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Authors: Bisi, Francesco, Martinoli, Alessio, D'Acunto, Davide, Gagliardi, Alessandra, Masseroni, Elisa, et al.

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SHORT COMMUNICATION

Habitat selection by Alpine Rock Ptarmigan *Lagopus muta helvetica* in the Italian Alps

Francesco BISI^{1,2}, Alessio MARTINOLI^{1,#}, Davide D'ACUNTO¹, Alessandra GAGLIARDI^{1,2}, Elisa MASSERONI², Chiara DE FRANCESCHI^{1,2}, Damiano G. PREATONI¹, Lucas A. WAUTERS¹ and Adriano MARTINOLI¹

¹ Dipartimento di Scienze Teoriche e Applicate. Università degli Studi dell'Insubria. Via J. H. Dunant, 3–I–21100 Varese. Italia

² Istituto Oikos. Via Crescenzago 1, 20134 Milano. Italia

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Abstract We analysed space use strategies in two populations of Alpine Rock Ptarmigan *Lagopus muta helvetica* considering three topographical variables (elevation, slope and aspect) to investigate whether populations living at range margins can adapt to suboptimal conditions by exploiting the available habitat differently. Selection for topographic features differed between populations, suggesting that Rock Ptarmigan adapt their habitat selection to local availability. Therefore, we suggest considering a wide range of habitat parameters when planning conservation strategies for species living at the margins of their range.

Key words Adaptation, Alps, Management, Rock Ptarmigan, Suboptimal habitat

Recent increase in human pressure and global warming (Sala et al. 2000; Houghton et al. 2001) is reshaping species distribution and causing local extinctions in species with narrow ecological niches (Moss et al. 2001; Thomas et al. 2006). In this context, studying the behavioural ecology of critical species is important in order to plan appropriate management strategies. However, extrapolating ecological information from a few sample populations to the whole species range may result in management guidelines that are too generalised. This may be particular true for species with wide or disjointed distributions. In this study we focussed our attention on the Rock Ptarmigan *Lagopus muta*, a species that occurs across most of the Arctic and alpine tundra of the northern hemisphere (Storch 2007; Potapov & Potapov 2011). The species is currently considered to be of “Least Concern” in the IUCN Red List, although local populations appear to be declining (BirdLife International 2015).

In the Italian Alps subspecies *L. m. helvetica* occurs from the Maritime Alps in the southwest to the Giulie Alps in the east with a discontinuous dis-

tribution related to the availability of suitable habitat (De Franceschi 1992; Favaron et al. 2006). At the southern limit of its distribution (Alps and Pyrenees) Rock Ptarmigan populations are patchy and have low densities (Storch 2000). Moreover, recent studies in the Swiss and Italian Alps have highlighted how climate changes may strongly affect population distribution, causing altitudinal shifts and local extinctions of populations living at lower elevations (Revermann et al. 2012; Imperio et al. 2013; Pernollet et al. 2015). In addition to climate, topographical features, both at the micro- and macro scale level, can markedly shape a species distribution and use of space (Revermann et al. 2012; Nelli et al. 2013; Visinoni et al. 2015). Although well-studied, research into the behavioural ecology and habitat selection of the Rock Ptarmigan has frequently only considered single populations, sometimes in consecutive years (e.g. Magnusson et al. 2005; Favaron et al. 2006; Novoa et al. 2008), thus there is little information on effects of geographical location and microhabitat variation on populations (Scherini et al. 2003). Results of such studies are sometimes used to make statements presumed to be valid for all populations throughout the species range: unfortunately, for species living in particularly harsh environments at the fringes of the spe-

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Corresponding author, E-mail: alessio.martinoli@uninsubria.it

cies range, or in isolated areas, as in the Alps, local adaptations may render such generalisations of little use. In fact, populations living under extreme habitat conditions often make the best out of non-optimal situations (Kawecki 2008), and conclusions drawn from populations in the core area of the range may be misleading when planning conservation strategies for “marginal” populations.

In this study we compared two distinct Rock Ptarmigan populations in terms of their selection of topographical features, considering elevation, slope and aspect, to investigate whether or not distinct populations, living in similar environments, have different behaviour in response to local conditions.

