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Biology of alpine accentor (*Prunella collaris*) VII. Mountain tourism, climbing and hiking – a cause of drastic synanthropy in alpine accentors in the last 200 years

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Abstract. This study briefly describes the history of synanthropy in a high-altitude bird species, *Prunella collaris*. A list of food items that synanthropic individuals seek in garbage in the mountains is presented. Possible influences on behavioural changes and physiology of this protected species are discussed. The large number of synanthropic individuals of this species is evidence of how the development of alpine tourism in Europe over the last 200 years has seriously affected the life of alpine fauna.

Key words: Prunella collaris, bird synanthrophy, hiking and climbing

Introduction

The family Prunellidae is a relatively old family of songbirds. The group appears to split from outgroup families approximately 14.8 million years ago, in the middle Miocene (Drovetski *et al.* 2013). The divergence of the large *Prunella collaris* and *Prunella himalayana* group and other small accentors occurred during the late Miocene, approximately 7.31 million years ago according to Drovetskii *et al.* (2013) or 9.1 million years ago according to Liu *et al.* (2017). Ancestral area reconstructions indicate a Himalayan region origin breeding north of the Qinghai-Tibet Plateau. Later, new areas were facilitated during glacial periods, when suitable accentor habitats expanded west to east, and then subsequently northward from the Plateau and the great Asian mountain ranges (Liu *et al.* 2017). *P. collaris* and *P. himalayana* diverged from each other approximately 3 - 4 million years ago during the late Pliocene, in either the Himalayan region or the central Palearctic (Drovetski *et al.* 2013; Liu *et al.* 2017). The sympatric species in the Sino-Himalayan Mountains have divergent habitat preferences, with *P. collaris* residing at higher altitudes than the others, in alpine habitats. Most speciation events in accentors occured before the Pleistocene, but climatic oscillations during that period may have substantially modified their distribution. Liu *et al.* (2017) suggest that colonization of new areas by accentors was facilitated during glacial periods, when they expanded away from the great Asian mountain ranges across low-elevation areas, followed by the fragmentation of suitable habitats during interglacial periods. In the period 115,000 BP - 10,000 BP, the alpine accentor was already widespread in Euroasia, as well as in Europe, with a number of isolated populations in different mountain ranges, late Pleistocene fossils also exist from the lowlands between mountainous regions (Tyrberg 1991).

Recent studies show that alpine accentors can detect human activity in winter very quickly (Janiga 2021), therefore, it may be that the first associations between ancient humans and these birds occurred in Central Asia as early as 200 to 300 thousand years ago, at the time of the Denisovans. The age of Central Asian Denisovan fossils is estimated at 280,000 years (Jeenbaev 2007). Denisovans were likely adapted to life in the high mountains, where alpine accentors also lived. Living at high altitudes is hard. The air there carries less oxygen, making it harder to breathe and causing a host of problems; but modern inhabitants of Tibet have adapted. Many studies have linked their altitude adaptation to several genes including EPAS1; part of the system that helps the body react to low levels of oxygen. Huerta-Sánchez *et al.* (2014) discovered that genetic adaptation in modern Tibetans has its roots in Denisovans and that gene flow from this extinct group is found to have had important consequences. Alpine accentors may also have come into contact with Heidelberg or Neanderthal man in Europe. For example, many Würmian fossil records of alpine accentors are from SW Europe and link the populations in the Pyrenees, Massif Central and the Alps. Some records also exist from Greece (Tyrberg 1991).

Following the arrival of modern humans as many as 50,000 years ago (Svoboda 2014; Soukup 2015), most of the early relationships between larger birds and humans were ones of predation. In the case of small bird species, however, the relation was more of a commensalism, with birds visiting human settlements mainly in winter. Especially in the Gravettien, human populations became more and more settled with sufficient food sources in the mammoth steppe. After the onset of the Neolithic – Agricultural Revolution, significant changes also occurred in the biology of many wild bird species, including alpine accentors.

