.26</td>
<td>4.84</td>
<td>0.71</td>
<td>9.99</td>
<td>5.06</td>
</tr>
</tbody>
</table>

Figure 1. — Distribution of preferential (dark grey) and occasionnal (light grey) home ranges in Vanoise National Park.
North

Figure 2. — Limits of the eight groups of Chamois populations in Vanoise National Park.

TABLE III

Pastoral pressure in the respective home ranges of the ten groups of populations.

<table>
<thead>
<tr>
<th>Area</th>
<th>D × MC</th>
<th>D × BC</th>
<th>D × SH</th>
<th>D × GO</th>
<th>D × U.G.B.</th>
</tr>
</thead>
<tbody>
<tr>
<td>VNP-1</td>
<td>11 596</td>
<td>23 209</td>
<td>299 513</td>
<td>0</td>
<td>7.97 × 10^4</td>
</tr>
<tr>
<td>VNP-2</td>
<td>24 585</td>
<td>17 093</td>
<td>824 050</td>
<td>57 619</td>
<td>17.1 × 10^4</td>
</tr>
<tr>
<td>VNP-3</td>
<td>36 538</td>
<td>40 175</td>
<td>385 168</td>
<td>9 426</td>
<td>13.54 × 10^4</td>
</tr>
<tr>
<td>VNP-4</td>
<td>20 443</td>
<td>13 966</td>
<td>820 230</td>
<td>8 905</td>
<td>17.83 × 10^4</td>
</tr>
<tr>
<td>VNP-5</td>
<td>20 158</td>
<td>58 582</td>
<td>17 084</td>
<td>1 382</td>
<td>8.14 × 10^4</td>
</tr>
<tr>
<td>VNP-6</td>
<td>70 819</td>
<td>29 918</td>
<td>755 290</td>
<td>28 906</td>
<td>11.33 × 10^4</td>
</tr>
<tr>
<td>VNP-7</td>
<td>16 540</td>
<td>13 372</td>
<td>303 354</td>
<td>9 855</td>
<td>7.64 × 10^4</td>
</tr>
<tr>
<td>VNP-8</td>
<td>1 991</td>
<td>22 210</td>
<td>9 884</td>
<td>7 872</td>
<td>2.65 × 10^4</td>
</tr>
<tr>
<td>BGR-9</td>
<td>44 672</td>
<td>76 289</td>
<td>0</td>
<td>66 490</td>
<td>12.76 × 10^4</td>
</tr>
<tr>
<td>ENP-10</td>
<td>710</td>
<td>53 170</td>
<td>778 960</td>
<td>18 840</td>
<td>11.68 × 10^4</td>
</tr>
</tbody>
</table>

(D × MC = duration (number of days) × number of milk cows, D × BC = duration × number of beef cattle, D × SH = duration × number of sheep, D × GO = duration × number of goats, D × U.G.B. = duration × number of U.G.B., with U.G.B. being a unit corresponding to a 500 kg cow-equivalent ruminant).
From 1978 to 1996, the pastoral pressure fluctuated moderately in our study areas (under ten per cent), which explains that, for each population home range, a mean value (evaluation taking into account the duration of the sampling period) was considered as a good estimate.

**DIVERSITY AND EVENESS INDICES**

Table IV gives the values of the selected diversity indices. These were related to environmental factors. A mathematical relationship between environmental factors and $H'$ leads to believe that they might cause real impacts on the structure of helminth communities (particularly affecting common species). On the other side, the increase of species richness, correlated with a descriptive variable, suggests that the latter might influence parasite species recruitment. We further argue about this.
TABLE IV

Diversity indices: values corresponding to the ten tested areas.

<table>
<thead>
<tr>
<th>Population unit</th>
<th>$H'$</th>
<th>$N_1 = \exp(H')$</th>
<th>$S$</th>
</tr>
</thead>
<tbody>
<tr>
<td>V.N.P.-1</td>
<td>1.46</td>
<td>4.31</td>
<td>23</td>
</tr>
<tr>
<td>V.N.P.-2</td>
<td>1.88</td>
<td>6.58</td>
<td>32</td>
</tr>
<tr>
<td>V.N.P.-3</td>
<td>2.25</td>
<td>9.46</td>
<td>20</td>
</tr>
<tr>
<td>V.N.P.-4</td>
<td>1.88</td>
<td>6.55</td>
<td>31</td>
</tr>
<tr>
<td>V.N.P.-5</td>
<td>1.13</td>
<td>3.10</td>
<td>24</td>
</tr>
<tr>
<td>V.N.P.-6</td>
<td>1.67</td>
<td>5.29</td>
<td>22</td>
</tr>
<tr>
<td>V.N.P.-7</td>
<td>1.39</td>
<td>4.01</td>
<td>26</td>
</tr>
<tr>
<td>V.N.P.-8</td>
<td>1.48</td>
<td>4.41</td>
<td>16</td>
</tr>
<tr>
<td>B.G.R.-9</td>
<td>1.87</td>
<td>6.46</td>
<td>36</td>
</tr>
<tr>
<td>E.N.P.-10</td>
<td>1.50</td>
<td>4.49</td>
<td>22</td>
</tr>
</tbody>
</table>

