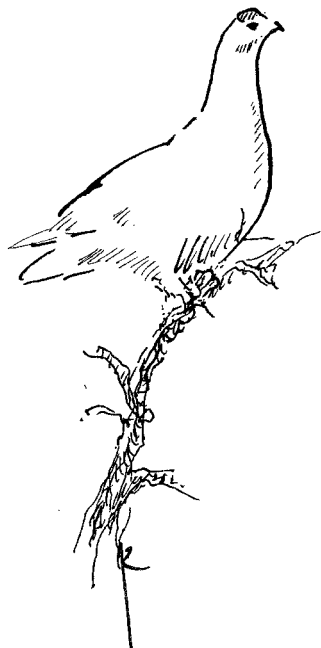


SOCIAL BEHAVIOUR, REPRODUCTIVE BIOLOGY AND BREEDING SUCCESS OF ALPINE ROCK PTARMIGAN *LAGOPUS MUTUS HELVETICUS* IN NORTHERN ITALY

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We monitored social behaviour, nest site selection, clutch size and survival, and breeding success (number of fledglings per successful hen in late August) in two Alpine Rock Ptarmigan *Lagopus mutus helveticus* populations in the South-central Alps, Italy, 1992-97. Phenology of flock formation and territory occupancy was similar as in northern populations, and, in spring, cocks outnumbered hens in most years. Not all cocks found a partner, but all paired cocks appeared to be monogamous. Few hens that lost their eggs during incubation laid a repeat brood. Adult hens (more than one year old) laid larger clutches than yearlings and clutch size was larger for first than for repeat broods. Nest losses were high (50%) and mainly due to predation of the incubating hen or her eggs. Probability of nest loss was not significantly affected by the amount of cover around the nest or nest type. Average clutch size, nest predation rates, and breeding success fluctuated annually, and clutch losses were higher in years with poor weather during incubation, suggesting that stochastic factors (weather, predators) strongly influenced brood survival in Alpine Rock Ptarmigan.

Key words: *Lagopus mutus helveticus* – nest site selection – reproductive biology – clutch size – nest predation

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INTRODUCTION

Adult hens of ground-nesting game birds are known to be vulnerable to predators while laying or incubating (e.g. Angelstam 1986; Cotter 1999). Therefore, selecting a safe nest site has been considered an important component of fitness for ground-breeding birds (e.g. Lack 1968; Wiebe & Martin 1998a). Since incubating hens of ground-nesting grouse are cryptic and their nests are generally well hidden, nest site selection, nest building behaviour and inconspicuous movements and foraging of incubating hens are considered anti-predator behaviour (Watson 1972; Giesen & Braun 1979; Wiebe & Martin 1998a). In high-arc-

tic and alpine grouse populations, the hen's condition and the microclimate around the nest also affect nest site selection (Wiebe & Martin 1997, 1998a).

In northern populations of grouse and ptarmigan species, annual variation in breeding success strongly affects the size of autumn stocks, and the size of the breeding population in the following year (Choate 1963; Hannon & Smith 1984; Myrberget 1984; Watson *et al.* 1984, 1998). Clutch size, clutch survival and egg hatchability (% eggs that hatch and produce chicks), and chick survival are important components of breeding success (Steen & Unander 1985; Watson *et al.* 1998; Rørvik *et al.* 1999). In Scottish Rock Ptarmigan

Lagopus mutus scoticus breeding success was determined by annual variation in clutch size and chick survival, which varied with the hen's condition, and there was a positive feedback between recruitment of young in one year and the next (Watson *et al.* 1998). Delayed density dependence of clutch size, breeding success and summer loss occurred on poorer soils, while grouse numbers fluctuated more erratically on rich soils (Watson *et al.* 1998). Although, rises in predator numbers and predation can increase losses of entire clutches and thus lead to lower ptarmigan numbers (Moss & Watson 1984; Cotter 1999), cyclic changes in Scottish Rock Ptarmigan populations living on rich or poor soils were inconsistent with expectations from predator-prey hypotheses for cycles (Watson *et al.* 1998).

The Alpine Rock Ptarmigan *Lagopus mutus helveticus* is a small (adult body mass in autumn about 350-525g), territorial and mainly social monogamous tetraonid (Bossert 1977; Desmet 1988). The alpine population is a glacial relict, and the Italian Alps constitute the southern border of the distribution area of Rock Ptarmigan. The species occurs as a sedentary breeding bird from the Maritime Alps in the southwest to the Alpi Giulie in the east, with a discontinuous distribution in favourable habitats, determined by bedrock and soil composition, elevation and orientation of mountain slopes and alpine meadows (De Franceschi 1992). In contrast with populations studied on subarctic and arctic grounds in Scotland, Iceland and northern Fennoscandia (Watson 1972; Moss & Watson 1984; Mortensen *et al.* 1985; Steen & Unander 1985; Unander & Steen 1985; Nielsen & Pétursson 1995; Watson *et al.* 1998; Cotter 1999), the social organisation and reproductive biology in these alpine populations are poorly known, and there is no information on the relationship between nest site selection, nest predation, clutch size, and final breeding success of individual hens. In this paper we describe social behaviour of Alpine Rock Ptarmigan, and nest site selection and foraging habitat of incubating hens. We then investigate the effects of the amount of cover, formed by high vegetation and

large rocks, around the nest and of various environmental parameters on clutch survival, clutch size and brood size.

