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Geographic variation in body mass of rock ptarmigan *Lagopus mutus* in the Alps and the Pyrenees

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We compared the body mass of adult rock ptarmigan *Lagopus mutus* shot in autumn in the French Pyrenees (Ariège), the French Alps (Hautes-Alpes) and the Italian Alps (Province of Verbania). Mean body mass of adults was greater in the Ariège than in the Hautes-Alpes both for cocks (466 vs 433 g) and hens (429 vs 406 g), with the body mass of Italian birds being intermediate (cocks 448 g, hens 418 g). The relatively large mass of rock ptarmigan in the Pyrenees contrasts with the geographic trends found in capercaillie *Tetrao urogallus* and grey partridge *Perdix perdix* in France. For the last two species, birds in the Pyrenees are smaller than those further north. The site differences that we observed in body mass of rock ptarmigan may be related to differences in availability of high quality foods, particularly ericaceous shrubs. However, at the continental scale within Europe, the body mass of rock ptarmigan appears to be greatest in northern latitudes.

Key words: autumn, body mass, France, geographic variation, Italy, Lagopus mutus, rock ptarmigan

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Data on body mass in tetraonids are useful for investigating taxonomic relationships (Kahn et al. 1999), and for explaining the evolution of life history traits, including social organisation and demographic parameters (Wiley 1974, Trouvilliez et al. 1987, Sæther & Andersen 1988, Stearns 1992). In grouse, body mass may also be

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Table 1. Models employed to first test the effect of date of shooting (D) on body mass of rock ptarmigan mass and then the effects of sex (S) and location (L). Y(L) = year (nested in location), + = additive effect, * = interactions.

Model	Tested Effect	F	df	P
S + L + S*L + D + S*D + L*D + S*L*D	S*L*D	0.07	2, 165	0.931
S + L + S*L + D + S*D + L*D	L*D	0.23	2, 167	0.794
S + L + S*L + D + S*D	S*D	0.0001	1, 169	0.994
S + L + S*L + D	D	1.11	1, 170	0.293
S + L + S*L + Y(L) + S*Y(L)	S*Y(L)	0.63	14, 137	0.836
S + L + S*L + Y(L)	Y(L)	1.59	20, 151	0.061
S + L + S*L	S * L	0.46	2, 171	0.634
S + L	S	39.08	1, 173	< 0.001
S + L	L	10.89	2, 173	< 0.001

helpful in interpreting the effects of environmental stress on individuals (Sherfy & Pekins 1994). Such studies require accurate information on both inter- and intraspecific variation in body mass. In this paper we report on differences in body mass of two subspecies of rock ptarmigan in three areas: *Lagopus mutus pyrenaicus* in the French Pyrenees and *L. m. helveticus* in the French and Italian Alps.

Material and methods

Data collection

In France, we examined 53 adult rock ptarmigan shot by hunters during 1994-1999 in four communes in the Pyrenees, department of the Ariège (~42°30'N, 1°30'E) and 51 birds shot during 1979-1996 in nine communes in the Alps, department of the Hautes-Alpes (~44°30'N, 6°45'E). In Italy, the sample included 73 adults shot during 1997-2001 in two hunting districts in the Province of Verbania (~46°00'N, 8°30'E). We did not consider juveniles (3-4 months old) because they only occurred in small numbers in the shooting bags.

Dates of shooting varied from 15 September to 12 October in the Ariège and from 9 September to 11 November in the Hautes-Alpes. Shooting dates in Italy were 1 October to 28 November.

In France, we determined the sex of most birds by internal examination of the gonads. Age (adult or juvenile) was established by the presence or absence of the bursa of Fabricius. In the case of 18 birds not examined internally, age was determined by colour of primary wing feathers (Ellison & Léonard 1996), and sex was assessed by external plumage characteristics, including the colour and pattern of barring on body feathers. Jean-François Brenot verified this method of sex determination by examining the gonads of several birds.

In Italy, birds were not examined internally. Sex was determined by the presence or absence of the black loral stripe. This eye stripe appears in late September in males and is a reliable indicator of sex from October to May (Weeden 1964). Age was assessed from the wear and pigmentation of the two outermost primary wing feathers (Bocca 1984).

In all locations, body mass of birds, including the crop and its contents, was measured to the nearest 5 g either by us or by field assistants that we had trained.