$H'$ = Shannon & Weaver index; $N_1$ = Hill index; $S$ = species richness.

PARASITE DIVERSITY AND ENVIRONMENTAL RESTRAINTS

Parasite diversity and pastoral pressure

We found a significant linear relationship between the whole pastoral pressure and parasite diversity indices:

$S = 8.73 \times 10^{-5} (D \times U.G.B.) + 15.5 \quad r^2 = 0.44$

$H' = 4.75 \times 10^{-6} (D \times U.G.B.) + 1.13 \quad r^2 = 0.46$

$N_1 = 2.56 \times 10^{-5} (D \times U.G.B.) + 2.63 \quad r^2 = 0.42$

As spatial interactions with livestock are thought to influence the structure of helminth communities, we looked for species-area relationships.

Species-area relationship

First of all, no correlation (either linear, or power or exponential function) was found either between diversity indices and the surface of summer and winter Chamois home ranges (preferential and occasional), or with the total surface of Chamois home range ($r^2$ from 0.0001 to 0.177, $p > 0.05$).

Table V summarizes the main relationships between parasite diversity and home range surfaces on one side, overlapping surfaces (between pastures grazed by livestock and chamois home range) on the other side.

It clearly emphasizes a mathematical relationship between parasite diversity and spring home ranges. $H'$ and $N_1$ are significantly correlated with the total surface of the Chamois spring home range. $H'$ is correlated with the area grazed by livestock in the Chamois preferential spring home range.

On another side, species diversity is significantly correlated with the surface grazed by livestock in the chamois' preferential summer home range.
TABLE V

*Significant regression equations of species-area relationships.*

<table>
<thead>
<tr>
<th>Surface (A)</th>
<th>Regression equations</th>
<th>$r^2$</th>
<th>F-test proba. %</th>
</tr>
</thead>
<tbody>
<tr>
<td>Surface grazed by livestock in the Chamois preferential spring home range</td>
<td>$H' = 0.1303 \ln (A) + 1.5911$</td>
<td>0.5313</td>
<td>3.95</td>
</tr>
<tr>
<td><strong>VA NOISE</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total surface of chamois spring home range</td>
<td>$H' = 0.038 (A) + 1.249$</td>
<td>0.6396</td>
<td>1.72</td>
</tr>
<tr>
<td></td>
<td>$H' = 0.3583 \ln (A) + 0.8934$</td>
<td>0.6306</td>
<td>1.85</td>
</tr>
<tr>
<td></td>
<td>$N_1 = 0.2250 (A) + 3.1329$</td>
<td>0.6826</td>
<td>1.16</td>
</tr>
<tr>
<td></td>
<td>$N_1 = 2.006 \ln (A) + 1.2800$</td>
<td>0.5978</td>
<td>2.42</td>
</tr>
<tr>
<td>Surface grazed by livestock in the chamois preferential summer home range</td>
<td>$S = 1.2851 (A) + 16.9362$</td>
<td>0.4700</td>
<td>4.59</td>
</tr>
<tr>
<td></td>
<td>$\ln (S) = 0.0498 (A) + 2.8830$</td>
<td>0.4020</td>
<td>8.96</td>
</tr>
<tr>
<td><strong>ALPS</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total surface of chamois spring home range</td>
<td>$H' = 0.0285 (A) + 1.3272$</td>
<td>0.4037</td>
<td>4.70</td>
</tr>
<tr>
<td></td>
<td>$H' = 0.2892 \ln (A) + 1.0104$</td>
<td>0.4494</td>
<td>3.29</td>
</tr>
<tr>
<td></td>
<td>$N_1 = 0.1668 (A) + 3.5756$</td>
<td>0.4247</td>
<td>4.00</td>
</tr>
<tr>
<td></td>
<td>$N_1 = 0.5836 + 1.9705$</td>
<td>0.4116</td>
<td>4.42</td>
</tr>
<tr>
<td>Surface grazed by livestock in the chamois preferential spring home range</td>
<td>$H' = 0.104 \ln (A) + 1.5884$</td>
<td>0.3879</td>
<td>6.58</td>
</tr>
</tbody>
</table>