METHODS

Rock Ptarmigan were studied from 1992-97 in two sites in the Bormio Hunting District (27650 ha) in the Lombardian Alps, in northern Italy. The main study area Monte Sobretta of 890 ha consisted of a high-altitude alpine valley, Valle dell'Alpe, and the northeastern slopes of Monte Sobretta at elevations of 2200m to 3090m (46°24'N, 10°26'E). The substrate was moraine and other detritus formed by surrounding glaciers and their streams, with podzol soils at lower elevations. Six main vegetation types occurred: mountain ridges, unstable detritus and cliffs without vegetation (11.1%), or partially covered by patches of different pioneer vegetation types (27.6%); natural alpine meadows (28.1% of the study area); secondary degraded grasslands, due to grazing by domestic livestock, boags and a skipiste with artificial grassland (16.2%); alpine shrubland (9.6%), dominated by Alpine Rose *Rhododendron ferrugineum* and Bilberry *Vaccinium myrtillus* with various *Erica* spp. and abundant Juniper *Juniperus nana*; and dwarf-shrub vegetation (7.4%), characterised by Crowberry *Empetrum hermaphroditum*, Mountain Avens *Dryas* spp. and Alpine Azalea *Loiseleuria procumbens*. The climate was of the continental intra-alpine type, characterised by annual precipitation of 800 to 1000mm, mean minimum monthly temperature (Jan) around -10°C and mean maximum monthly temperature (Jul) around +10°C, >180 days of snow cover per year above 2000m, and between 6 and 8 months per year with frost. Permanent snow occurred above 3000m, and snow depth varied strongly monthly and annually.

Additional data on brood size and number of chicks per hen in autumn were gathered in a second study area, Val Federia (851 ha), a high-altitude valley at elevations of 2300-2794m (Monte

Blesaccia), near Livigno (46°32'N, 10°06'E). Distance between the two sites was 27 km. Substrate, soil and vegetation types were similar to study area Monte Sobretta, but with slightly different proportions of the main vegetation categories. Potential predators of eggs, chicks and/or adult birds occurred in both study areas: Alpine Chough *Pyrrhocorax graculus*, Raven *Corvus corax*, Peregrine Falcon *Falco peregrinus*, Golden Eagle *Aquila chrysaetos*, Alpine Marmot *Marmota marmota*, Fox *Vulpes vulpes*, and Stoat *Mustela erminea*. Disturbance related to human presence in different seasons was higher in Val Federia than in Monte Sobretta. The population of Rock Ptarmigan in Monte Sobretta, within the Stelvio National Park, has been protected since 1978, while only one bird was shot during the study period in Val Federia. Population size in the whole Bormio Hunting District is among the largest of the Lombardian Alps, with a long-term average autumn stock of 400 to 450 birds (density 1.45-1.63 km⁻²).

We located territorial pairs in spring (early May-mid Jun) by seeing and hearing territorial cocks, which crowed frequently during the first hours after sunrise and could be heard for 1 km. In summer (early June to first decade of July), nests were found by (1) observing male parental care, which consisted of males defending the nest site and showing distraction display ('walking in a circle', Watson 1972); and (2) looking for 'clocker' droppings, the large pellets left by the female during the laying and incubation period (Watson 1972; Giesen & Braun 1979). When a nest was located, we recorded date, exact location (on a 1:10 000 map), and nest type. Each nest was assigned to one of two types: (1) exposed nests that had no boulders or rocks nearby and were not overhung by plants and partly sheltered nests that were made in a slight depression near a tiny mound or against a rock, or were partly sheltered by plants; and (2) completely sheltered nests that were made in a small cavity and completely overhung by rocks or plants (see also Watson 1972). In Monte Sobretta, we trapped birds in May-early Jun by setting three sets of mist nets (15m long,

3m high) in close proximity within a male's territory, and a group of four drivers chased the local pair towards the nets. All caught birds ($n = 28$) were aged and sexed based on plumage characteristics (Weeden & Watson 1967). A total of 22 adult Rock Ptarmigan (9 males, 13 females) were fitted with necklace radio transmitters (Cotter & Gratto 1995) (type RI-2B, diameter 25 mm, width 11 mm, weight 13.6 g about 3-3.5% of adult body mass; Holohil Inc., Canada). Transmitter range (ground to ground) in our study area was 450m and battery lifetime was 18 months. A RX-81 receiver (151-152 Mhz, Televilt, Sweden) and a hand-held 3- or 4-element Yagi antenna were used to locate the radio-tagged birds. In late Aug-early Sep a count was made of hens on the study areas and the chicks accompanying them using trained dogs and drivers. We used these counts to calculate two measures of breeding success: the number of chicks per hen in autumn (n chicks/ n hens) and brood size (n chicks/ n hens accompanied by chicks). Direct observations were made of the behaviour of single birds and of social interactions between individuals when occurring in flocks. In the latter case, flock size and flock composition were described.

