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Biology of the Alpine Accentor *(Prunella collaris)* XI. Inter-individual transfer of information about the wintering site. 16-year study

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Abstract. This study represents a 16-year effort to learn about the transfer of overwintering habitat information in Alpine Accentors, encompassing at least three generational replacements. The effects of individual age, position in the flock hierarchy, and presence at local wintering sites were consistently examined. Banding with a combination of colored rings made it possible to identify birds individually over many years. Banded birds were given specific names to better differentiate their behaviour. The study is supported by many minute records of the maintenance activities of individual animals. Of the 27 birds accurately identified between 1987 and 2022, only four were important for the transmission of wintering location information among birds. The birds first arrived there as yearlings, gradually adapted to the environment as residents, and became -dominant individuals in the wintering flocks. Yearlings usually show little caution when feeding on the site, while young adults, two to three years old, appear to be the most cautious. Six- and seven-year-old adults exhibit less cautious behavior, likely related to their experience. If these birds occupy dominant positions in the hierarchy of a wintering flock, they can feed quickly on familiar food sources and consequently spend considerably more time resting, drilling and preening in safe places. Subordinate birds spend more time trying to feed, which increases their risk of predation. The research provides important insights into how wintering grounds for birds disappear after a ski resort undergoes complete reconstruction. Maintaining wintering grounds requires not only suitable food sources, but also habitual conditions for rest, sunbathing, protection, and temperature regulation. In November and December, two groups arrived that behaved differently and only formed a more cohesive structure as winter progressed in January and February. The distance they kept from humans decreased from November and December to March in the spring. They arrive at their wintering grounds in November, well-fed, with adults weighing over 40 g. Size and weight do not necessarily determine alpha position in the flock (e.g., No. 25). Moreover, hierarchy among adults in winter flocks can change from a year to year. The history of some individuals, such as No. 119, shows that even though they were older and smaller, they had an alpha position in the flock. This suggests that dominance may be based not only on size, but also on experience.

Research shows that not all of the flock remains at the wintering site. Some used the location as a temporary stopover in November during migration (No. 9 or 11), while others used it as a stopover in March on their return from other wintering grounds (No. 6), and some only occasionally stayed at the site, for example, in December (No. 24). Some individuals stayed at the site permanently (residents) but remained on the surrounding rocks and did not fly down to search for food from people (No. 4). These individuals flew away with the others from the site to their roosts in the evening. Information transmission obviously requires experienced resident individuals who return to the site for several years. From them, new individuals learn to know not only the location of the site but also the local conditions, and where and how to forage. It is the resident bird that shows several incoming birds the site over several years. Some of them get used to the site in the process of learning this information. In the following years, these newer individuals become residents and play a key role in transmitting information about the wintering site to subsequent generations. Research shows that it is important for the long-term existence of the wintering site and for information transmission, that adults arrive with young yearlings. Some of these yearlings become residents of the wintering site, transmitting information to different generations each year. Some young birds may stay in their wintering grounds for 5–6 years after settling in, while other young birds that appear there in their first year never return. Some individuals observed alone at various wintering sites may play a vital role in helping other birds remember information about those sites in subsequent years (e.g., individual No. 119 in 1993/1994).

To realistically study the impact of size or age on the evolution of differential migration, we must cover all age groups of birds in a flock. In the case of Alpine Accentors, it is incorrect to

conduct a study for only three or four years and categorize individuals based on their external appearance as yearlings or older adults. This leads to misleading results that do not reflect actual natural processes. This study is exceptional because the age of most individuals was known, allowing us to compare the behavior of several age categories.

Key words: Alpine Accentor, *Prunella collaris*, *winter site information transmission*, the Great Fatra National Park, the West Carpathians