Humans began to impact the original biota in a number of ways, including: the institution of agri-

culture, storing of foodstuffs, modification of surface of terrestrial ecosystems (including wetlands, lakes and rivers), use of fire, fragmentation of wild nature, and the introduction of invasive or alien organisms. In late autumn, winter or early spring, some alpine accentors are commonly found close to farms, and they exploit feeding opportunities offered by this association with agriculture (Schiferli *et al.* 1980; Del Hoyo *et al.* 2005), such as feeding in barns, close to livestock, or nearby mountain chalets (Fig. 1). The muscular gizzard and crop that characterize acentors are adaptations to cope with their seed-dominated autumn and winter diet. The process of digestion of seeds is further assisted by the consumption of grid. Therefore, some alpine accentor individuals are commonly found close to human habitation in winter. In this period of intense medieval pastoralism, birds undoubtedly found food in the vicinity of haylofts or stables sheltering sheep, cows or horses. Such phenomena persist in suitable conditions today, and accentors are often seen at horse farms, where they will search for and collect seeds and grain from horse manure (Géroudet 1957; Dyrcz 1976; Šťastný and Hudec 2011). Millet or wheat, for example, has been found in the stomach of birds caught in winter (Kovshar 1966).

A radical change in the relationship of alpine accentors to humans has occurred in Eurasia over the last 200 – 300 years with the development of alpine tourism, which is seriously impacting breeding sites of this species. In the past, a chalet in the alpine area was mainly used by shepherds as a shelter for themselves and their flocks. Herders often visited the mountains to pasture their livestock and store milk and butter. This was often the practice with herders in all Eurasia. During the winter months, chalets were usually left unattended because herders would take their livestock and products to the flatlands. As time went on, outdoor enthusiasts started traveling to these mountains for holidays and the herders gave out their homes as shelter. Then as more people started visiting the alpine for holidays, the herders discovered the market for these vacationers (Fig. 1). More so, this was also largely the advent of mountain travel, leading to a boom in tourism. The most important buildings of this type in the High and Low Tatras were built in the 19th and 20th centuries: 1841 – Skalnatá chata, 1883 – Ťatliakova útulňa, 1893 – touristic path in Veľká Studená dolina (Great Cold Valley), 1895 – Chata pri Zelenom plese, 1899 – Téryho chata, 1932 – Chata Plesnivec, 1933 – Chata Rysy. In 1920, one of today's most popular valleys, Žiarska dolina, was almost unvisited, with the mountain cottage there completed in 1939. In 1936 work began on the cableway to Skalnaté pleso and in 1949 the cableway reached one of the highest summits of the Tatras, Lomnicky Peak. In 1964 the cableway transported 270,000 people. In 1949 - 1950 the construction of the cableway to Chopok summit began the development of the largest ski resort in Jasná. The history of the development of alpine summer and winter resorts in the Alps dates back about 100 years earlier than in the Carpathians, and a boom in the construction of mountain resorts in the Tian Shan mountains is currently underway. More recently, the market for chalets in Eurasia is even stronger than that of hotels, and one can often rent luxurious private accommodation with many amenities. Chairlifts, cable cars and these accommodations allow many more tourists to visit high mountain valleys or accesses mountain peaks. However, as a result a huge amount of biological waste and litter is left behind. The impact of tourism greatly affects the lifestyle of alpine accentor, as these birds scavenge this waste throughout the year (Géroudet 1957; Praz 1976; Martí *et al.* 1988), often congregating close to winter centres and hotels (Hudec 1983; Cramp 1988; Heer and Fraenkel 1999) or around ski-lift stations during winter (Dick and Holupirek 1978; Janiga 2020). The birds can also be found looking for food left by hikers on the tops of mountains or in camps for climbers during the summer months (Martín-Vivaldi *et al.* 1995) (Fig. 2). Sometimes relatively few sites (mountain huts and refuges) may highly influence the life of accentors in several valleys (Janiga 1998). Accentors regularly and actively forage on food leftovers of hikers (Delestrade 1995; Henry 2011). As accentors often consume cakes, fat or bread on mountain tops, feeding on rubbish can be expected to have an adverse effect on their general body condition (Dyrcz and Janiga 1997). The aim of this study is to provide a summary of the food that these birds feed on in human-influenced environments. The findings come from both the summer and winter seasons.

Fig. 1. Switzerland. Left: For many alpine accentors, seasonal movement to lower elevations introduces them to more heavily vegetated habitats and often brings them into cultivated areas, where they are commonly associated with mountain villages and livestock. Right: As more people started visiting the alpine, herders discovered the market for these vacationers, and birds discovered new sources of diet (e.g., garbage left in the wake of tourists) (Photo: M. Janiga, 2013).