MATERIALS AND METHODS

The study was carried out in two different areas 140 km apart in the Piedmont region of the Italian Alps. One area, PNGP (800 ha) was located inside Gran Paradiso National Park, close to the Aosta Valley and the Nivolet lakes (45°28'01"N, 7°09'31"E). The elevation varies from 2,100 to 3,400 m asl. The other area, CACN4 (1,000 ha) is at the top of Stura valley near the border with France (44°13'43"N, 7°02'10"E). The elevation there varies from 1,900 to 2,700 m asl. According to the Forestry Map of Piedmont Region (hereinafter FMPR) four land cover categories are identifiable in the two areas: rocks and screes (PNGP 90%; CACN4 70%), rupicolous vegetation (PNGP 5%; CACN4 15%), high altitude grassland (PNGP 5%; CACN4 10%), and alpine shrubs (CACN4 5%). The Rock Ptarmigan is protected in PNGP, but hunted in CACN4 (according to Italian wildlife protection law, the hunting season is limited to October and November). Ptarmigan censuses were carried out from May to October in 2010–2011 in PNGP, and in 2011 only in CACN4. Different weather conditions occurred during the study years: 2010 was characterized by a wet spring and a hot summer, while 2011 had a dry spring and a cool summer. Birds were located using different methods in relation to the period of the breeding season. In May ptarmigan were located with the help of recorded cock calls. In June and July they were located with the help of recorded juvenile calls. From August to October we used trained dogs. When possible we recorded sex (80% of total locations). Every localisation was recorded using a handheld GPS device recording to the nearest 3–10 m. Throughout the study period animals were located also by periodic

active searches in the study areas.

Data on elevation, aspect and slope were measured using a Digital Elevation Model (DEM, 50 m cell size). Land cover was classified according to FMPR categories. This map was developed based on photointerpretation and field surveys performed in 2000 (reference scale 1:25000, smallest mapping unit 1 ha).

Initially, we tested for differences in frequency distribution (availability) of the two study areas with chi-square test. We performed an analysis of variance (ANOVA) followed by post hoc tests (Tukey's range test) to assess for effects of elevation, aspect and slope on ptarmigan locations during the study period, and to check for differences between the two study areas. We also checked for differences in use of space between males and females by running the same analysis on males and females separately, because dispersal from breeding territories among various species of grouse is often female-biased (Martin & Hannon 1987; Warren & Baines 2002). Elevation and slope data met the assumptions of normality (Shapiro-Wilk test, $W > 0.90$). For circular data (aspect), non-uniform distribution of data was appropriately tested using the Watson test.

Subsequently, we tested for habitat selection by ptarmigan in the two study areas. First, we computed the Ivlev Electivity Index (Ivlev 1961) for each variable (elevation, slope, aspect and land cover) after categorization of continuous variables (breaks every 100 m for elevation, 10° for slope, 22.5° for aspect) both for PNGP and CACN4. Given the proportions of available and used habitat categories, positive habitat selection is defined for index values in the range $\geq 0.5 - 1$. Second, a logistic regression was performed for each area separately in order to evaluate the effects of elevation, slope, aspect and land cover on ptarmigan localizations. For this purpose we randomly generated an equal number of pseudo-absences within the study areas. A final model was selected using a backward stepwise variable selection procedure excluding step by step from the complete model the factor that was least significant ($p > 0.05$) until only significant factors were left.

All analyses were performed using R software, ver. 3.1.3 (R Core Team 2015), in particular using the functions provided by the *stats* and *circular* (Agostinelli & Lund 2011) packages.

RESULTS

The frequency distribution of all of the topographic variables revealed differences between the two study areas (elevation: chi-square=4047.3, df=9, $p<0.001$; slope: chi-square=840.7, df=6, $p<0.001$; aspect: chi-square=1769.6, df=15, $p<0.001$).

