The collection includes 16 articles, 5 of them concern Marmota bobac, the
two - M. marmota, M. flaviventris, M. menzbieri, M. baibacina and M.
camtschatca. The articles discuss different aspects of marmot ecology, impact of
man activity on the populations state in different parts of the species areas,
conservation of marmots and their habitats. Articles devoted to the problems of
marmots behavior and morphology occupy comparatively small volume, and there
is almost no discussion of the questions on marmots systematics, phylogeny,
biosystematic and medical importance.

The subject and geography range of present collection have undoubtedly been
affected by the modern political situation: breach of broad interregional
connections in the former USSR created the absence of traditional works on the
participation of marmots in natural plague centers as well as articles from
Kazakhstan and Middle Asia - the regions inhabited by 4 marmot species, with
maximum biological diversity of Marmota genus representatives, containing
numerous and extended zones of interspecies contacts, variety of habitats.

For the last years center of activity of marmots investigators has shifted to
Europe, as a result main attention is being concentrated now upon the two species
bobac and Alpine marmots. In the nearest decade regional localization of research
activity is likely to lead to predominant intensification and improvement of
methods of stationary investigation of marmots population structure and social
organization. Nevertheless, further activation of international co-operation in this
field, that has yet began may stimulate development of broad comparative
investigations.

The collection compilers hope that international society will aim not only at
preservation of these wonderful animals, but at restoration, consolidation and
expansion of "interpopulational" connections between scientists investigating
marmots as well, and publication of the present collection is also intended to
contribute this very goal.

We highly appreciate publishing house ABF for the assistance in preparation
of the collection.

The Bureau of Marmots Investigation Committee of the USSR within RAS
Survivorship of young and adult females was markedly reduced over the winter of 1991-92. In addition, reproduction by females in the summer of 1992 differed from that of the three previous summers. This report describes the patterns of mortality and reproduction and explores possible causes of the patterns.

METHODS

Each year each marmot in our study area is trapped and marked. When a marmot is trapped for the first time, an individually numbered tag is inserted in each ear. The animal also receives a unique dye-mark of blotches or stripes for individual recognition during behavioral observations. Upon each capture, the marmot is weighed and reproductive condition and sex are noted. Young, yearlings, and 2-year-old adults can be aged on the basis of body mass. Thus, the age of most individuals is known because most individuals are first-trapped as either young or yearlings. Frequent trapping throughout the active season provides a series of body-mass determinations from which growth curves can be calculated.

The trapping data were used to determine reproductive success for adult females. The study area was divided into two regions: Lower Valley and Upper Valley because the active season of the animals in the Lower Valley is advanced about 15 days in comparison to the active season of the animals in the Upper Valley (Van Vuren, Armitage, 1991).

The weight records were used to determine growth rates by regression analysis (Sokal, Rohlf, 1981) for the following: young, reproductive females, and non-reproductive females. The regression statements were used to predict body mass at the end of the period of mass-gain for the summer of 1991 and the three previous summers. The increase in body mass terminates at different times for different age-sex groups and varies between early August and early September, which is about the latest time that any gain in mass can be expected for this population (Armitage, unpublished data).

Body-fat was determined for 14 young in mid August in 1991 in the Upper Valley by calculating the body fat from the measure of total body water by D20 dilution injected 3 hours before a blood sample was collected for measurement of D20 concentration (Nagy, Costa, 1980).
Weather data were obtained from records kept by the Rocky Mountain Biological Laboratory or from U.S. Weather Bureau records for the town of Crested Butte, Colorado, about 13 km from the study area.

RESULTS

Reproduction

The percentage of adult females that were reproductive varied among years (Table 1).

Table 1.

The percentage of adult females that were reproductive

<table>
<thead>
<tr>
<th>Year</th>
<th>Lower Valley</th>
<th>Upper Valley</th>
</tr>
</thead>
<tbody>
<tr>
<td>1989</td>
<td>0.40</td>
<td>0.72</td>
</tr>
<tr>
<td>1990</td>
<td>0.31</td>
<td>0.63</td>
</tr>
<tr>
<td>1991</td>
<td>0.50</td>
<td>0.60</td>
</tr>
<tr>
<td>1992</td>
<td>0.88</td>
<td>0.23</td>
</tr>
</tbody>
</table>

1) The low values in the Lower Valley in 1989 occurred because there were many 2-year-old females present and they reproduce at a lower rate than females aged 3 or older (Armitage, Downhower, 1974). In 1989, the reproductive rates of females aged 3 or older was 0.78. The low value in the Lower Valley in 1990 occurred because most of the 3-year-old females did not breed, possibly because of reproductive suppression by the older, dominant females (Armitage, 1986). This pattern of non-breeding continued into 1991. In 1992, the rate of reproduction was well above the long-term population mean (0.48, calculated for all adults) in the Lower Valley, but much lower in the Upper Valley (Table 1).