Introduction

All avian social systems are fundamentally determined by the states of the individuals within them and the social relationships between those individuals. Many bird species show an irregular mixture of social and individual behavior. In birds, the transfer of information about what individuals have found can occur either at a roost or at one of the feeding sites used in the morning feeding bout (Lefebvre and Giraldeau 1984). At roosts, especially early in the morning or later in the commuting flight, the physical behavior of successful individuals is likely to signal their intent to forage. These individuals may attract followers. The transmission of information may also be more direct, as perching birds see other commuting individuals flying rapidly to the feeding area. These birds may be "driven" or attracted by those in flight. Although the initial intention to forage occurs at the roosting site, the first feeding site represents the primary center for direct information transfer (Lefebvre and Giraldeau 1984), because individuals that congregate at the feeding site in one day may roost overnight at different sites (Nakamura *et al.* 1996). Transfer from individual to social structure behaviour changes pathways of information transmission. In addition to the enhanced communication provided by groups, other feeding advantages of group foraging, especially in severe winter conditions, lie in the number of trained eyes that are used to search for food. Some birds are better at finding food than others, which influences their daily behavior (Janiga 2020), and the others usually take advantage of what the former have found (Giraldeau and Lefebvre 1986). Learning individuals acquire information about novel food sources from those with whom they forage. Furthermore, unexperienced individuals preferentially use the information provided by the bird that produces the relevant information (Firth *et al.* 2016). Individuals who search and follow may well differ from one foraging situation to another, so that sometimes the search efficiency of an individual foraging in subset A benefits individuals in subset B, and sometimes the opposite is true. This is called the skill-pool effect (Giraldeau 1984). The behavior can also be formatted into the second hypothesis, wherein producers locate the food and start eating, and then are quickly joined by scroungers, or other individuals that do not locate their own food source. Former scroungers may become producers when former producers die or disappear. Moreover, individuals exchange roles in response to food type and group composition, and the producer-scrounger effect cannot be explained by dominance or variation in individual learning ability (Giraldeau and Lefebvre 1986). This suggests that there is a variable flock membership that characterizes, for example, winter groups of Alpine Accentors (Nakamura *et al.* 1996).

Individual age is an important and relevant state to consider when understanding any social system, as age shapes many aspects of avian social behavior (Forslund and Pärt 1995; Froy *et al.* 2013). The interaction between individual age and sociality has multiple consequences for individuals, groups, and the broader population (Firth *et al.* 2024). It is likely that all young accentors, regardless of native endowment, will be scroungers, at least for a time. Although the term has a pejorative ring, young birds may as well be considered learners, which would make the phenomenon of a teacher-student effect common to many vertebrate groups. Individuals will adopt a novel behavior if they have seen it leading others to food (Lefebvre 1986). This novel foraging behavior can then spread naturally through a bird population. The ability of young birds to learn by observation and local reinforcement facilitates the rate at which the behavior spreads through the population (Lefebvre 1986). Many bird species, including Alpine Accentors, have been observed to use repeated flight paths to wintering sites, suggesting that they may "know" where they are going (Janiga 2020, 2021; Monier 2024) and young birds may learn the directions of the paths (Henry 2011). Birds can search for food directly using visual, olfactory, and auditory cues. However, many species, including accentors, may also look for indicators of the presence of the food source. Indirect food cues include, for example, the concentration of many species of small birds at feeders or the presence of tourists and skiers at winter resorts. The search strategy used may depend on environmental factors such as food availability, as well as the memory, condition, or preferences of the individual bird, and many studies have omitted the quality of the winter roosting site (Walsberg and King 1980). If there is enough food at the feeding site in winter, birds may spend more time roosting, sitting, preening, sleeping or singing (Janiga 2020; Monier 2024)

The mixture of social and individual behaviour in accentors is complex (Davies *et al.* 1995, 1996 ; Heer 1998) and worth investigating, particularly during the winter season (Martí *et al.* 1988; Nakamura *et al.* 1996; Heer and Fraenkel 1999; Henry 2011). Considering that age, roost quality, sufficient food, dominance and sex play a very important role in information transfer in Alpine Accentors, short-term studies of one to four years are not sufficient to understand how information transfer on wintering location occurs in this species. (Martí *et al.* 1988; Martín-Vivaldi *et al.* 1995; Nakamura *et al.* 1996; Henry 2011). Based on colour ringing, we know that a certain proportion of experienced individuals live to be six years or older, therefore, it was particularly necessary to consider a longer study period when investigating the effect of age. This study represents a 16-year effort to learn about the transfer of overwintering habitat information in Alpine Accentors, encompassing

at least three generational replacements. The effects of individual age, position in the flock hierarchy, and presence at local wintering sites were consistently examined. Banding with a combination of colored rings made it possible to identify birds individually over many years. Banded birds were given specific names to better differentiate their behaviour. In addition, this study, which is exceptional in its own way, is supported by many minute records of the maintenance activities of individual animals.