Overall, 73 locations were recorded: 51 at PNGP (19 in 2010, 32 in 2011) and 22 at CACN4. A first comparison between years at PNGP (Fig. 1) showed that there were no differences in altitude selection (average altitude in 2010 and 2011 respectively, $2,882\pm 509$ m and $2,824\pm 509$ m asl, ANOVA: $F_{1,49}=3.67$; $P=0.06$), choice of aspect (2010: 250 ± 44 degree; 2011: 225 ± 40 degree; circular one-way ANOVA: $F_{1,50}=0.91$; $P=0.35$), or slope (2010: 14.7 ± 2.9 degree; 2011: 13.1 ± 2.4 degree, circular one-way ANOVA: $F_{1,49}=0.29$; $P=0.60$), therefore for

successive analysis we pooled data from 2010 and 2011. Land cover categories use was not compared between years since all locations in PNGP lie in the same category (rocks and screes).

Next, we tested for differences between the sexes in the selection of topographic variables for each area separately. There were no differences between males and females in the selection of any of the topographic variables: elevation (ANOVA: PNGP $F_{1,50}=0.57$, $P=0.46$; CACN4 $F_{1,21}=0.48$, $P=0.50$), aspect (circular one-way ANOVA: PNGP $F_{1,50}=0.23$, $P=0.64$; CACN4 $F_{1,21}=1.04$, $P=0.32$) and slope (circular one-way ANOVA: PNGP $F_{1,50}=0.05$, $P=0.83$; CACN4 $F_{1,21}=1.05$, $P=0.32$). Based on these results, the locations of both sexes were pooled in successive analysis.

Ptarmigan locations in the PNGP study area were on average at higher elevations than at CACN4

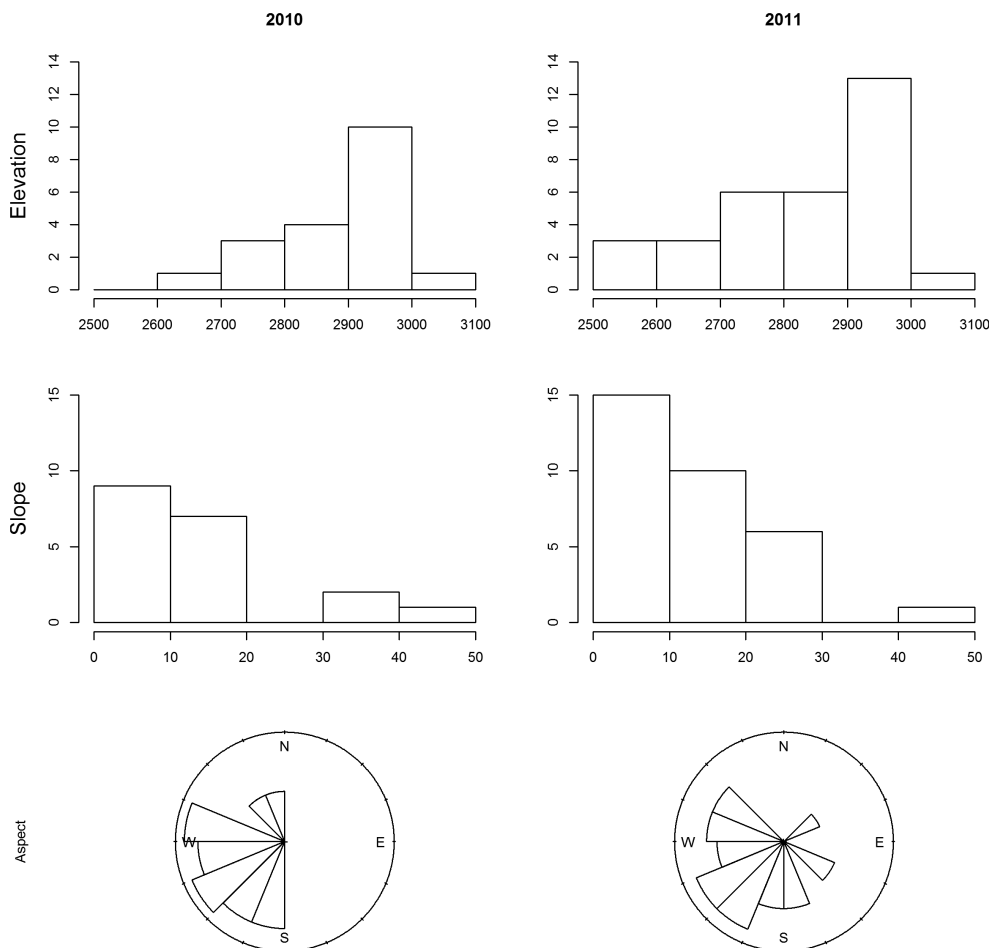


Fig. 1. Elevations at which Rock Ptarmigan were located in relation to slope and aspect in 2010 (left) and 2011 (right) at PNGP.