Fig. 2. Left: Racek Mountain Camp, Ala Archa National Park, Kyrgyzstan. Alpine accentors feed on biological waste. The waste was stored in barrels behind the mountain hut. Right. Rozsutec summit, The Malá Fatra National Park, the West Carpathians, Slovakia. A young alpine accentor feeds on bread. In an undisturbed environment, the parents feed the chicks with insects; after flying out of the nest, the fledglings learn to hunt insects and thus to be predators. If the parents feed them bread, the animals' foraging behaviour changes, potentially resulting in lower survival rates. The physiology of individuals is also affected by changing nutrition based on this artificial diet (Photo: M. Janiga, 2012 - left, 2017 - right).

Material and Methods

As noted in many of our previous studies, alpine accentors are the subject of long-term research at the Institute of High Mountain Biology. The first data on this bird species was systematically collected in 1984, and various types of research have continued to the present day. In addition to systematic data collection, we have had many opportunities to observe many other phenomena in the life of this species. The results herein are the summary of long-term observations of accentor feeding patterns on garbage near mountain summits and near mountain chalets, hotels and huts. The data mainly originate from the West Carpathians, but observations from the Alps, Pyrenees, Apennines, Tian Shan, Balkan mountain range, and Krkonoše are also included. The observations date from 1984 to the present.

Results

An overview of the diet of alpine accentors offered by people is presented in Table 1. Alpine accentors usually arrive at their wintering grounds in November, and if they find places without snow, they forage for grass seed. They seek anthropogenic food sources particularly in times of snowfall, frost, snowstorms, or heavy snow cover. In cases of bad weather, one individual can eat up to 7.5 g of poppy seeds or 3 g of bread in the morning. Of these anthropogenic foods, birds prefer poppy seeds to bread, bread to biscuits, and biscuits to cheese. In the case of poppies, they make approximately 40 to 60 pecks per minute. During sunny winter days, birds actively hunt for insects (flies) under the roofs or along the windows of hotels. In March, they visibly switch to foraging for animal food.

Discussion

Organisms that cohabit with humans may be called synanthropic. Many species leave habitats modifieds by human activity. Some experienced populations decline, and a few have been extirpated. However, a good number of other species of birds accommodated to habitat modification. The existence of such synanthropic is no secret, but the degree to which the birds of a continental avifauna use habitats modified by humans has not been historically and comprehensively evaluated until recently. Species of early ecological succession and those known to be habitat generalists are likely to be synanthropic in at least part of their distribution. A large proportion of Eurasian birds could likely be designated as synanthropic, a distinction probably owing to a longer period of exposure to land use by humans. The enormous number of feeding associations of birds with other taxa, including primates, suggests the possibility that, in the past, birds foraged with some of our human and pre-human ancestors (see Introduction). Thus, evolution has played a role in bird-human feeding associations and the associations of birds with humans might be an example of very ancient symbiosis (Haeming *et al.* 2015). The alpine accentor is no exception; its winter occurrence has long been observed on castles (Ferianc 1979), roads (Boehme 1926), or in towns (Schmidt 1985).

However, fundamental changes in the life of alpine accentors and other mountain bird species occurred following the Industrial Revolution with the start of construction of hotels and restaurants beginning to occur in the alpine. Cable cars and chairlifts allowed ever greater concentrations of people on summits. The result is huge amounts of litter at mountaineering campsites, on high mountain peaks or at mountain huts and hotels. Birds frequently visit these sites, particularly outdoor serving areas to feed on scraps and leftovers (Heer 1998; Janiga 2020). Such summer and autumn food supplementation could have deleterious impacts. It may result in an unbalanced diet and consequently to changes in phenotypic structures of breeding populations (Jones and Reynolds 2008; Robb *et al.* 2008; Plummer *et al.* 2013a). The food list in Table 1 confirms that the alpine accentors seek out bread scraps (Fig. 3), chocolate and sweet biscuits, sausage, bacon, and butter. A large body of scientific literature, as well as the experience of songbird breeders, warns that these food sources are not healthy for wildlife. They can cause disease, mouth and throat injuries, and even death. Songbirds must be very ef-

Food	Jan	Feb	Mar	Apr	May	June	July	Aug	Sep	Oct	Nov	Dec	Sum
Breads, rolls and buns	9	7	3	1	2		4	5	8	3	4	16	62
Chocolate and sweet biscuits	6	14	4	1				1		1		7	34
Sausage, salami, bacon		2	2		1		2	1					8
Butter, bread and butter		3	5	1	1							2	12
Poppy seed rolls, poppy		16									4	13	33
Rice, hotel garbage			7										7
Cheese, milk products												2	2
Synathropic insect on hotels		7	23	1							2		33
Melted grassy spots near hotels	1	6	5	6							2	2	22