Material and Methods

Field work

Field work was conducted between 1984 and 2005 in the Great Fatra Mountains National Park, at the Malinô Brdo ski resort (Fig. 1.). In general, birds were monitored from the beginning of November to the end of April. The survey area was limited to the ski resort, approximately 1 km long and 2 km wide, where accentors were found near hotels, guesthouses or restaurants. Daily visits lasted a minimum of five hours, but many visits lasted from dusk to dawn. 27 birds were captured using a cheese/millet-baited fall trap. Each bird was individually marked with color rings and measured. Ringed birds were individually distinguished and resighted in subsequent years. Binoculars of various powers were used for observation. Behavioral notes were simply written or dictated on tape. Many ringed individuals were also videotaped. To better facilitate observation of dominance, one or two artificial feeding grounds were established. Beginning in the 1988/89 season, a food consumption and food preference survey was conducted at a feeding site (feeder) where birds were offered different types of food. A portable video cassette recorder (SONY) was placed 7-10 m from the artificial feeding site. Video observation lasted several hours, depending on weather conditions, frost, snow, storm, etc. The number of visits made by each individual, the duration of stay, and the number of pecks were analyzed. In some cases, the weight of food consumed was measured. The recordings were later analyzed in the laboratory. A detailed classification of behaviors has been described in studies by Janiga and Romanová (1996, 1997) and Janiga (2020). The following episodes were recorded: feeding, standing (sitting alert), sitting drowsily (often sleepy). For this study, maintenance activities such as grooming, drilling, sunning, or singing are included in the category of drowsy sitting. The term general maintenance activities is used according to McFarland (1987). The feeding category includes foraging. The sitting alert category reflects a stressful time for a bird, while the opposite category, sitting drowsily, reflects rest and security.

Social dominance

The following types of interactions were observed at the feeding grounds to determine dominance rank: A bird is said to demonstrate dominance over another when it successfully chases the other away from a food source. This could mean that a bird made a successful attack and displaced another bird from the food source, or that a bird approached the feeder and the other birds withdrew. Another possibility is that a bird causes another bird to wait until it has finished feeding. At feeding grounds where food was offered by tourists, or at natural feeding grounds, such as snow-melting islands or meadows, hierarchy was determined by observing winners and losers. A bird was considered a winner if it displaced a competitor. Avoidance at the resting site was also considered a hierarchical relationship between two birds. Each ringed member of a wintering group was classified. A bird ranked first was classified as alpha (dominant); a bird ranked second was classified as beta; and so on. The order of Greek alphabet letters indicates the hierarchy among individuals.

Fig. 1. A very suitable wintering place for the birds was a hotel in the area, completed in 1960 (left). Under the roof, the birds could walk around the perimeter, rest in the shelter during snowstorms, sing in spring and catch emerging insects from the cracks in the wood. It is very likely that this has been a wintering site for *Prunella collaris* since the 1960s. The first decline in wintering birds between 1989 and 1994 seems to correlate with the changing political situation, namely, the end of socialism and the major reconstruction of the resort. When the hotel began to under reconstruction, an attic was added and the roof was replaced, making it impossible for birds to rest under the eaves (right). The completion date for the extension was 1999. Until the winter of 2001/2002, birds continued to visit the wintering site. The last one left in the winter of 2002/2003. After that, the wintering site virtually disappeared (Photos: www/hotelmalina.sk/historia and M. Janiga)

Age and sex

The distinction between males and females was confirmed in several ways: through the discriminant analysis proposed by Heer (1994), the sometimes markedly different coloration of the chin and throat, and the thickness of the tarsometatarsus. Males often sang subsongs (trills). Subsong and subsequently also song activity increased in spring and was particularly intense on sunny days in March and early April, but also in November. On such sunny days, several males could be seen singing in close proximity on the roof of the hotel. The males usually change from sub-song to full song in late April, usually when the females arrive at the breeding sites. Females have their own distinctive song, which is distinct from the sub-song of the males. Females start singing and trilling only during their fertile period, which is during nest building and usually one week before the laying of the first egg (cf. Hartley *et al.* 1995 or Langmore *et al.* 1996). Yearling birds differed from older individuals by primary feather and wing cover wear, sometimes also by eye color and morphometric characteristics (Heer 1994, 1999, Gil *et al.* 2007). Dominance was determined in a number of ways: subordinates were chased away from food or feeders by the dominant, or waited for the stronger individual to feed; and when roosting on the roof of a hotel, the subordinate bird stepped out of the way of the dominant or flew around it. A bird was considered stronger or more dominant if it exhibited this behavior at least five times in a given month in a conflict with another individual.

Birds

The overwintering site was already known in the early 1980s (Hudec 1983). In the winter of 1993/1994, there was only one individual wintering at the site. This was crucial for providing information about the site to new wintering birds. Individually marked birds were given names, the group up to 1994 had names ending in "- slav". Birds observed and marked from 1995 onwards were given names ending in "- mír". In Slavic languages, '-slav' usually means 'glory' and '-mír' can be translated as 'world' or 'peace'. An index number from the author's database of *Prunella collaris* specimens follows each name.