A total of 24 nests were monitored in 1992 and from 1995-97, and additional data of a repeat brood, with 2-3 day old chicks were gathered in 1997 (Appendix 1). The date for initiation of egg-laying (laying date) was determined by observing the hens' behaviour from the last week of May onwards, using a 30x telescope and/or by locating radio tagged birds (1995-97). The radio necklace did not affect the behaviour of the birds (Scherini unpubl. data; see also Cotter & Gratto 1995). Four nests were found on the day the first egg was laid (laying date). These nests were checked every second day to determine an average laying-rate of 29 ± 7 h which corresponded with literature data (24-36h, De Franceschi 1992). The remaining 21 nests were found at different stages of the laying period. Counting the number of eggs already laid and using the average laying-interval of 29h egg⁻¹ allowed us to calculate the laying date for 21 nests. The mean incubation period in the wild was

23d ($n = 7$ nests, see also Watson 1972, Moss & Watson 1984: 21-23d for Rock Ptarmigan in captivity). Clutch size and clutch survival until hatching (not depredated clutches) were determined by checking nests every second day throughout the incubation period in 1992 and 1995. We took care to visit nests when the hen was off foraging, and when no predators were seen in the vicinity. During the 3-4h after we checked nests, no predators were observed approaching the nest-site ($n = 32$). Although we can not exclude that night-active predators, mainly foxes, may have been attracted by our scent, we feel confident that study methods did not interfere with behaviour of the incubating hens, or with the probability a nest would be found by predators. In 1996-97 all monitored hens ($n = 13$) were radio tagged allowing to check whether they were still incubating from a distance (c. 100m). Nests were visited only two times during the laying phase, the second visit to determine clutch size, and a third time at 21-23d after incubation started, or when the hen's behaviour suggested the nest had been predated to determine clutch survival. Egg predators could be recognised by signs left on broken egg shells. Direct observations of predation on real or artificial nests (unpubl. data) revealed that Alpine Chough typically left some eaten eggs near the nest, with a hole where the bill perforated the shell. Marmots left teeth marks (incisors) on broken shells in and around the nest, while Foxes normally carried away entire eggs without breaking them. Two predation attempts by a Stoat were directly observed.

After hatching, the structure and composition of the habitat around a nest site was described using a 10x10m sampling plot, with the nest as centre (see Appendix 1). Throughout the entire incubation period, nest sites were monitored for half a day (from sunrise till midday, or from midday till sunset) using a 30x telescope from a hidden position about 100m from the nest. In 18 cases, we observed the incubating hen leaving the nest to feed ($n = 13$ different nests), and recorded the position and behaviour of the foraging hen

and its cock until the hen returned to the nest or moved out of our observation field.

Variables expressed as proportions (p_i) were arcsine $\sqrt{p_i}$ transformed before analyses. Because of annual variation in laying dates, normalised laying dates per year were calculated for first clutches, giving for each clutch the divergence from the mean annual laying date. In a set of normalised data, the mean = 0 and SD = 1. All other continuous dependent and independent variables that were used in the analyses were normally distributed (Shapiro-Wilk test all $P > 0.1$, SAS 1989), thus multivariate, parametric tests were used. If not specified otherwise data are presented as means $\pm$ SD. We used multiple ANCOVA models (Proc glm, SAS 1989) to investigate the effects of continuous independent variables and categorical variables (factors) on a continuous dependent variable. In a first step a full model was calculated containing all the parameters tested. In a second step a stepwise backward procedure was used to select a final model containing only significant variables and/or factors with the level of significance set at $P < 0.05$. We used a logistic regression to test the effects of nest-type (exposed or partly sheltered versus sheltered) and of several environmental variables on the probability of nest loss versus nest survival. In grouse species, several consecutive days of extreme weather conditions have negative effects on both egg and juvenile survival (e.g. Moss & Watson 1984). Therefore, an index of weather conditions during incubation (period between earliest date a hen started incubating and latest date of hatching) was derived from the occurrence of at least two periods of more than three consecutive days of bad weather (maximum daily temperature below 10°C with heavy rain- or snowfall). This way, weather was classified as 'bad' in 1992 and 1997, as 'good' in 1995 and 1996. Since several variables were intercorrelated, they could not be fitted in the model simultaneously. Therefore, we first tested the effect of each variable or class on the binary dependent variable separately, and then used a stepwise forward procedure to produce a model that best fitted the data (Baker & Nelder 1978).

Model building was stopped when addition of another variable no longer significantly increased the total deviance (Table 2).