($2,845 \pm 502$ m and $2,564 \pm 453$ m asl respectively; ANOVA: $F_{1,71}=97.6$; $P<0.01$). Monthly variation in the elevations of locations was significant in PNGP (ANOVA: $F_{5,45}=6.26$; $P<0.01$), but not in CACN4 (ANOVA: $F_{4,17}=0.33$; $P=0.85$). At PNGP, birds were at lower elevations in May than in August, September and October (Tukey test: all $P<0.01$), and in July they used lower elevations than in August and September (Tukey test: $P<0.05$).

Rock Ptarmigan also selected different slopes between study areas (circular one-way ANOVA: $F_{1,71}=11.0$; $P<0.01$, Figs 2 & 3). They preferred gentler slopes at PNGP and steeper slopes at CACN4, where there was a more uniform selection of different slopes. Likewise, aspect was not uniformly distrib-

uted (Watson $U^2=0.74$; $P<0.01$) and aspect selection differed between study areas (circular one-way ANOVA $F_{1,72}=21.9$; $P<0.01$; Figs 2 & 3).

A logistic regression model was calculated for each area, considering both topographic variables and land cover classes; the stepwise procedure selected for different variables in each area. In both areas land cover variables were first removed and only topographic variables were selected in the final models. In PNGP the only significant variables were slope (coefficient estimate = -0.067 , z value = -3.478 , $p<0.01$) and elevation (coefficient estimate = 0.004 , z value = 2.923 , $p<0.01$) and the explained variance was low (14.7%). In CACN4 only elevation showed a significant effect (coefficient estimate 0.017 , z value = 0.005 , $p<0.01$),

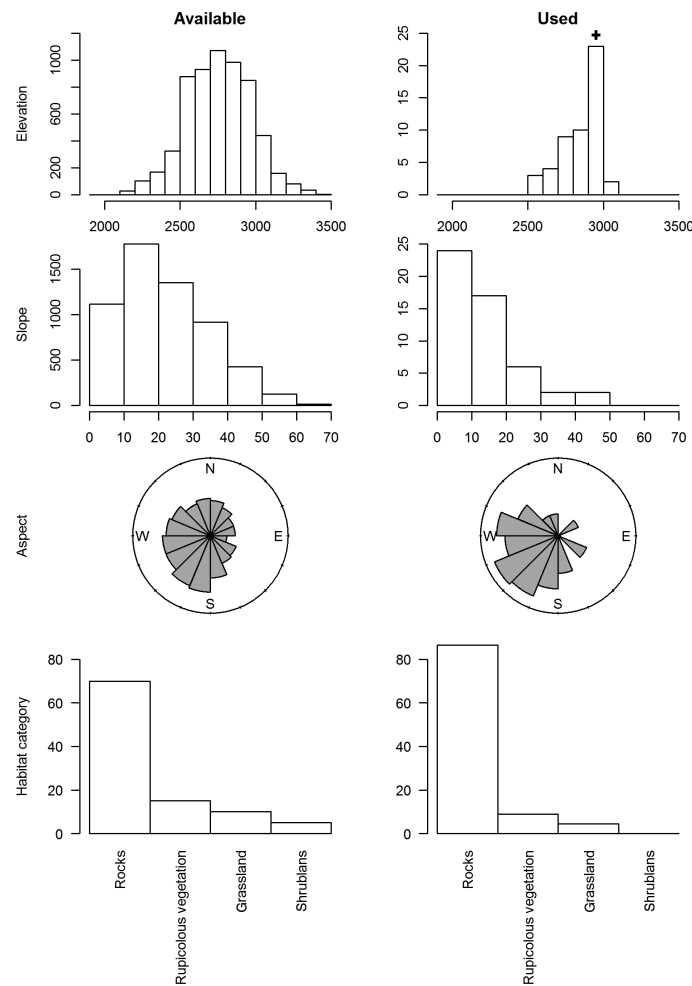


Fig. 2. Frequency of elevation, slope, aspect and habitat category at PNGP study site (left) and frequency of the same topographic variables for the Rock Ptarmigan locations (right). "+" indicates positive selection $\geq +0.5$ (range: -1.0 , $+1.0$) according to Ivlev Electivity Index (Ivlev 1961).