Víťazoslav – 3. Young bird: Length (mm): wing – 90, tarsometatarus – 24.8, tail – 64, body weight - 35 g (26/03/88), parasites – *Philopterus, Analges, Proctophylodes* – examined but not found. Less than one-year-old (1987/88), at least **three years** old in 1990.

Radoslav – 4. Adut: Length (mm): wing – 105, tarsometatarus – 26.2, tail – 73.5, (26/03/88) parasites – *Philopterus, Analges, Proctophylodes* – examined but not found. At least **four years** old in 1990.

Jaroslav – 5. Adult: Length (mm): wing – 102.6, tarsometatarus – 28, tail – 74, body weight 41g (26/03/88) parasites – *Philopterus, Analges, Proctophylodes* – moderately parasitized (mites) in 1988. At least **six years** old in 1992.

Svätoslava – 6. Adult: Length (mm): wing – 102.4, tarsometatarus – 26.9, tail – 71, body weight 40g (26/03/88) parasites – *Philopterus, Analges, Proctophylodes* – heavily parasitized (mites, mainly *Proctophylodes*) in 1988.

Branislav – 7. Adult: Length (mm): wing – 102.4, tarsometatarus – 30.2, tail – 69, body weight 44g (02/04/88) parasites – *Philopterus, Analges, Proctophylodes* – Moderately parasitized (mites, mainly *Proctophylodes*) in 1988.

Vratislav – 8. Adult: Length (mm): wing – 105.6, tarsometatarus – 30.3, tail – 64.5, body weight 44.5g (04/04/88) parasites – *Philopterus, Analges, Proctophylodes* – A few parasites (*Proctophylodes*) in 1988. At least **six years** old in 1992. It was a key bird for transmitting information about the wintering site to other individuals.

Dobroslav – 9. Adult: in 1988. Ringed: 05/04/1988. At least **three years** old in 1989.

Stanislav – 10. Young: Length (mm): wing – 100.7, tarsometatarus – 31.1, tail – 69, body weight 35g (15/04/88). Moderately parasitized (mites, mainly *Proctophylodes*) in 1988.

Miloslav – 11. Adult: Length (mm): wing – 104.8, tarsometatarus – 30.4, tail – 73, body weight 45g (15/04/88), 43g (22/11/88). Moderately parasitized (mites, *Analges*, mainly *Proctophylodes*) in April 1988. At least **three years** old in 1989.

Ladislav – 23. Adult: Length (mm): wing – 102, tarsometatarus – 30.4, tail – 68, body weight 43g (22/11/88). Parasites not found in November 1988. At least **five years** old in 1991. Dominant, nice male.

Ľuboslava – 24. Adult: Length (mm): wing – 102.4, tarsometatarus – 30.3, tail – 73, body weight 44.5g (08/12/88). Moderately parasitized (lice) in December 1988. At least **two years** old in 1989. The bird flew to the site very rarely. It was observed only this winter.

Bohuslav – 25. Adult: Length (mm): wing – 104.5, tarsometatarus – 31, tail – 73.3, body weight 47g (11/12/88), 43.5g (23/02/91) Moderately parasitized (mites - *Proctophylodes*) in April 1988. At least **five years** old in 1991.

Vladislav – TB. Adult: an individual that has not been captured, but which could be distinguished by the original patches on the plumage. At least **two years** old in 1989.

Levoslav - 39. Young bird: Length (mm): wing – 103.1, tarsometatarus – 31.3, tail – 77, body weight 37g (03/03/90). Moderately parasitized (mites, more *Analges, Proctophylodes*) in March 1990.

Kvetoslav – 40. Old adult: Length (mm): wing – 102, tarsometatarus – 30, tail – 76, body weight 41g (03/03/90). Moderately parasitized (mites - *Analges, Proctophylodes*) in March1988. At least **two (but surely more) years** old in 1991.

Miroslav - 119. Young bird: Length (mm): wing – 100.2, tarsometatarus – 30, tail – 69, body weight 36,5g (10/02/91), 42,5g (09/01/96). At least **seven years** old in 1997. It was a key bird for transmitting information about the wintering site to other individuals.

Bronislav – 168. Young adult: Length (mm): wing – 106.7, tarsometatarus – 33, tail – 80, body weight 45g (15/03/92), At least **two years** old in 1992.

Drahoslav – 169. Old adult: Length (mm): wing – 106, tarsometatarus – 30, tail – 78, body weight 44g (20/03/92), At least **two (probably more) years** old in 1992. An individual with a very worn feather.