(**: B.G.R. + É.N.P. + V.N.P. = 10 groups of populations).**

DISCUSSION

ABOUT SPECIES-AREA RELATIONSHIPS, WIDESPREAD RULES IN ECOLOGICAL COMMUNITIES

Besides the well-known relationship between parasite diversity and latitude (Fischer, 1960; Pianka, 1966), the increased number of species of a taxonomic group related to home range surface has been studied for a long time (Preston, 1960, 1962; Williams, 1964; Mc Arthur & Wilson, 1967; Simberloff, 1972). This phenomenon was formerly underlined in phytocoenosism (e.g. Arrhenius, 1921) as well as in zoochoeoensis (e.g. Judas, 1988, Lumbricidae; Newmark, 1985, terrestrial mammals; Eadie et al., 1986, river and lake fishes; Nangasawa, 1987, butterflies; Bevanger, 1987, birds).

In our study, exponential and linear functions proved to be good fitting models for characterizing species-area relationships.

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1 According to Cabaret (oral comm.), this relationship does not work for Nematodes.
HYPOTHESIS OF SPECIES-AREA RELATIONSHIPS

Within the context of species-area relationships, three hypotheses may help to explain a positive correlation:

i) a passive sampling hypothesis,

ii) an increase of habitat heterogeneity with home range surface,

iii) a balance between extinction and immigration processes, which results in an increase of species richness and abundance with surface.

About the passive sampling hypothesis

This one is not considered as a relevant hypothesis. First, we point out that no mathematical relationship was found between diversity indices and either the total surface of chamois home ranges, or the summer home ranges (which are the largest chamois home ranges). Secondly, considering, for each group of populations, the [preferential range/occasional range] ratio, for each biological season, great differences are noted, which brings out important differences in home range occupancy. Further, a recent study, performed in V.N.P. (unpublished data) pointed out heterogeneous spatial and feeding behaviour of chamois, according to season, day-time, presence of cattle within the seasonal home range and chamois sex and age.

As a consequence, we can assume that passive sampling, itself, does not explain the observed mathematical relationship between species and area.

Habitat diversity in home ranges

According to Williams (1964), the surface of home ranges is correlated with the diversity of microhabitats.

The great biogeographic contrasts which characterize French Alps (Ozenda, 1985), make difficult an exhaustive evaluation of habitat diversity in study areas. Table I gives a succinct outline of biogeographic characteristics of Vanoise, Écrins and Bauges mountains, which hold a great variety of suitable habitats for wild and domestic ruminants. Whereas northern Prealps are much rainy and submitted to oceanic influences, the climate of central Alps is a continental-like one.

Concerning bedrock, soil and plant diversity, an important heterogeneity is noted in Vanoise National Park (Gensac, 1972, 1974, 1979). As well, the eastern side of the B.G.R. holds various plants and soils, on an heterogenous dominant chalky bedrock (Manneville, 1983). The Lautaret district of Écrins National Park, which is in a transition area between northern and southern Alps and holds complex soil and rock structures, is also characterized by a very great plant diversity (Dubost & Jouglé, 1981; Chalaux, 1982, 1983), submitted to the joint action of continental and mediterranean meteorological influences.

As availability of habitats for free living stages of helminths depends on plant distribution, on microclimatic parameters (precipitation, frost-defrost alternance, sun exposure, wind exposure...), and since the regional scale of our study results in a lack of local-scale data, we could not make a reliable estimate of micro-habitat diversity in the ten selected group home ranges.

Immigration and extinction processes: the island theory

Thus, only species able to reach high density levels will be able to colonize a wide range. If low-sized populations are associated with high extinction probabilities, on the contrary, large populations, which either inhabit larger home ranges or show higher densities, are unlikely to go extinct.

These three mechanisms are probably acting altogether, defining a complex species-area relationship, characterized by an increasing mathematical function.

THE PRESUMED INFLUENCE OF SAMPLING

Referring to Toma et al. (1996), we looked for the influence of sampling modalities on the result of our investigations.