RESULTS

Seasonal changes in social behaviour

Observations ($n = 6$) of Rock Ptarmigan in Oct-Nov suggest the formation of large groups, with both immature and adult birds of both sexes, consisting of about 30-50 ind, with maximum group size in the Bormio Hunting District of 87 birds (mean $\pm$ SD = 45 ± 22). By Dec, smaller groups of about four to ten Rock Ptarmigan of both sexes were formed ($n = 6$, 7 ± 2 birds). Two cases (9%) of pair formation were observed in Jan or Feb, when the birds still moved around in small winter groups (see also De Franceschi 1992). By the end of Mar-early Apr, cocks started to occupy and defend territories, frequently with 'song in flight' displays, and in a few cases attacking and driving off an intruder while uttering a short, sharp and rapid 'kwa-kwa-kwa' ('attack call' Watson 1972). Territorial behaviour became more intense by early May, continuing throughout May and the first part of Jun, with calling frequency of cocks concentrated during the first 2-3h after sunrise and just before sunset. Twenty out of 22 cases of pair formation (91%) occurred within the cock's territory when hens joined territorial cocks in Apr-May. In our study areas, hens engaged very little in calling activity, remaining mostly silent. No female - female interactions for territorial cocks were observed, probably because there was little competition among hens for territorial cocks probably due to male-biased sex-ratios (between 1.3 and 2.1 males per female in spring, mean 1.5) throughout the study period. Courtship behaviour and mate-guarding by cocks was very intense from May-early Jun. Because of male-biased sex-ratios in both study areas in all years, there were always unpaired cocks in May-Jun. In 1992 and 1993, respectively, three out of four (75%) and five out of six (83%) unpaired cocks called and defended territories at Monte Sobretta,

while none of the three to six unpaired cocks present between 1994 and 1997 were observed calling or defending a territory. At Val Federia, one unpaired cock was found calling in 1992, 1993 and 1994 (respectively, 33%, 25% and 50% of all unpaired cocks), but none in 1995. All paired cocks appeared to be monogamous, and all hens, yearlings included, joined a territorial cock and laid eggs.

Nest building and nest site selection

One or a few days before starting to lay, all the hens ($n = 4$) were observed scraping a small depression for a nest. Cocks were alert, often standing on a main lookout point. All 24 nests were in a natural or a scraped hollow, lined with dry grasses, lichens and sometimes dry leaves of *Vaccinium* or *Rhododendron*, and some moulted feathers. Four (17%) were exposed nests, five (21%) partly sheltered nests, and 15 (62%) completely sheltered nests. The partly sheltered and completely sheltered nests that were found at lower elevations were hidden among bushes of Alpine Roses or Junipers. Most nests (65%) faced south-west or south, 23% faced north-west or north, 8% east and 4% west, which did not differ from the expected distribution (one-sample goodness-of-fit test $\chi^2_3 = 0.87$, $P = 0.83$). Twenty-five nests of Rock Ptarmigan were found between elevations from 2310-2780m, with an additional nest (not included in further analyses because the fate of the clutch was unknown) at 2895m. Number of nests per 100 m intervals was similar between 2300 and 2800m (appendix 1). For statistical analysis, we pooled categories and distinguished three elevation classes, from 2200-2499m, 2500-2699m, and above 2700m. The observed nest distribution according to elevation did not differ from the expected distribution (one-sample goodness-of-fit test $\chi^2_2 = 1.33$, $P = 0.52$). Nest sites were not randomly distributed in the six main vegetation types. No nests were in areas with bare detritus rocks or gravel, or in dwarf shrubland (appendix 1), only one nest was in artificial grassland (ski piste; Ivlev's electivity index $E = -0.60$). The proportions of nests in patchy pioneer vege-

tation types ($E = 0.02$) and natural alpine meadows ($E = 0.10$) were close to the expected values, but a significantly higher proportion of nests than expected was in *Loiseleuria-Vaccinium* shrubland (Appendix 1, $E = 0.55$).

The amount and type of vegetation cover around the nest varied strongly (percentile range: herbs 4-100, bushes 0-72, patchy vegetation 0-49), and the amount of ground covered by small (range 0-50%), or large rocks (range 0-48%), varied greatly in relation to the main vegetation type at the nest (Appendix 1). Several environmental variables were intercorrelated, as a result of the typical zonation of the main vegetation types, or due to the effects of slope steepness on vegetation development. The amount of cover around a nest was strongly correlated with the proportion of shrubs (Spearman rank correlation $r_s = 0.78$, $df = 22$, $P < 0.001$), and there was a negative correlation between the amount of nest cover and elevation ($r_s = -0.61$, $df = 22$, $P < 0.01$). The steepness of slopes where nests were found ranged from 10 to 50° with a mean of 27.2° ($\pm 11.0^\circ$). Most nests were on slopes (19 of 25 nests, 76%), with the remainder in the valley bottom (12%), on mounds (8%) and in hollows (4%). No nests were found on mountain ridges. For two repeat broods, the second nest site was 620m (with an elevation difference of 200m), and 380m (elevation difference 60m) away from the first nest site. The nest site of one hen was located in three consecutive years, and that of two others in two consecutive years. Distances between sites were 570, 350 and 220m (elevation difference 50m), 280m (elevation difference 30m), and 185m (elevation difference only 5m), respectively.

Behaviour during egg-laying and brooding

All four nests with eggs checked during egg-laying were covered with loose grass and/or lichens when the hen was off the nest. After clutch completion, cocks defended the nest site during the first week of incubation ($n = 8$ observed). They positioned themselves on a lookout point from where they could see the nest, and, when approached by an observer, showed 'walk-

ing in a circle' distraction display. All cocks ($n = 13$) followed their incubating hens (94%, $n = 18$ observation bouts) when they left the nest for feeding bouts and in all cases remained on the lookout while the hen was foraging, during feather preening or dust bathing. Cocks displayed different degrees of brood attentiveness. Of eight cocks, six left the nest site five to seven days after incubation started, while two stayed until, respectively, three and four days after the eggs hatched.