Data analysis

We analysed the variations in body mass using linear models (McCullagh & Nelder 1989). Because birds might gain or lose mass during autumn, we studied the effect of date of shooting on mass by fitting the model: Mass = Sex + Location + Sex*Location + *Date* + *Sex*Date* + *Location*Date* + *Sex*Location*Date*. We then tested the effects written in italics with an analysis of variance, beginning with the interactions. In a second analysis, we studied the effects of sex and location by fitting the model: Mass = Sex + Location + Sex*Location

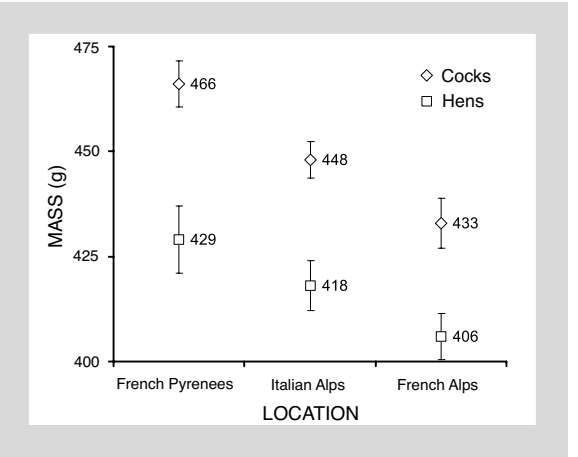

Figure 1. Body mass (in g) of adult rock ptarmigan in the French Pyrenees (Ariège), the Italian Alps (province of Verbania) and the French Alps (Hautes-Alpes) with error bars indicating ± 1 standard error.

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Table 2. Mean body mass (in g), standard error (SE) and range of adult rock ptarmigan in the French Pyrenees (Ariège), the French Alps (Hautes-Alpes) and the Italian Alps (Province of Verbania).

	Ariège				Hautes-Alpes				Italy			
Sex	Mean	SE	Range	N	Mean	SE	Range	N	Mean	SE	Range	N
Cocks	466	5.50	400-540	32	433	5.92	360-475	22	448	4.36	385-520	56
Hens	429	7.93	350-485	21	406	5.47	350-460	29	418	5.97	385-470	17

+ Year(Location) + Sex*Year(Location). Note that Year was nested within Location, i.e. it was assumed that a given year did not have the same effect in different locations. In this model, we first tested all interactions and then the main effects. We conducted all analyses using R software (R Development Core Team 2004).

Results

In the first analysis, after we withdrew the non-significant interaction terms, the effect of date was not significant (Table 1). Because mass showed no trend during the hunting season, we did not retain date in the second analysis. In the second analysis, the effect of year within location was nearly significant (see Table 1), but we removed this effect from the model because the P value of 0.061 was caused by one unusually small hen (350 g), which was the only hen weighed in 1998 in the Ariège. We also removed the other non-significant interaction terms from the initial model, allowing us to test for sex and location, both of which were highly significant (see Table 1). In the model Sex + Location, variances were homogeneous in cocks and hens, as well as in the three locations. Residuals of the model were also normally distributed. We conclude that body mass of both cocks and hens is greater in the Ariège than in the Hautes-Alpes, with birds in Italy occupying an intermediate position (Fig. 1, Table 2). The body mass of cocks exceeded that of hens by about 30 g in all three areas.

Discussion

Our data on mean body mass of adult rock ptarmigan in the Hautes-Alpes are similar to those reported by Couturier (1964) for adults shot in autumn in the French Alps (Table 3). Mass of birds in the Italian Province of Verbania is similar to that of ptarmigan shot about 120 km to the east in the Italian Province of Sondrio (Scherini 1984; see Table 3). The Italian ptarmigan appear to be about 10-20 g heavier than those in the Hautes-Alpes. Couturier (1964) reported that rock ptarmigan were heavier in the Pyrenees than in the French Alps, and our results suggest a difference of about 20-30 g. Nevertheless, we believe that other populations in both mountain ranges should be sampled before concluding that this difference characterises the subspecies *L. m. pyrenaicus* and *L. m. helveticus*.