Ľubomír – 203. Young bird: Length (mm): wing – 99, tarsometatarus – 30, tail – 73, body weight 38g (08/01/95). Known to site by old bird (Miroslav) but not seen in subsequent years. Worn feathers. Even young birds may have worn feathers at the beginning of the year. The appearance of this young bird, which no doubt flew in to follow the adult Miroslav, can be seen as Miroslav's first attempt to bring other birds into the wintering area, after having been here on his own last year. This attempt failed. In the area, a major reconstruction of the winter sports centre has begun.

Vladimíra – 212. Young bird: Length (mm): wing – 98.6, tarsometatarsus 29.5, tail – 75, body weight – 38.5 (17/02/96). Known to site by old bird (Miroslav) but not seen in subsequent years. Worn feathers. Even young birds may have worn feathers at the beginning of the year. **This female was seen together with other Alpine Accentors in the Malá studená valley in the Central Tatras on October 11th, 1999.** The linear distance between the place of wintering and the place of autumn sighting was about 70 km. The bird was at least **four years old** at that time. She only stayed in the wintering grounds for a year, after which she didn't appear there again. It is very likely that she also followed Miroslav. The same is true of the males - Mojmír and Slavomír - who appeared the following year and took over the wintering grounds.

Mojmír – 210. Young bird: Length (mm): wing – 97, tarsometatarsus 29.6, tail – 70, body weight – 40g (09/01/96), 37g (22/03/98). Known to site by old bird (Miroslav), At least **three years** old in 1998. Parasites examined, not found in March 1998.

Slavomír – 211. Young bird: Length (mm): wing – 100, tarsometatarsus 29.8, tail – 70.4, body weight – 39g (17/02/96). Known to site by old bird (Miroslav), At least **three years** old in 1998. It was a key bird for transmitting information about the wintering site to other individuals.

Jaromír – 230. Young bird: Length (mm): wing – 100.4, tarsometatarsus 30.5, tail – 73, body weight – 36.5g (22/03/98). At least **six years** old in 2003. Moderately parasitized (mites – both *Analges* and *Proctophylodes*) in March 1998 Jaromír, as a young bird, was shown the wintering grounds by both Slavomír and Mojmír in the winter of 1997/98. In the following years Jaromír became an important transmitter of information about this wintering site to other accentors. 2002/2003 was the last season when Jaromír appeared alone at the location. In the following years, the accentors did not appear at this wintering site anymore.

Tichomír – 247. Adult: Length (mm): wing – 105.7, tarsometatarsus 30.6, tail – 74, body weight – 41.3 g (20/02/99). Judging by the grey colouring, it was an old bird, more than three years old. It was heavily parasitised by mites (*Analges* and *Proctophylodes*) in February 1999.

Radomír– 254. Young adult: Length (mm): wing – 10O, tarsometatarsus 31, tail – 71, body weight – 42.5 g (20/01/2000). Heavily parasitised by mites (*Analges* and *Proctophylodes*) in January 2000. At least **four years** old in 2002.

Drahomír – 255. Young adult: Length (mm): wing – 99, tarsometatarsus 30, tail – 69, body weight – 42 g (06/03/2000), 46g (09/01/2002). Heavily parasitised by mites (*Analges* and *Proctophylodes*) in March 2000.). At least **four years** old in 2002.

Kazimír – 265. Adult: Length (mm): wing – 104.5, tarsometatarsus 30.4, tail – 75, body weight – 48 g (12/01/2002). At least **two years** old in 2002.

Results

Description of wintering behavior and numbers in different years

1984/1985

There were 10 birds on the site, they stayed until March 31, 1985 (Fig. 2). They collected ski leftovers from around the restaurant by the ski lifts, and around the hotel. In March they started to catch insects (flies) from under the hotel roof, as well as food on the asphalt. When the grass islands appeared in March; they had already begun to collect food on them. Birds were present here on sunny days, especially in February. On April 8, they were no longer seen at the site. It was a typical winter at the site, with a lot of snow and the beginning of the snow melt in March. The birds usually kept a distance of at least one metre from each other, both when resting and feeding, in the middle of the winter they also fed on bread.