Breakdown of territorial behaviour in summer

In the Italian Alps, from June onwards, single adult cocks that did not defend a territory and remained unpaired, aggregated in groups of two to three birds. In July, these birds were joined by territorial, paired cocks that had abandoned the incubating hen, and by adult hens that had lost their brood. Hens with chicks remained within the territory at least until the chicks were 14d old, and could be considered fledglings. Until late August-early September, family groups composed of the adult hen with her chicks remained separated from the groups of adult cocks and unsuccessful hens. Thus, counts carried out in this period gave good estimates of annual breeding success (brood size, number of chicks per successful hen).

Laying date and clutch size

We gathered brood size data for 24 nests, with complete information on 22 broods: 19 first broods (86.5%) and 3 repeat broods (13.5%). The hen's age (yearling or adult) could be determined in 18 cases: 15 first broods and 3 repeat broods. The earliest repeat brood had 29 June as laying date. Mean laying dates of 15 first broods differed significantly between years but not between age groups (two-way ANOVA, year effect $F_{2,11} = 5.00$, $P = 0.03$, age effect $F_{1,11} = 0.25$, $P = 0.63$; one-year old birds, 10 June ± 8 d, $n = 7$; >1-year old birds, 11 June ± 6 d., $n = 8$), with the laying date in 1995 significantly later than in other years (Table 1, Tukey test on differences between means). In three out of 22 cases, incubation was initiated the day before the last egg was laid, in the other cases when the clutch was complete. We

Table 1. Rock Ptarmigan breeding success at two study areas in the Lombardian Alps. Annual averages for first broods and repeat broods (mean $\pm$ SD, sample size between brackets) of laying date (date first eggs was laid) and clutch size (number of eggs) for Monte Sobretta. Mean brood size (n = number of hens accompanied by chicks in August) and mean number of young per hen (n = total number of hens counted in August) for both study sites.

Year	Mean laying date Monte Sobretta	Mean clutch size Monte Sobretta	Mean brood size (n)		Young per hen (n)	
			MSobr	Val Fed	MSobr	Val Federia
1992	(2) 10 Jun $\pm$ 6d.	(4) 8.0 $\pm$ 1.6	6.3 (3)	7.0 (2)	3.8 (5)	2.8 (5)
1993			5.0 (1)	5.0 (2)	1.0 (5)	2.0 (5)
1994			5.0 (4)	7.5 (2)	3.3 (6)	5.0 (3)
1995	(4) 17 Jun $\pm$ 5d.	(4) 6.3 $\pm$ 0.5	3.5 (2)	3.7 (3)	0.6 (11)	1.8 (6)
1996	(8) 6 Jun $\pm$ 5d.	(8) 6.5 $\pm$ 1.2	4.0 (3)		0.9 (14)	
1997	(3) 8 Jun $\pm$ 4d.	(3) 8.0 $\pm$ 1.0	4.0 (3)		0.9 (14)	
Repeat broods	(3) 9 Jul $\pm$ 10d.	(3) 5.0 $\pm$ 1.0				

Table 2. Logistic regression model predicting nest loss (nest lost versus not lost) of Alpine Rock Ptarmigan. Models B-I were compared with model A (the selected model), using the difference in total deviance explained by adding another variable, by computing a goodness-of-fit test for each variable added ($\Delta\chi^2$ with Δdf , see methods).

Model	Variables included	Total deviance (%)	$\Delta\chi^2$	Δdf	P
A	Weather	20	6.511	1	0.012
B	Weather + nest type	20	0.13	1	0.72
C	Weather + elevation	20	0.22	1	0.64
D	Weather + large rocks	20	0.01	1	0.92
E	Weather + shrubs	20	0.20	1	0.66
F	Weather + herbs	20	0.22	1	0.64
G	Weather + patch	20	0.09	1	0.76
H	Weather + nestcover	22	0.74	1	0.40
I	Weather + nestcover x elevation	22	0.69	1	0.41

tested the effects of normalised laying date, vegetation cover (independent variable), nest-type, year, brood (first versus repeat brood) and age (factors) on clutch size of 18 hens of known age using an ANCOVA model. The partial effects of laying date, vegetation cover and nest-type were not statistically significant (all $P > 0.1$). A selected model with age, year and brood explained 74% of variation in clutch size. Mean clutch size of first broods over all years was higher than for repeat broods (15 first broods, 6.8 ± 1.1 ; three repeat broods, 5.0 ± 1.0 ; $F_{1,13} = 12.9$, $P = 0.003$).

Older (> 1 -year-old) hens laid, on average, larger clutches than yearlings (yearling, $n = 9$, 5.8 ± 0.8 eggs per clutch, adults, $n = 9$, 7.2 ± 1.2 eggs per clutch, age-effect, $F_{1,13} = 7.37$, $P = 0.02$), and mean clutch size was larger in 1997 than in 1995 and 1996 (see also Table 1, year effect, $F_{2,13} = 4.14$, $P = 0.04$, and Tukey test on differences between means).