In wildlife investigations, sampling by lot is almost impossible. Most of the time, samples obtained at hunting, as well as those collected from mortality inquests are not representative of the corresponding populations. In our study, by chance, the distribution of samples according to age and sex of the chamois, corresponded to those expected in the population, except in the first sample of the Lautaret district of É.N.P., collected from 1990 to 1992. A complementary sampling campaign was necessary to obtain a sample distribution which parameters almost correspond to the population ones. Further, looking for the influence of sample sizes, and for the prevalence and abundance of the various parasite species, we conclude that we found a good approximate of Shannon & Weaver and Hill indices.

On the opposite, taking into account the size of the respective chamois populations, because of the narrow-sized samples of V.N.P.-1, V.N.P.-3, V.N.P.-6 and V.N.P.-8, the probability to detect parasite species which prevalence is under 10 %, is inferior to 95 %. Nevertheless, the mathematical relationship between species richness and area, is worth taking into account, since it rouses pertinent and interesting hypotheses.

ECOLOGICAL SIGNIFICANCE OF OUR FINDINGS

Our results suggest a possible influence of the structure of home ranges on parasite species diversity in Chamois. They agree with the hypothesis that spring may be the most risky season for parasite infection in chamois populations.

Field studies performed in V.N.P.¹ revealed an heterogeneous feeding behaviour of Chamois, according to the structure of habitat. When intense feeding is noted in preferential districts, feeding intensity decreases considerably as Rupicaprinae feed in occasional ranges, which are mainly covered during daily and seasonal migrations (between refuges).

The size of spring preferential districts might influence core species recruitment (see good correlations with Shannon’s index), the species-area relationship involving species richness means that the recruitment of Chamois rare parasite species might be mainly caused by cattle grazing on alpine pastures included in the summer Chamois preferential home range. This suggests a negative sanitary impact of livestock grazing within the preferential home ranges of Chamois populations.

¹ Pastoral activities and wildlife, II, research program of the Vanoise National Park.
Some authors previously noted some negative impacts of livestock breeding on the sanitary status of wild ungulates in alpine mountains (Genchi et al., 1984a, b; Müller, 1984; Rossi et al., 1985; Gauthier et al., 1991, Pinget & Gibert, 1993; Gauthier & Duran, 1996). Further, some parasite species (Dictyocaulus filaria, Cystocaulus ocreatus Trichostrongylus colubriformis, Haemonchus contortus, Moniezia expansa, Dictyocaulus viviparus, Ostertagia ostertagi, Capillaria bovis, Cooperia punctata, Oesophagostomum venulosum, Moniezia benedeni, Trichostrongylus axei) found in chamois digestive tracts, are usually considered as adapted to domestic hosts (Euzeby, 1961, 1963, 1966). Their occasional presence in wildlife suggests that the intrusion of domestic ungulates within Chamois home ranges sometimes results in wildlife infection by sheep, goat and cow parasites.

Because of a great anthropic pressure on French landscape (roads, tourism, town expansion...) protected areas are considered as “insular-like” ecosystems, most of them holding great numbers of transhumant domestic ungulates.

Our hypotheses (which should be confirmed experimentally) and previous research lead to worry about pastoral practices, especially free roaming of flocks, which often results in great disturbance of wild ungulates, inter-specific transmission of pathogens and frequent penetrations of uncontrolled sheep in spring and summer preferential home ranges of Rupicaprinae.

As parasite species richness is a bio-indicator of interspecific spatial competition, its fluctuations could be taken into account (besides the presence of helminth species highly specific of domestic ungulates) to manage wildlife health, and to reveal situations at risk for interspecific flow of contagious or abortive diseases such as brucellosis (Gauthier & Durand, 1996), Queensland fever and tuberculosis.

**CONCLUSION**

Besides pastoral pressure which seems to influence species diversity and richness, the occurrence of species-area relationships suggests the role of spring home ranges as reservoirs of parasites, since infected lawns are mainly involved in the fluctuations of diversity indices characterizing Chamois helminth fauna. As the presence (in chamois digestive tracts) of parasites mainly adapted to domestic ungulates argues for interspecific transmission of pathogens, we can assume that domestic cattle intrusion within Chamois preferential home ranges probably results in an increased recruitment of parasite species in wildlife.

Recent studies performed in V.N.P. (Durand, 1997b) make evidence of the influence of cattle management on interspecific cohabitation modalities, and suggest a global management policy for domestic and wild ungulates, minimizing inter-specific contacts and preventing from roaming of flocks within chamois preferential home ranges. Such statements plead for a necessary increase of sanitary care on wildlife, so as the actual agricultural policy often results in free-roaming of sheep and cattle flocks in vulnerable insular ecosystems.

**REFERENCES**