Within subspecies of rock ptarmigan and spruce grouse *Dendragapus canadensis* in North America, birds of northern populations tend to be heavier or larger in body dimensions than birds of southern populations (Browning 1979, Holder & Montgomerie 1993, Boag & Schroeder 1992). These trends coincide with Bergmann's rule, which states that mass is higher in cooler climates because small animals lose heat faster than large animals. However there are exceptions in tetraonids. For example, the opposite latitudinal trend occurs in ruffed grouse *Bonasa umbellus* (Rusch et al. 2000). Likewise, in our study, birds in the Ariège are heavier than those further north in the Hautes-Alpes and in Italy, despite

Table 3. Mean body mass (in g) and range (figures in parentheses) of adult cocks and hens of four subspecies of rock ptarmigan in autumn in Europe.

Subspecies	Area	Reference	Months	Adult cocks	Adult hens
L. m. pyrenaicus	French Pyrenees (Ariège)	This study	September - October	466 (400-540)	429 (350-485)
L. m. helveticus	French Alps (Hautes-Alpes)	This study	September - early November	433 (360-475)	406 (350-460)
L. m. helveticus	French Alps	Couturier (1964)	Most in October - early November	428 (375-515) N = 39	401 (347-471) N = 22
L. m. helveticus	Italian Alps (Verbania)	This study	October- November	448 (385-520)	418 (385-470)
L. m. helveticus	Italian Alps (Sondrio)	Scherini (1984)	September-November	449 (360-520) N = 42	414 (350-455) N = 26
L. m. millaisi	Scotland	Watson (1987)	September-November	530[1]	490[1]
L. m. hyperboreus	Norway	Mortensen et al. (1985)	September-November	514[2]	465[2]

[1] Estimated from graph of Figure 1 in Watson (1987).
[2] Estimated from graph of Figure 1 in Mortensen et al. (1985).

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the generally colder temperature in the Alps (Izard et al. 1985). On the other hand, the greater mass of *L. m. millaisi* in Scotland and of *L. m. hyperboreus* in Norway (see Table 3) suggests that at a continental scale in Europe, mass may increase with latitude.

The relatively large mass of rock ptarmigan in the Pyrenees does not correspond to the geographical trends observed in two other galliformes in France. The subspecies of capercaillie inhabiting the Pyrenees *Tetrao urogallus aquitanicus* is smaller than *T. u. major* living further north in the Jura and the Vosges (Ménoni & Corti 2000). Similarly, the grey partridge of the Pyrenees *Perdix perdix hispaniensis* is smaller than the subspecies *P. p. perdix* inhabiting the plains further north in France (Lescourret et al. 1987). The relationship in the partridges cannot be a simple matter of temperature because the climate is colder in the Pyrenean Mountains than in the lowland plains.

To explain the differences reported here, we believe that mass will have to be measured in many populations in the Pyrenees and the Alps because both environment (e.g. soil fertility, food quality, temperature) and genetics likely contribute to variation in body mass. Indeed habitat quality may contribute to large body size in the Pyrenees. Nearly all birds from the Ariège were shot in the commune of Aston, where summer and autumn habitats are comprised of areas with a rich ground cover of herbaceous and ericaceous plants, including bilberry *Vaccinium myrtillus*, bog whortleberry *V. uliginosum* and heather *Calluna vulgaris*. Bilberry is a nutrient-rich food (Moss & Watson 1984) that, if available, is selected by rock ptarmigan in all seasons (Watson 1964, Martinez 1985, Boudarel & Garcia-Gonzalez 1991). Bog whortleberry is the only ericaceous plant readily available to rock ptarmigan in the Hautes-Alpes (Bernard 1982), where the habitat tends to be composed of a sparse cover of sedges, grasses and decumbent woody plants, for example mountain azalea *Loiseleuria procumbens*, along with large expanses of stony ground (screes) and boulder fields. These habitats are also often heavily grazed by sheep, which may reduce food available to ptarmigan. On the average, habitats in the Italian Province of Verbania tend to be of intermediate quality. Birds were harvested on both poor areas resembling those in the Hautes-Alpes and on better areas where the vegetation is dominated by bilberry, whortleberry, willow *Salix* spp. and rhododendron *Rhododendron ferrugineum*.

Finally, it would be interesting to investigate in further studies if differences in body mass of rock ptarmigan in the Pyrenees and the Alps are correlated with demographic parameters. Across species of tetraonids, incubation period and clutch mass (egg mass times clutch size), but not clutch size, increase with body mass (Sæther & Andersen 1988) and within galliformes low population turnover rates, and thus low sustained harvests, tend to be associated with high body mass (Trouvilliez et al. 1987).

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