Clutch survival

Of 24 clutches checked until hatching, 12 were lost prior to hatching (11 because of preda-

tion, one clutch incubated for 36 days with one dead chick and five unhatched eggs), and 12 hatched. One hen was taken by a Peregrine Falcon and two by a Stoat. Of the other eight clutches lost due to predation, two were taken by Alpine Choughs and six by mammals (three probably by Foxes, two by Alpine Marmots, one by a Stoat). In the logistic regression predicting the probability of nest loss, only weather during the incubation period ('good' in 1995 and 1996, 'bad' in 1992 and 1997, see methods) had a significant effect on the probability of nest loss (Table 2). In years when weather conditions during incubation were bad eight out of ten nests (80%) were predated (60% in 1992, 100% in 1997, appendix 1), but only four out of 14 nests (29%) were lost in years with better than average weather in June – mid July (20% in 1995, 33% in 1996, appendix 1). The effect of nest type, 33% of 15 sheltered nests were robbed, against 67% (6 out of 9) partly sheltered or exposed nests, was not significant (Table 2).

Chicks hatched and brood size in late August

The number of hatched chicks, counted between the first and third day after hatching, in 12 nests that escaped nest predation ranged from 3 to 6 for yearlings and from 4 to 10 for older hens (yearlings, $n = 7$, 4.7 ± 1.4 chicks; older hens, $n = 5$, 6.2 ± 2.5 chicks; t -test $t_{10} = 1.33$, $P = 0.21$). Clutch size and number of eggs hatched were positively correlated ($r = 0.59$, $n = 12$, $P = 0.044$), but hatchability of a clutch, the proportion of eggs that hatched, was not related to clutch size ($r_s = -0.01$, $n = 12$, $P = 0.98$). Hatchability varied between 44% - 100% and did not differ between yearling and older hens (yearlings $84 \pm 17\%$, older hens $76 \pm 27\%$; Mann-Whitney U -test $U = 0.15$, $P = 0.67$). The two measures of breeding success, the number of chicks per adult hen in August and mean brood size in August, were strongly correlated (Table 1, combining data of both study sites $r = 0.85$, $n = 10$, $P = 0.002$). Dividing the number of hens with chicks counted in August by the total number of hens counted (see Table 1), we calculated the proportion of hens that were successful in raising a brood. At

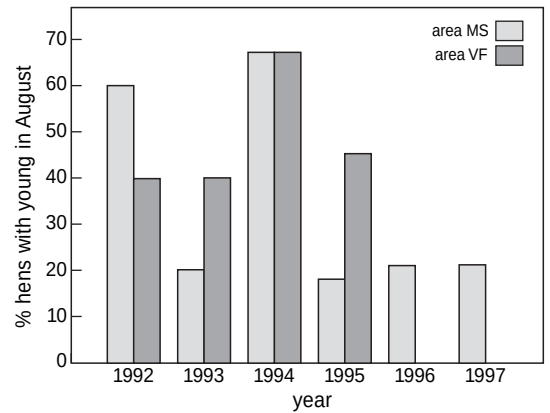


Fig. 1. Annual percentages of Alpine Rock Ptarmigan hens with fledged young in late August at two study areas in the Lombardian Alps. See Table 1 for sample sizes.

Monte Sobretta, the proportion of hens that raised a brood varied between 18 and 67% (Fig. 1). In four out of six years only about one fifth of female Rock Ptarmigan fledged chicks, while in two favourable years this increased to about two-thirds of all hens (Fig. 1). At Val Federia about 40% of hens fledged chicks in three years, and 67% in one year (Fig. 1). Mean clutch size per year and mean brood size tended to vary in parallel, but with a sample size of only four years at Monte Sobretta, the correlation was not significant (Table 1, Spearman rank correlation $r_s = 0.83$, $n = 4$, $P = 0.17$).

DISCUSSION

Phenology of flock formation and of territory occupancy by male and female Alpine Rock Ptarmigan did not differ from the behaviour described in northern populations (Watson 1972; Unander & Steen 1985; Cotter 1999). As in Svalbard, Scotland and the Canadian Arctic (Unander & Steen 1985; Watson *et al.* 1998; Cotter 1999), cocks outnumbered hens in most years and these male-biased sex-ratios, ranging from 1.3 to 2.0 cocks per hen, seemed to result in strict

monogamy of Rock Ptarmigan in the Lombardian Alps. This was in contrast with Rock Ptarmigan populations in northern Alaska and Svalbard where polygynous cocks occur (Bart & Earnst 1999). Similar as in northern ptarmigan populations (Watson 1972; Bart & Earnst 1999; Cotter 1999), several cocks in our study areas remained without a partner. In contrast with arctic Rock Ptarmigan populations (e.g. Unander & Steen 1985), hens with chicks in our alpine population remained within the natal territory until chicks were fledged, although their partner had already left its territory and thus showed no brood care. In contrast with Scottish Rock Ptarmigan (Watson 1972), Alpine Rock Ptarmigan did not engage in territorial behaviour in autumn, and autumn flock formation was similar as on Svalbard (Unander & Steen 1985).