1985/1986

Individuals maintained a distance of at least one meter when feeding or roosting. In November 1985 there were 9 birds, but two of them behaved distinctly from the other seven. The birds can pick up bread, bring it under the roof and feed there, they make contact by trilling while feeding. In November, birds also looked for insects under the roof, and fed on biscuits, sausage scraps and greasy leftovers like bread with butter. The dominant individual could make all the others in the hierarchy fly away. If one saw himself alone during an evening flight, he would

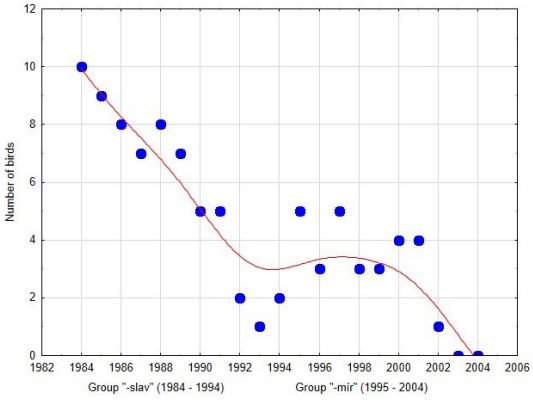

Fig. 2. Maximum number of wintering *Prunella collaris* birds observed at Malinô Brdo, Great Fatra National Park in the corresponding winter season. The presence of birds was monitored from November to April. The years on the x axis mark the beginning of the winter season. Often fewer birds were observed at the site. The numbers indicate their maximum abundance, which was determined by direct observation of the birds and later by ringing them with coloured rings. The curve represents a line of distance-weighted least squares (STATISTICA 12 software, Stat Soft CR).

fly to the roof and call the others. Their presence depended on the weather; if it snowed all day (e.g. in February or March), they stayed at the feeding place all day. With the beginning of March, the escape distance from humans was shorter than in November, as if they had gotten used to skiers. They were very attracted to the scraps of meat; subordinates kept a distance of about 4 meters from dominants when waiting to be fed. **There were at least two different groups meeting at the wintering grounds.**

1986/87

A hotel employee fed them butter and poppies through a feeder at the window, they preferred poppies, when searching for food the subordinates had to try to find food elsewhere than at the feeder and had to warm their feet more by rubbing against their fluffy feathers. They also fed on plant seeds on the ground or on the hotel garbage dump, they used every moment when people were not around to bring their food scraps to the roof (bread - December, January). When islands of grass appeared after the snow melted, they moved to them, feeding in places already without snow (warm February). When a sparrowhawk (*Accipiter nisus*) flew over, they all became immobile (this is how they react to the sparrowhawk even in the summer season). The one that flew first into the trees near the hotel gave the order to leave in the evening. It is likely that there were two groups of 4 + 4, the other four did not show up at the site when the weather was unfavorable, as if the site was more suitable for roosting than for feeding.

1987/88

This was the winter season when research by color ringing began. Vratislav was a known bird from the previous year. The birds fed on scraps of meat, bread, butter, biscuits, rolls, and in March and April, after the snow melted, they fed on islands of grass (April - Radoslav, Branislav, Vratislav, Dobroslav, Stanislav and Miloslav – for the names see Tables 1 and 2). Accentors are rarely seen **bathing**. In summer they often take advantage of the rain in the mountains, but in winter after the frost they don't bathe, they just clean themselves quite often. On wintering grounds, when temperatures rise above freezing in March, bathing is probably also a way to get rid of parasites. The procedure is as follows: First, the bird simply walks up to the puddle and dips its head, or just its bill, as if testing the water. Then it goes into the water with its whole body, feet submerged. Then it dips its head and throws the water back on its body. After swimming with its head, it begins to shake its tail in the water until it is completely wet. Then it comes out, preens with its beak, stretches its tail and wings wide in the sun, shakes off the water, and dries in the sun. Sometimes it sits down and preens. The position of Vratislav in the hierarchy of the wintering flock is noteworthy. He didn't appear as often as some of the other individuals living in the wintering grounds (Table 2 – common), but in the future proved that he was a very important individual for the transmission of information.

Fig. 3. Radoslav (Tables 1 and 2), March 26th, 1988. Radoslav was a bird that did not feed at the site in March 1988, he sat alert and was the individual that alerted the other foraging accentors. In the winter of 1988/89, he was the most alert individual, he did not feed near people at all, he also perched on nearby birch trees, and he was especially able to activate Vratislav (8) when he flew out. Radoslav must have noticed the behavior of the other accentors in the winter resort from the surrounding rocks, because he knew in the evening that they wanted to fly away, and he was the fourth to join them when they flew away. In the winter of 1989/90 it was only a March migrant, feeding little and using the site for both drowsily and alert sitting. So more for resting. This season the bird was very low in the hierarchy, an ε - subordinate individual. Photo: M. Janiga

1988/89

November. The arrival of accentors on their wintering grounds in November was undoubtedly triggered by the first intense snowfall. On November 14, 20 cm of snow fell in this area within two hours. There was more heavy snowfall on November 21 and 23. Miloslav and Dobroslav appeared with Vratislav and one un-ringed bird. The first two birds were only visitors in November and likely moved on to other wintering sites. Malino Brdo was only a temporary stopover for them. They were not seen at the site from December

onward and did not show up again in subsequent years (see Tables 1 and 2). However, Vratislav's role is important to note. He was dominant at the site the previous year and became key in transmitting information about the wintering site to other birds.