Table. 1. Anthropogenic food of alpine accentors. The numbers indicate the number of times a particular bird was observed feeding on a given food source. They depend on the possibility of daily field visits as well as the possibility of food identification. Numbers therefore characterize qualitative food sources; they do not represent seasonal changes in foraging. Identified food sources in the months November to April come from the winter ski resort of Malinô Brdo, observations from May to October come from mountain peaks and chalets. Data on the capture of synanthropic insects by birds and on the change of their diet in places with melted snow and exposed grass come only from the Malinô Brdo ski resort. To identify the problem of synanthropy in alpine accentors, observations must be multiplied by the huge number of days and the number of individuals that visit feeding sites and consume anthropogenic food every day in summer, autumn or winter.

Fig. 3. Left: A female alpine accentor collecting bread leftovers after tourists on Malolučniak summit, High Tatras, Polish – Slovakian border. The female was bringing bread to her young. When young wild animals learn to depend on humans for food, they become less experienced in foraging and consequently less likely to survive. Right: Furthermore, wild birds that are accustomed to food provided by humans commonly lose their fear of people (Photo: M. Janiga, 2021).

ficient eaters due to rapid metabolism and the small size of their stomachs. For example, bread robs birds of the opportunity to take in the true nourishment their bodies require to survive. Bread has zero nutrition for wild birds. It is heavily processed and contains chemicals and preservatives that are not suitable for wild birds. Bread contains very little protein, calcium, phosphorus, or other vitamins and trace minerals (Burt *et al.* 2021), which birds need to develop muscles and feathers. As a carbohydrate-rich food, these bread products do not contain sufficient fat, and while it will provide momentary satiety, does not provide much nutrition (Burt *et al.* 2021). This is a deadly combination of factors, considering how many calories birds need to eat in order to survive. The same is true for similar bread-like products such as buns, bagels, crackers, chips, pretzels, cookies, cereal, and donuts. For a small bird, this can lead to tragedy very quickly. It can freeze to death overnight, with its stomach full of bread. Foods such as chips, cookies, and crackers are reported as terrible food choices for birds because they are full of trans fats and crammed full of sugar and salt. Bacon drippings are another dangerous diet to offer wild birds. Bacon is full of nitrates, salt and other additives which are very harmful to wild birds' health. Fresh milk products or chocolate are also not a good food for wild birds because birds are lactose intolerant. Small chocolate residues can be fatal to a bird, due to the theobromine and caffeine.

They cause a bird digestive distress as well and heart and breathing difficulties. These snippets of information from veterinary literature and guides for songbird enthusiasts are just a very brief overview of what anthropogenic food can do to birds in the high mountains. Moreover, feeding a bird can change its normal behaviour and cause it to lose

its natural fear of humans and pets (Fischer and Miller 2015). A food-conditioned animal is likely to approach other people looking for food (Clark *et al.* 2015). Birds can become dependent on artificial food sources, less able to survive on their own (Plummer *et al.* 2013b) and pass important survival skills onto their young (Fig.3).

Humans are influencing food supply for birds directly by providing feeders, but also indirectly via waste treatment and through the creation of urban spaces at the expense of natural habitats (Chace and Walsh 2006). In this study, the important findings on the effects of food supplementation on alpine accentor ecology were highlighted. It can be estimated that between 10 and 30 percent of the alpine accentor population may be fed in this way during the summer and autumn months in the Tatra mountains. Perhaps this phenomenon may be corrected only by different feeding preferences among individual birds (Janiga and Novotná 2006). It is known that some accentors visit places with plenty of anthropogenic food frequently, while others do so only sporadically (Heer 1998). However, many young birds can be observed on summits collecting food from humans (Fig. 2). The distance they must travel to do so are likely farther than previously imagined. This indicates that the effects of supplementary feeding on alpine acccentors are likely to extend far beyond just one mountain valley. Thus, learning and information transfer between generations can be a serious phenomenon that threatens the population stability of this protected species in the high mountains (Janiga 1998). As incidental supplementary provisioning of wildlife is hugely prevalent and increasing in these habitats, this may have large and widespread ramifications for biodiversity conservation in many mountain national parks, and we urge caution upon policy makers in national parks to ensure hygiene and enforce maintenance of tourist destinations in affected areas.