In our study area, Rock Ptarmigan nests were found on arctic-alpine ground, above the tree-line, at elevations between 2300 and 2800 m. Other alpine populations also occur above the tree-limit, at elevations from 1500 to 1900 m in the eastern part of the Italian Alps, where mountains are less high, up to 2850 m in the central and western Italian Alps, the French and Swiss Alps, on mountain chains reaching well over 3000 m (Marti & Bossert 1985; Desmet 1988; De Franceschi 1992). Most nests were on southwest- or south-facing slopes, where snow-cover disappeared early. These microhabitat, and thus microclimate, preferences of nesting sites were also found in other studies on Rock Ptarmigan and White-tailed Ptarmigan in mountainous areas (De Franceschi 1992; Wiebe & Martin 1998a), and for grouse and ptarmigan in areas or years with late snowmelt, indicating that nest site selection is related to site exposure (Choate 1963, Giesen & Braun 1979; Steen & Unander 1985; Unander & Steen 1985; Clarke & Johnson 1992).

All nests were covered with loose grass and/or lichens when the hen was off the nest. This behaviour, also found in Scottish Rock Ptarmigan (Watson 1972), is considered a typical anti-predator behaviour, but it may also serve to protect the eggs from frost. Distraction behaviour by the

cock, when the hen is incubating, and staying on the lookout while his partner is foraging, might serve to protect the hen (and the eggs) from mammalian predators (e.g. Artiss & Martin 1995). However, most cocks (75%) abandoned the nest site after the first week of incubation, leaving nest defence exclusively to the hen. In one case, an incubating hen stayed on the nest while attacked by a Stoat and successfully defended her clutch by hissing and pecking at the predator: during a second attack the following day, however, the Stoat succeeded in killing the hen.

Factors affecting nest predation

Placing nests near suitable feeding sites may reduce time away from the nest for foraging. This behaviour may be an adaptation to reduce clutch predation by avian predators hunting by sight (Picozzi 1975; Erikstad *et al.* 1982), and/or to maximise incubation time (Wiebe & Martin 1997). In fact, only 27% of all predation events occurred while the hen was away from the nest: one was killed during the incubation period while returning from the feeding site by a Peregrine Falcon (direct observation); and in another two cases the nest site was discovered and the clutch predated by Alpine Choughs. These birds are incapable of driving off an incubating hen and can only predate unattended nests. On grouse moors in Scotland and NE England where predator-control was intensive, losses of brooding hens due to predation were low (e.g. Watson *et al.* 1984; Hudson *et al.* 1992) suggesting that site-related differences in predator density can have a strong effect on clutch survival. In our population of Alpine Rock Ptarmigan, only three of 24 incubating hens (12%) were predated and another eight clutches were lost due to predation of the eggs. Since in one clutch no eggs successfully hatched, total nest-loss during the brood period was 50%, comparable with the 54% to 67% nest-loss found for White-tailed Ptarmigan in alpine habitats (Giesen & Braun 1979; Wiebe & Martin 1998a), and with the 52-56% of clutch losses documented for Svalbard Rock Ptarmigan (Steen & Unander 1985). Similarly as on Svalbard, the proportion of nest

loss in our population (mainly due to predation) differed between years, and was higher when weather conditions during incubation (June-early July) were worse than average. Number of predator sightings per day (our unpubl. data) was constant throughout the years, suggesting that predator densities remained stable. We hypothesise that annual variation in weather conditions during incubation affects the probability of a nest being predated in relation to a hen's condition: when weather is bad, hens will be forced to increase the duration of incubation recesses (feeding bouts) to prevent a strong decrease in body mass, leaving the nest unattended for longer periods of time than during good weather (see also Wiebe & Martin 1997).

The proportion of nests robbed according to nest-type, 33% of 15 sheltered nests robbed against 67% of nine partly sheltered or exposed nests, were not significantly different. Hence, our data did not confirm the hypothesis that direct cover decreases a predator's chances of finding and robbing a nest. Since the lack of statistical significance might be a consequence of only 24 nests being monitored, larger sample sizes might confirm that completely sheltered Rock Ptarmigan nests are less likely to be found and robbed by predators, as was the case for White-tailed Ptarmigan, *Lagopus leucurus*, living in similar alpine habitats in North-America (Wiebe & Martin 1998a). However, for the latter species, concealed sites, with fewer escape routes, were more risky for the incubating hen, suggesting a fitness trade-off with the amount of cover at the nest (Wiebe & Martin 1998a).

Also in Rock Ptarmigan populations in Scotland and on Svalbard, the proportion of hens accompanied by chicks in August varied greatly between areas and years (Moss & Watson 1984; Steen & Unander 1985), and decreased strongly at one Scottish site (from 35 - 92% of hens with chicks, to a low of only 11%; Moss & Watson 1984) in a year when many Crows appeared. When predation occurs during egg-laying, which is found regularly in Rock Ptarmigan populations in Scotland (Watson 1972) and on Svalbard (Steen

& Unander 1985), and in nordic Willow Grouse (Myrberget 1985), a high proportion of females lay a repeat brood (40 - 100%). In our population, however, only three out of nine females (33%) that lost their clutch during incubation and could have produced a repeat brood did so. Also in other grouse and ptarmigan populations, renesting by hens that had already initiated incubation was rare (e.g. Watson 1972; Giesen & Braun 1979; Myrberget 1985, 1986; Wiebe & Martin 1998b; Cotter 1999).