December. At the end of November, Ladislav was ringed in the company of Vratislav. In early December, Ľuboslava and Bohuslav were ringed; Bohuslav was not present in November. There was also a change in the birds' hierarchy in this year. In December, Vratislav was subtly dominant over Ladislav and equal to Bohuslav. With the arrival of spring, the hierarchy changed, and Ladislav became dominant (Tables 1, 2). In December, the birds fed on bread, poppy seeds, and biscuits left by tourists. Vratislav often fed with Bohuslav or let him feed while Vratislav remained alert. The most impressive feat was making 62 pecks per minute when food was found, which was approximately one peck per second. During snowstorms, the birds would swoop down to feed after the skiers vacated the outdoor seating on the benches. Subordinate Bohuslav flew in first, followed by Vratislav; Ladislav was the last to come down and feed. The bird was always the most careful. The sequence was the opposite when humans flushed them out. Ladislav was the first to fly out, followed by Vratislav. Bohuslav, the subordinate, attempted to feed for as long as he could. He was the bravest. Due to his dominant position, Ladislav spent the least time feeding. The other individuals had to wait when a food source was found. The three birds behaved this way throughout the entire winter period.

January and February. A young bird Vladislav appeared at the site. The birds were feeding on a similar diet as in December. In late January, the snow on the southern slopes disappeared, as it was warm. At that time, the birds did not appear at the site, although people were skiing and leaving garbage. February was also a relatively warm month. Ladislav, Vratislav, and Bohuslav took turns showing up at the site, proving that birds behave differently during a warmer winter. Sometimes young birds like Vladislav or another uncaptured, unringed bird accompanied them. During this time of year (February and March), when it was wet during the day and starting to frost in the evening, the danger of ringing birds with metal rings became apparent. For example, the snow froze on Vratislav's ring, covering about one cubic centimeter. This bothered him very much in the evening when walking, and the bird kept trying to remove it with his beak. This never happened with plastic-colored rings. On frosty days, the birds used the snow as a water source. Although Vratislav was subordinate to Ladislav, he, as the most experienced bird, decided when to leave the site for the roost in the evening. He flew up to the roof of the hotel and called to the other accentors to fly away. Only then did Ladislav and finally Bohuslav join him.

March. At the beginning of March, the cold and snow returned. Bohuslav still had the slightest fear of people, but Vratislav and Ladislav were much more cautious. Ladislav began singing subsongs intensively, and by the end of March, Bohuslav started singing as well. Vratislav, the most experienced, also sang, but not as often or as intensely as Ladislav. During their songs, the birds sat about one meter apart. In March, they sometimes came to feed as early as 3:00 a.m. Once the snow melted, they started looking for food in the fallen grass. Vratislav always initiated the evening departure from the site, and Bohuslav was always the last one to depart. Radoslav (4), a spring transmigrant, had to stay in the rocks near the hotel all day. He never flew to feed on people's garbage. Instead, he flew with the birds to the site in the morning and with them again from the site in the evening. Radoslav must have been able to perceive the birds from a great distance. He arrived in the evening to activate their departure and flew to the roosting sites first. The others joined him. Vratislav and Ladislav were close at times, sometimes managing to sit drowsily side by side, even within 30 cm of each other.

1989/90

During this winter, Ladislav was the strongest bird on the site. He behaved aggressively toward Bohuslav and, especially, Vratislav. Vratislav could no longer drive Bohuslav away from the feeder; their hierarchy was clearly established this year. During the spring migration, two birds were caught: Kvetoslav, who was second in the hierarchy after Ladislav, and Levoslav, a young bird who was low in the hierarchy. The spring transmigrants — the relatively old birds, Víťazoslav and Radoslav — also had low subordinate positions (Table 1, Fig. 3). In November, while grass seeds were still available under the snow, the birds fed on them. During this winter, the resident birds were threatened by a domestic cat. This was especially dangerous for the inexperienced, low-ranking juvenile Levoslav, who tended to feed for as long as possible. Bohuslav was also used to feeding for long periods despite the danger from the cat. He would often stand on one leg while feeding and look in the direction where he could see the cat. Subordinate birds spend more time trying to feed, which increases their risk of being caught by a predator.