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References

Arntzen, J.W., Goudie, I.B.J., Halley, J., Jehle, R. and Boehme, L.B. 1926: The birds of North Ossetia and Ingoushia (with the adjoining regions). *Bulletin Scientifique de l´ Institut de l´ Exploration Regional du Causase du Nord*, **1**: 1-274.

Burt, S.A., Vos, C.J., Buijs, J.A. and Corbee, R.B. 2021: Nutritional implications of feeding free-living birds in public urban areas. *J. Anim. Physiol. Anim. Nutr.*, **105**: 385-393.

Chace, J.F. and Walsh, J.J. 2006: Urban effects on native avifauna: a review. Landsc. Urban Plan., **74**: 46-69.

Clark, D., Whitney, J.J., MacKenzie, K.G., Koenen, K.K.G. and DeStefano, S. 2015: Assessing gull abundance and food availability in urban parking lots. *Hum.-Wildl. Interact.*, **9**: Article 7.

Cramp, S. (ed.) 1988: Handbook of the birds of Europe the Middle East and North Africa. The birds of the Western Palearctic. Volume V. Tyrant Flycatchers to Thrushes. Oxford University Press, Oxford, New York.

Del Hoyo, J., Elliott, A. and Christie, D. (eds.) 2005: Handbook of the birds of the world. Volume 10. Cuckoo-shrikes to Thrushes. Lynx Editions, Barcelona.

Delestrade, A. 1995: Impact of human activity on foraging flocks and populations of the alpine chough *Pyrrhocorax graculus*. *Avocetta*, **19**: 189-193.

Dick, W. and Holupirek, H. 1978: Über die Alpenbraunelle auf dem Territorium der DDR. *Falke,* **25**: 308-312.

Drovetski, S.V., Semenov, G., Drovetskaya, S.S., Fadeev, I.V. Red'kin, Y.A. and Voelker, G. 2013: Geographic mode of speciation in a mountain specialist avian family endemic to the Palearctic. *Ecol. Evol.*, **3**: 1518-1528.

Dyrcz, A. 1976: Contributions to the biology of Alpine Accentor. *Notatki Ornitologiczne,* **17**: 79-92.

Dyrcz, A. and Janiga, M. 1997: Alpine Accentor – *Prunella collaris*. In: *The EBCC atlas of European breedingbirds: their distribution and abundance* (eds. E.J.M. Hagemeijer and M.J. Blair), pp. 510. T & AD Poyser, London.

Ferianc, O. 1979: Vtáky Slovenska 2. Veda, Bratislava.

Fischer, J.D. and Miller, J.R. 2015: Direct and indirect effects of anthropologic bird food on population dynamics of a songbird. *Acta Oecol.*, **69**: 46-51.

Géroudet, P. 1957: L´ Accenteur alpin. In: *Les Passereaux III,* pp. 49-54. Delachaux et Niestlé, Neuchätel, Swiss.

Haemig, P.D., Sjöstedt de Luna, S., Blank, H. and Lundqvist, H. 2015: Ecology and phylogeny of birds foraging at outdoor restaurants in Sweden. *Biodivers. Data J.*, **3**: e6360.

Heer, L. 1998: The polygynandrous mating system of the Alpine Accentor *Prunella collaris,* indivdual reproductive tactics, breeding adaptations on high mountain conditions and winter ecology. PhD thesis, Institute of Zoology, University of Bern.

Heer, L. and Fraenkl, A.C. 1999: Zur Verbreitung, sozialen Organisation, Raum- und Habitatnutzung der Alpenbraunelle *Prunella collaris* in Winter. *Orn. Beob.*, **96**: 25-36.

Henry, P.-Y. 2011: Differential migration in the polygynandrous Alpine Accentor *Prunella collaris*. *Bird Study*, **58**: 160-170.

Hudec, K. (ed.) 1983: Fauna ČSSR. 23. Ptáci – Aves. Díl III/1. Academia, Praha.

Huerta-Sánchez, E., Jin, X., Asan, Bianba, Z., Peter, B.M., Vinckenbosch, N., Liang, Y., Yi,X., He, M., Somel, M., Ni, P., Wang, B., Ou,X., Huasang, Luosang,J., Cuo, Z.X.P., Li, K., Gao, G., Yin, Y., Wang, W., Zhang, X., Xu,X., Yang, H., Li, Y., Wang, J., Wang, J. and Nielsen, R. 2014: Altitude adaptation in Tibetans caused by introgression of Denisovan-like DNA. *Nature,* **512**: 194-197.