Clutch size and breeding success

As for Rock Ptarmigan in Scotland and on Svalbard (Moss & Watson 1984, Steen & Unander 1985), and White-tailed and Willow Ptarmigan in North-America (Wiebe & Martin 1998b), older hens with larger clutches produced more chicks. For our Alpine Rock Ptarmigan population, we have no complete data on survival of individual hatchlings from hatching to fledging (15-days old) in the wild. However, the three cases in which chick corpses were found by monitoring radiotagged hens, suggest that extremely bad weather conditions, for three or more days during the first week of life, can cause high mortality even of complete broods (Scherini, unpubl. data). Also predators may take several chicks from a single brood before they fledge. Consequently, the proportion of hens that successfully raised a brood, varied markedly between years, confirming that environmental factors (weather, predators) seemed to have a strong influence on brood survival in this Alpine Rock Ptarmigan population. Similarly, predation of eggs or young, and extremely harsh weather conditions determined annual variation in breeding success of White-tailed Ptarmigan in naturally fragmented high alpine habitats in the Colorado Rocky Mountains (Martin *et al.* 2000).

Older (>one-yr of age) Alpine Rock Ptarmigan hens did not initiate egg-laying earlier than yearlings. This was in contrast with arctic Rock and Willow Ptarmigan and White-tailed Ptarmigan, where adult hens, that were heavier, laid eggs earlier and produced larger clutches with

higher hatching success than hens in poor condition (Steen & Unander 1985; Wiebe & Martin 1998b). We must underline that our sample was small. It might be, however, that as for Red Grouse in Scotland (Moss *et al.* 1981) there is no selective advantage for a hen in good condition to lay early (or late) with respect to the median laying date in the population. Unpredictable temperature fluctuations and duration of snow-cover in May and June in high-alpine environments, which affect the onset of vegetation growth, make selection for early breeding unlikely. Therefore, hens probably react each single year on the temporal development of food plants, and laying may simply be delayed when a hen has difficulties in increasing its body condition as weather reduces or retards the growth of protein-rich shoots and flowers. This was confirmed by the retarded laying dates in 1995, when late frost periods and several days of snow-fall or heavy rains prolonged into June, delaying the onset of vegetation growth with respect to other years, and thus reducing food availability and food quality for ptarmigan hens. Also in boreal Willow Grouse and arctic Rock Ptarmigan populations, laying date varies annually and regionally, in relation to weather conditions, in particular the disappearance of snow cover (Steen & Unander 1985; Unander & Steen 1985; Myrberget 1986), and breeding success of White-tailed Ptarmigan in the Sierra Nevada mountains was negatively affected by spring snow depth (Clarke & Johnson 1992).

In most years, mean brood size in August in the two alpine populations was lower (3.5 – 5.0 chicks/successful hen) than in Svalbard Rock Ptarmigan (5.5 – 7.1, Steen & Unander 1985). Only in 1992 (both sites) and in 1994 (Val Fedèria, see Table 1) brood size was similar to that in high production years on Svalbard (6.1 – 7.1, Steen & Unander 1985). Thus, our data confirm that, on average, clutches are larger in arctic than in alpine populations of Rock Ptarmigan (Bossert 1977; Steen & Unander 1985; De Franceschi 1992; Cotter 1999).

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SAMENVATTING

In tegenstelling tot de goed bestudeerde populaties van het Alpensneeuwhoen *Lagopus mutus* in Schotland en meer arctische streken, weten we maar weinig van deze soort in de Alpen. Deze studie vult deze leemte op en geeft een mooie vergelijking tussen het gedrag en de reproductie van dit ijsstijdrelict met de noordelijk levende populaties. Tussen 1992 en 1997 werden twee populaties in de Italiaanse Alpen bestudeerd. Evenals in noordelijker streken vormden zich in het najaar grote groepen bestaande uit jonge en oude vogels van beide seksen. In deze groepen vond in enkele gevallen al paarvorming plaats. Vanaf eind maart verdedigden de hanen territoria. Ieder jaar waren er meer hanen dan hennen en sommige hanen bleven daardoor ongepaard. Polygamie werd niet waargenomen. De meeste hanen verlieten hun partner na de eerste week dat met broeden was begonnen, hoewel enkele bleven tot na het uitkomen van de eieren. De legdatum varieerde tussen jaren, afhankelijk van de temperatuur in het voorjaar. De helft van de legsels ging verloren door predatie van de hen en/of de eieren door Slechtvalken *Falco peregrinus*, Alpenkauwen *Pyrrhocorax graculus*, Vossen *Vulpes vulpes*, Alpenmarmotten *Marmota marmota* of Hermelijnen *Mustela erminea*. Vervolglegsels waren na het mislukken van het legsel zeldzaam. De predatiekans was het grootst in koude jaren en verschilde niet tussen nesten die meer of minder beschut waren. Reproductie is een belangrijke factor die de populatiedynamica van het Alpensneeuwhoen bepaalt. Het lijkt erop dat de jaarlijkse variatie in reproductie vooral door externe factoren, zoals weersomstandigheden en predatoren, wordt bepaald. (CB)

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