Rock Ptarmigan topography adaptation

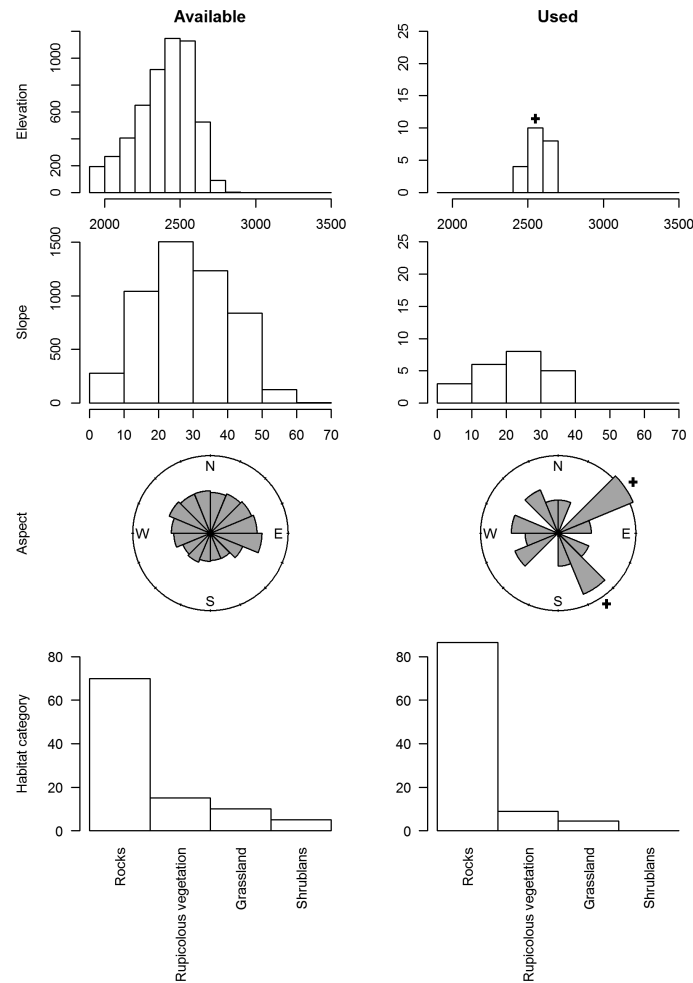


Fig. 3. Frequency of elevation, slope, aspect and habitat category at CACN4 study site (left) and frequency of the same topographic variables for the Rock Ptarmigan locations (right). “+” indicates positive selection $\geq +0.5$ (range: -1.0 , $+1.0$) according to Ivlev Electivity Index (Ivlev 1961).

but in this case the explained variance was higher (47.1%).

The effect of elevation on ptarmigan locations shown by the logistic regression is consistent with the results of the Ivlev Electivity Index in both areas (PNGP: 2,901–3,000 m, Ivlev index=0.52; CACN4: 2,601–2,700 m, Ivlev index=0.57) (Figs 2 & 3). No selection for specific land cover categories or slopes emerged from the analyses. Easterly aspects were selected in CACN4 (45°–67.5°, Ivlev index=0.53; 135°–157.5°, Ivlev index=0.70), but not in PNGP.

DISCUSSION

We found differences in selection for topographic variables between two study areas near the southern

margin of the range of the Rock Ptarmigan, suggesting local adaptation to different topographic conditions. Our results agree with Levins (1968) hypothesis that populations living at range margins often experience suboptimal habitat conditions and are pushed towards a certain degree of plasticity in order to survive.