In the Lower Valley, six females that did not reproduce in 1991, did so in 1992 and of the five adult females that reproduced in 1991 and survived to 1992, three weaned litters in 1992. In the Upper Valley, no female that weaned a litter in 1991 did so in 1992. The three females that produced litters were all 3-years-old and reproduced for the first time.

Survivorship

The percentage of adult females surviving over-winter varied little among years or between the Upper Valley and the Lower Valley, except for 1988-89, when survivorship in the Lower Valley was reduced and for 1991-92 when survivorship in the Upper Valley was markedly reduced (Table 2). The average survivorship for the three winters prior to 1991-92 was 0.8 for the Lower Valley, which is not biologically significantly different from the rate of 0.77 for 1991-92. Similarly, the mean rate of adult female survivorship in the Upper Valley for the three winters prior to 1991-92 was 0.78, which is not biologically significantly different from 3-year mean for the Lower Valley. By contrast, survivorship in the Upper Valley for the winter of 1991-92 was only 0.46, which is 58% of the 3-year-mean rate of survivorship (Table 2).

Table 2.

Rate of overwinter survivorship for adult females

<table>
<thead>
<tr>
<th>Winter season</th>
<th>Lower Valley</th>
<th>Upper Valley</th>
</tr>
</thead>
<tbody>
<tr>
<td>1988-89</td>
<td>0.67</td>
<td>0.83</td>
</tr>
<tr>
<td>1989-90</td>
<td>1.00</td>
<td>0.73</td>
</tr>
<tr>
<td>1990-91</td>
<td>0.73</td>
<td>0.77</td>
</tr>
<tr>
<td>1991-92</td>
<td>0.77</td>
<td>0.46</td>
</tr>
</tbody>
</table>

Survivorship of young may be measured as reproductive success (RS): 

\[ RS = \frac{\text{Number of Young}}{\text{Number of Yearlings}} \]

That is, the number of young weaned in one year is divided by the number of yearlings captured the next year. RS is recorded for the year in which the yearlings were captured. RS varied among years (Table 3). RS was low throughout the study area in 1989, and was above average (long term average is 0.46) in 1990, 1991, and in the Lower Valley in 1992. The major difference between the Lower and Upper Valley occurred in 1992 when RS in the Upper Valley was one-third of that in the Lower Valley.
Table 3.
Reproductive success measured as the fraction of young that were recovered as yearlings

<table>
<thead>
<tr>
<th>Year</th>
<th>Lower Valley</th>
<th>Upper Valley</th>
</tr>
</thead>
<tbody>
<tr>
<td>1989</td>
<td>0.28</td>
<td>0.37</td>
</tr>
<tr>
<td>1990</td>
<td>0.67</td>
<td>0.78</td>
</tr>
<tr>
<td>1991</td>
<td>0.83</td>
<td>0.55</td>
</tr>
<tr>
<td>1992</td>
<td>0.75</td>
<td>0.24</td>
</tr>
</tbody>
</table>

Growth: Mass Gain

All animals gained mass during the active season, but the predicted mass at the end of the season varied among years and between the Lower and Upper Valley. Young in the Lower Valley were heavier each year than young in the Upper Valley. The larger size of the Lower Valley young probably occurs because they have a longer growing season, and young in the Lower Valley were weaned two weeks earlier than young in the Upper Valley. This difference in body mass of young is consistent with the report that mass of young on 1 August is negatively related to time of 50% snow cover (Van Vuren, Armitage, 1991). Snow cover remains longer in the Upper Valley, thus reducing the time for growth.

DISCUSSION

The variation in survival and reproduction among years complicates finding reasonable explanations for the reduced survival and reproduction in the Upper Valley in 1992. The low rates of reproduction in the Lower Valley in 1989, 1990, and 1991 can be explained by the large number of 2-year-old and subordinate females in the population. Some of the females that did not reproduce in 1990 had not reproduced for the first time as late as 1993. It is not my intent to attempt to explain all the variation in survival and reproduction, but focus on a pattern evident in the data.

In the Upper Valley, 1992 was characterized by low survivorship of adult females in the winter of 1991-92, the lowest rate of reproduction, and the lowest reproductive success (RS). These results were preceded in the summer of 1991 by the smallest body masses in young and reproductive females, but not in the non-reproductive females except for one small non-reproductive female that did not survive (Table 4). Furthermore, the fat content of Upper Valley young was less than 90% of total body mass in mid-August. Thus, both survivorship in the winter of 1991-92 and reproduction in the summer of 1992 are related to body mass prior to emigration into hibernation.

Table 4.
Predicted body mass (kg) at the end of the period of gain in mass. The number in parentheses (N) is the number of individuals used in the analysis. LV - Lower Valley, UV - Upper Valley.