Janiga, M. 1998: Diet, the reason of the first steps of synanthropy in high altitude birds. In: *Proceedings of the VII International Congress of Ecology, 19-25 July 1998*, (eds. A. Farina, J. Kennedy and V. Bossú), pp. 206. Firenze, Italy.

Janiga, M. 2020: The biology of the Alpine accentor *Prunella collaris*. IV. Maintenance activities and their clusters from late autumn to early spring. 20 year observation. *Oecologia Montana,* **29**: 28-38.

Janiga, M. 2021: Biology of alpine accentor (*Prunella collaris*) VI. Interspecific relationships among alpine accentors and other species of birds during winter. *Oecologia Montana*, **30**: 85-99.

Janiga, M. and Novotná, M. 2006: Feeding preferences and foraging behaviour in the Alpine Accentor *Prunella collaris*. *Ornis Fenn.*, **83**: 170-180.

Jeenbaev J.J. (ed.) 2007: Problems of mountainous countries (by the example of Kyrgyzstan). Threats and challenges of modern times. National Academy of Sciences of the Kyrgyz Republic, Bishkek.

Jones, D.N. and Reynolds, S.J. 2008: Feeding birds in our towns and cities: a global research opportunity. *J. Avian Biol.,* **39**: 265-271.

Kovshar, A.F. 1966: [Birds of Talas Alatau.] Kainar, Alma Ata (in Russian).

Liu, B., Alström, P., Olsson, U., Fjeldsa, J., Quan, Q., Roselaar, C.S., Saitoh, T., Yao, C.-t., Hao, Y., Wang, W., Qu, Y. and Lei, F. 2017: Explosive radiation and spatial expansion across the cold environments of the Old World in an avian family. *Ecol. Evol.*, **7**: 6346-6357.

Martí, R., Gómez-Manzaneque, A. and Perales, J.A. 1988: Invernada del acentor alpino (*Prunella collaris* Scop.) en los altos niveles de la Sierra de Gredos (Sistema Central). *Ardeola*, **35**: 143-146.

Martín-Vivaldi, M., Marín, J.M. and Villar, M. 1995: Seleccion de habitat, tamaño de bando y movimientos locales del accentor alpino (*Prunella collaris*) en Sierra Nevada (se de Espaňa). *Ardeola,* **42**: 11-30.

Plummer, K.E., Bearhop, S., Leech, D.I., Chamberlain, D.E. and Blount, J.D. 2013a: Fat provisioning in winter impairs egg production during the following spring: a landscape-scale study of blue tits. *J. Anim. Ecol.*, **82**: 673-682.

Plummer, K.E., Bearhop, S., Leech, D.I., Chamberlain, D.E. and Blount, J.D. 2013b: Winter food provisioning reduces future breeding performance in a wild bird. *Sci. Rep.*, **3**: 1-6.

Praz, J.C. 1976: Notes sur l, Accenteur alpin *Prunella collaris* dans le Val d´ Hérens (Valais). *Nos Oiseaux*, **33**: 257-264.

Robb, G.N., McDonald, R.A., Chamberlain, D.E. and Bearhop, S. 2008: Food for thought: supplementary feeding as a driver of ecological change in avian populations. *Front. Ecol. Environ.,* **6**: 476-484.

Schifferli, A., Géroudet, P. and Winkler, R. 1980: Verbreitungsatlas der Brutvögel der Schweiz/Atlas des oiseaux nicheurs de Suisse. Schweizerische Vogelwarte/ Station ornithologique suisse, Sempach.

Schmidt, E. 1985: The Alpine Accentor (*Prunella collaris*) in Hungary. *Aquilla,* **92**: 105-111.

Šťastný, K. and Hudec, K. (eds.) 2011: Ptáci – Aves. III/1. Academia, Praha.

Svoboda, J.A. 2014: Předkové. Evoluce člověka. Academia, Praha.

Soukup, V. 2015: Prehistorie rodu Homo. Karolinum, Praha.

Tyrberg, T. 1991: Arctic, montane and steppe birds as glacial relicts in the Western Palearctic. *Orn. Verh.*, **25**: 29-49.

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