Altitude was the main factor affecting the use of space by Rock Ptarmigan in both study areas, as shown both by the logistic regression and Ivlev Electivity Index. The effect of altitude, linked with temperature, is consistent with recent studies on the species that show that the temperature in July is a major factor shaping distribution, at both the macro and micro scales (Revermann et al. 2012; Visinoni et al. 2015; Furrer et al. 2016). In area CACN4, where

the range of topographical values for the Rock Ptarmigan was limited compared with PNGP, microhabitat selection was less pronounced. In fact, according to the logistic regression, birds only selected for altitude, using slope and aspect based on availability, although the model might not have detected the effect of aspect effectively, as two non-contiguous ranges result to be selected by the Ivlev Electivity Index. Slight differences between the regression and the Ivlev index were found for aspect selection in CACN4, but this inconsistency may have been due to the low number of locations available for this area.

The search for a cooler climate can also explain the lack of seasonal differences in the altitudes of ptarmigan locations in CACN4, which is located in the fringe of the Alpine range and only 65 km from the Mediterranean coast. Even though no climatic data were used in our study, we speculate that temperature rising beyond the species' tolerance prevents ptarmigan from using lower altitudes in CACN4, confining them to more elevated sites. Rock Ptarmigan densities in the two areas were similar between years (2 birds per 100 ha, Bisi et al. 2012) suggesting that in CACN4 they are well adapted to a suboptimal environment where both topographical and climatic constraints prevent individuals from exploiting a wider range of microhabitats.

PNGP provides a wider range of topographic values than CACN4 and it is centrally located in the Alps, where climate has more continental traits. Under these conditions, the model shows that Rock Ptarmigan show a significant preference for gradual slopes (see also Pedersen et al. 2014). This result differs from the study of ptarmigan by Visinoni et al. (2015), in an area located 60 km from PNGP in the core of Haute Savoie (France), in which they were found not to select any particular slope category at the micro scale level, albeit small depressions were clearly preferred with respect to control points. Hence, we believe that the preference for gradual slopes is related to the presence of depressions. Moreover, depressions are places where snow patches are found, a habitat feature that is positively correlated with Rock Ptarmigan presence (Pedersen et al. 2014).

Our model explained only 15% of observed variance in PNGP, revealing that other variables, such as vegetation, may affect ptarmigan space use more than topography. To test this, fine-scaled phytosociological maps are needed (Nelli et al. 2013). In fact, the scale and resolution of the maps used to anal-

yse ptarmigan distribution may affect model results (Revermann et al. 2012; Nelli et al. 2013; Schweiger et al. 2012; Pedersen et al. 2014) as microhabitat features are very important in Rock Ptarmigan habitat selection. Nelli et al. (2013) have previously used the FMPR for modelling male Rock Ptarmigan territories, although its predictive capability proved to be weaker than a phytosociological map due to insufficient spatial resolution. It must be noted, however, that topography can explain much of the Rock Ptarmigan's habitat preferences at the territory scale (Revermann et al. 2012; Pedersen et al. 2014).

As previously shown for ptarmigan in the Italian Alps (Favaron et al. 2006), we found no sex difference in habitat use in any season during our study. In contrast, in North America, where ptarmigan seasonal migration movements are more significant than in Europe (Storch 2007), females are known to move further than males from their breeding territories in autumn and winter (Weeden 1964).

Although still considered a game species in many Italian hunting districts, the size of local Rock Ptarmigan populations is decreasing in many areas of the Alps (Martinoli et al. 2015). Studies of ptarmigan behavioural ecology and improvements to monitoring schemes (Pedersen et al. 2014) could help explain this reduction in numbers and help management authorities to plan appropriate strategies to deal with it. This study shows that two populations of the same species can survive under different environmental conditions even in marginal areas. Since Rock Ptarmigan can change their habitat selection locally, it is important to evaluate local adaptation of single populations. In fact, Revermann et al. (2012) highlighted that as many as 13 different geomorphological and vegetational habitat variables can influence the species distribution at a local scale. This information is important for planning different *ad hoc* management strategies for the two populations, according to their different habitat selection: for example information on choice of aspect and slope at the local level can be used to determine areas for strict protection, avoiding activities such as hiking and hunting that cause high levels of disturbance to grouse species (Formenti et al. 2015). Hence, management strategies should consider local adaptation and different populations should be managed independently (Ficetola & De Bernardi 2005). In general, we recommend that conservationists consider a wide range of habitat parameters when planning conservation strategies for species living at range margins.