<table>
<thead>
<tr>
<th>Year</th>
<th>Young</th>
<th>Reproductive females</th>
<th>Non-reproductive females</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>LV</td>
<td>UV</td>
<td>LV</td>
</tr>
<tr>
<td>1988</td>
<td>1.653</td>
<td>1.332</td>
<td>3.211</td>
</tr>
<tr>
<td></td>
<td>(29)</td>
<td>(30)</td>
<td>(5)</td>
</tr>
<tr>
<td></td>
<td>(13)</td>
<td>(37)</td>
<td>(5)</td>
</tr>
<tr>
<td>1990</td>
<td>1.779</td>
<td>1.433</td>
<td>3.219</td>
</tr>
<tr>
<td></td>
<td>(12)</td>
<td>(26)</td>
<td>(4)</td>
</tr>
<tr>
<td></td>
<td>(7)</td>
<td>(37)</td>
<td>(5)</td>
</tr>
</tbody>
</table>

1.741(1)

Two questions remain. What caused the low growth rate in the summer of 1991 and why did marmots in the Upper Valley respond differently from those in the Lower Valley? Rainfall in July and August was 4.5 cm less in 1991 than the average rainfall (13.6 cm) of 1989 and 1990. I suggest that palatability, digestibility, and/or protein content of the vegetation were negatively affected by the low summer rainfall. Any one of these three factors would reduce assimilated energy available for growth and fattening. That precipitation could be the major factor affecting growth, survivorship, and subsequent reproduction is
supported by correlation analyses between precipitation and demographic characters over an 18-year period. Survivorship of young was positively correlated ($r = 0.62$) with mean precipitation, the percentage of females reproducing was positively correlated ($r = 0.65$) with mean precipitation the previous year, and mean colony size was positively correlated ($r = 0.54$) with mean precipitation the previous year (Armitage, Schwartz, unpublished data). Mean colony size in part reflects better survivorship over-winter. Furthermore, all three correlations imply that animals in better condition have higher survivorship and rates of reproduction.

This interpretation was tested by examining the survivorship of young and adults in the winter of 1988-89 following the low rainfall of summer 1988 (94% of the 1991 summer rainfall). As predicted, survivorship of young was low (Table 3) and body mass of young was lower than that of the high survivorship years of 1989-90 and 1990-91 (Table 4).

Why did survivorship and reproduction differ between marmots in the Upper Valley and Lower Valley in the winter of 1991-92 and the summer of 1992? The most plausible explanation is that the animals in the Lower Valley initiated their active season earlier and completed most of their growth before the vegetation was impacted by the low rainfall. In 1991, marmots in the Lower Valley were born young about June 25 whereas marmots in the Upper Valley were born young about 3 weeks later on July 15. Reproductive females do not initiate mass-gain until lactation is completed whereas non-reproductive females initiate mass-gain by early June (Armitage et al., 1976). Non-reproductive females reach hibernation mass by early August (Armitage, unpublished data), thus they would have completed most or all of their mass-gain by the time vegetation was impacted. These females were in good condition and all of them weaned litters in 1992. Reproductive females achieve hibernation mass in late August or early September; the Upper Valley females would be more severely impacted because they initiated mass-gain 3 weeks later than the Lower Valley females. These females hibernated in poor condition, survivorship was poor, and none reproduced in 1992. In similar fashion, the young of the Lower Valley would have completed most of their mass gain before vegetation was impacted whereas growth of the young of the Upper Valley would occur primarily during the period when the vegetation would be most affected by the low rainfall.

This interpretation is supported by the timing of reproduction in 1988. Young appeared about July 5 in both the Upper and Lower Valley populations. Lower Valley young started post-weaning growth 10 days later than in 1991 and lost the advantage of early season growth. By contrast, Upper Valley young were weaned 10 days earlier than in 1991 and thus had 10 days of additional growth, which could add 190 gms of mass (mean growth rate in 1988 was 19 gms/day) to produce a mean mass of 1,373 gms ($1,183 \pm 0.190$). This value is close to the measured value of 1,332 for 1988 (Table 4). However, the mean mass of young in 1988 was larger than that of 1991 (Table 4). Thus, approximately equal survival rates would be expected. An inspection of growth of individual young revealed considerable variation in growth rates. I looked at the body mass of young on Aug. 15. The young that survived weighed an average of 1,587 gms, those that did not survive weighed only 1,123 gms. Although both groups probably gained additional mass before hibernation, the gain would be small because of the effects of low rainfall on the vegetation. Even in normal years, growth of vegetation reaches its maximum in early August (Kilgore, Armitage, 1978; Frase, Armitage, 1989). Thus, vegetation would be senescing during the time that young were attempting to prepare for hibernation. Why some young were affected more than others is not known.

I conclude that low body-mass was primarily responsible for low survivorship of young and reproductive females in the winter of 1991-92 and the subsequent low reproduction rate in 1992. Low body-mass was a consequence of poor quality food resulting from low summer rainfall. Marmots in the Lower Valley were less impacted because they initiated their growing season about 3 weeks earlier than did marmots in the Upper Valley.

ACKNOWLEDGEMENTS

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