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REFERENCE

- Agostinelli C & Lund U (2011) R package ‘circular’: Circular Statistics (version 0.4-3). Available at <https://cran.r-project.org/web/packages/circular/index.html> (accessed on 10 August 2016).
- BirdLife International (2015) *Lagopus muta*. The IUCN Red List of Threatened Species 2015: e.T22679464A85043765. Available at <http://www.iucnredlist.org/details/22679464/0>. (accessed on 22 January 2016).
- Bisi F, D’Acunto D, De Franceschi C, Gagliardi A, Masseroni E, Storaci S et al. (2012) *Catture di pernice bianca in aree protette e venabili. Progetto n 88. Galliformi alpini. I galliformi alpini sulle alpi occidentali come indicatori ambientali: Monitoraggio, conservazione e gestione delle specie. Programma Alcotra 2007-2013* (Rock ptarmigan captures in protected areas and hunting grounds. Project n 88. Alpine Galliforms. Alpine Galliforms in the Western Alps as environmental indicators: monitoring, conservation and species management. Alcotra Program 2007–2013). Regione Piemonte, Turin, ONCFS, Paris, CNR, Rome and Regione Autonoma Valle d’Aosta, Aosta (in Italian).
- De Franceschi P (1992) *Pernice bianca* (Rock ptarmigan). In: Brichetti P, De Franceschi P & Baccetti N (eds) *Fauna d’Italia, vol. XXIX: Aves I* (Italian fauna, vol. XXIX: Aves I). pp 708–721. Calderini, Bologna (in Italian).
- Favaron M, Scherini GC, Preatoni DG, Tosi G & Wauters LA (2006) Spacing behaviour and habitat use of Rock Ptarmigan (*Lagopus mutus*) at low density in the Italian Alps. *J Ornithol* 147: 618–628.
- Ficetola FC & De Bernardi F (2005) Supplementation or in situ conservation? Evidence of local adaptation in the Italian agile frog *Rana latastei* and consequences for the management of populations. *Anim Conserv* 8: 33–40.
- Formenti N, Viganò R, Bionda R, Ferrari N, Trogu T, Lanfranchi P et al. (2015) Increased hormonal stress reactions induced in an Alpine Black Grouse (*Tetrao tetrix*) population by winter sports. *J Ornithol* 156: 317–321.
- Furrer M, Schaub M, Bossert A, Isler R, Jenny H, Jonas T et al. (2016) Variable decline of Alpine Rock Ptarmigan (*Lagopus muta helvetica*) in Switzerland between regions and sites. *J Ornithol* 157: 787–796.
- Houghton J, Ding Y, Griggs D, Noguer M, van der Linden P, Dai X et al. (2001) *Climate change 2001: the scientific basis*. Cambridge University Press, Cambridge.
- Imperio S, Bionda R, Viterbi R & Provenzale A (2013) Climate change and human disturbance can lead to local extinction of Alpine Rock Ptarmigan: new insight from the Western Italian Alps. *PLoS ONE* 8(11): e81598.
- Ivlev V (1961) *Experimental ecology of the feeding of fishes*. Yale University Press, New Haven.
- Kawecki TJ (2008) Adaptation to marginal habitats. *Annu Rev Ecol Evol S* 39: 321–342.
- Levins R (1968) *Evolution in Changing Environments*. Princeton University Press, Princeton.
- Magnusson KG, Brynjarsdottir J & Nielsen OK (2005) Population cycles in Rock Ptarmigan *Lagopus muta*: modelling and parameter estimation. RH-19-2004. Science Institute, University of Iceland, Reykjavík.
- Martin K & Hannon SJ (1987) Natal philopatry and recruitment of Willow Ptarmigan in North Central and Northwestern Canada. *Oecologia* 71: 518–24.
- Martinoli A, Gagliardi A, Preatoni DG, Bisi F & Martinoli A (2015) *Valutazione del trend delle popolazioni italiane di Galliformi alpini attraverso l’analisi dei dati di prelievo venatorio* (Trend evaluation of Italian Alpine Galliforms populations using bag records analysis). Abstracts of ‘XXVII Italian Congress of Ornithology’, September 17–20 2015, Caramanico Terme (in Italian).
- Moss R, Oswald J & Baines D (2001) Climate change and breeding success: decline of the Capercaillie in Scotland. *J Anim Ecol* 70: 47–61.
- Nelli L, Meriggi A & Frantoi A (2013) Habitat selection by breeding Rock Ptarmigan *Lagopus muta helvetica* males in the western Italian Alps. *Wildlife Biol* 19: 382–389.
- Novoa C, Besnard A, Brenot JF & Ellison L (2008) Effect of weather on the reproductive rate of Rock Ptarmigan *Lagopus muta* in the eastern Pyrenees. *Ibis* 150: 270–278.
- Pedersen OÅ, Blanchet MA, Hörnell-Willebrand M,

- Jepsen JU, Biuw M & Fuglei E (2014) Rock Ptarmigan (*Lagopus muta*) breeding habitat use in northern Sweden. *J Ornithol* 155: 195–209.
- Pernollet CA, Körner-Nievergelt F & Jenni L (2015) Regional changes in the elevational distribution of the Alpine Rock Ptarmigan *Lagopus muta helvetica* in Switzerland. *Ibis* 157: 823–836.
- Potapov R & Potapov E (2011) Willow and Rock Ptarmigan monitoring in Russia: An historic overview. In: Watson RT, Cade TJ, Fuller M, Hunt G, & Potapov E (eds) *Gyrfalcons and Ptarmigan in a Changing World, Volume II*. pp 213–228. The Peregrine Fund, Boise.
- R Core Team (2015) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available at <http://www.R-project.org/> (accessed on 29 November 2016).
- Revermann R, Schmid H, Zbinden N, Spaar R & Schröder B (2012) Habitat at the mountain tops: how long can Rock Ptarmigan (*Lagopus muta helvetica*) survive rapid climate change in the Swiss Alps? A multi-scale approach. *J Ornithol* 153: 891–905.
- Sala OE, Chapin FSI, Armesto JJ, Berlow E, Bloomfeld J, Dirzo R et al. (2000) Global biodiversity scenarios for the year 2100. *Science* 287: 1770–1774.
- Scherini GC, Tosi G & Wauters LA (2003) Social behaviour, reproductive biology and breeding success of Alpine Rock Ptarmigan *Lagopus mutus helveticus* in northern Italy. *Ardea* 91: 11–23.
- Schweiger AK, Nopp-Mayr U & Zohmann M (2012) Small-scale habitat use of Black Grouse (*Tetrao tetrix* L.) and Rock Ptarmigan (*Lagopus muta helvetica* Thienemann) in the Austrian Alps. *Eur J Wildlife Res* 58: 35–45.
- Storch I (2000) *Status Survey and Conservation Action Plan 2000–2004 Grouse*. WPA/BirdLife/SSC Grouse Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK and World Pheasant Association, Reading.
- Storch I (2007) *Grouse: Status Survey and Conservation Action Plan 2006–2010*. IUCN, Gland, Switzerland and World Pheasant Association, Fordingbridge.
- Thomas CD, Franc AM & Hill JK (2006) Range retractions and extinction in the face of climate warming. *Trends Ecol Evol* 21: 415–416.
- Visinoni L, Pernollet CA, Desmet J-F, Körner-Nievergelt F & Jenni L (2015) Microclimate and microhabitat selection by the Alpine Rock Ptarmigan (*Lagopus muta helvetica*) during summer. *J Ornithol* 156: 407–417.
- Warren P & Baines D (2002) Dispersal, survival and causes of mortality in Black Grouse *Tetrao tetrix* in Northern England. *Wildlife Biol* 8: 91–97.
- Weeden R (1964) Spatial separation of sexes in Rock and Willow Ptarmigan in winter. *Auk* 81: 534–541.