1990/91

Surprisingly, the hierarchy between Vratislav and Ladislav leveled out during this winter. Vratislav, the older bird, no longer yields to Ladislav when feeding, as he did in the previous year. This shows that the hierarchy among adults in winter flocks can change, and it undoubtedly depends on the fitness of the individual. Bohuslav was lower in the hierarchy than these two birds. However, the two older birds brought a young yearling named Miroslav to the wintering site (Table 1). Miroslav was the lowest in the hierarchy, but his role in recognizing the wintering site was crucial for transmitting information about the location to the other accentors. It was also discovered that, even several years after ringing, birds attempt to remove the metal ring from their tarsus with their beak and do not become accustomed to it. Accentors have recorded this wintering site in the context of other limestone peaks in

the smaller mountains of Slovakia. This year, they flew in a westerly direction to the top of Šíp Peak. In February, they fed on visitors' garbage and grass seeds. They also pecked the fruits of dog rose and catkins of hazel trees and caught insects (perhaps flies) under the hotel's roof on warm days.

1991/92

This winter demonstrated the importance of resident birds in transmitting information about wintering sites. It is the resident bird—in our case, Vratislav—that shows several incoming birds the site over several years. Some of them—in our case, the young bird, Miroslav—get used to the site in the process of learning the information. The following year, they become residents and play a key role in transmitting information about the wintering site. After disappearing for a few years, Jaroslav appeared on the site. This old bird was looking for garbage left by tourists. In March, Jaroslav and Vratislav caught flies from under the beams after wintering under the hotel's roof. Vratislav often stood on one leg while feeding, warming the other in his belly feathers. He often sat with his legs curled under his belly and hopped from place to place. Vratislav and Jaroslav were close old birds and could sit side by side at a distance of 30-50 cm. Young Miroslav could carry his bread and cheese under the hotel's roof and eat there safely. The birds were constantly threatened by a cat, which even caught an un-ringed accentor during this year. The new birds, Bronislav and Jaroslav, were just spring transients, and Drahoslav was a very subordinate bird in the hierarchy.

1992/93 – 1995/96

The winter of 1992/1993 was almost snowless, and accentors were only on the site for two weeks in February. They were often only seen in flight, and their rings could not be identified. During the winter of 1993/94, Miroslav was alone at the site. The following winter, 1994/95, the bird stayed with his subordinate, Ľubomír. The winter of 1995/96 was pivotal for the dissemination of information regarding the wintering site. During this period, Miroslav introduced the site to three young birds, Vladimíra (female), Mojmír, and Slavomír (see Tables 1 and 2). At the site, Miroslav demonstrated to both Vladimíra and Slavomír the location of the feeding sites and strategies for searching for scraps left behind by skiers and tourists. Slavomír and Mojmír became crucial for transmitting information about the wintering site in the future.

1996/97 – 1997/98

Miroslav came with only Mojmír and Slavomír. As the dominant bird, he was very tolerant of the weakest, Mojmír. They often fed very close to each other, sometimes only 10 cm apart. Slavomír was most likely to scavenge for food scraps left by tourists. With a piece of bread, he could fly up to the hotel roof and feed there. Mojmír and Miroslav were much more vigilant. During this winter, all individuals were documented roosting on nearby rocks (Haliny, 950 m asl). In December, a common kestrel (*Falco tinnunculus*) was recorded attacking them. It did not catch any of them, but by then, they had all flown away abruptly. The presence and popularity of wintering sites are influenced by more than just the abundance of food; predators also play a role. In February, they were offered a variety of foods, including millet, poppy seeds, crackers, bread, flies, and seeds from other plants, in small bowls that could be filmed. Miroslav consumed up to seven grams of poppy seeds in one morning feeding. Slavomír preferred poppy seeds, while Miroslav and Mojmír fed partly on biscuits and flies in addition to poppy seeds. Miroslav was last seen at the site that winter. This information transmitter shared details about the wintering site with Slavomír and Mojmír. The following winter 1997/98, juvenile Jaromír flew with them and next two un-ringed birds (see Tables 1 and 2, Fig. 2). He was a key bird for future information transmission.

1998/99 – 2003/2004 – the birds finally disappeared from the wintering site

In 1998/1999, Jaromír flew with Tichomír, a subordinate, and one other un-ringed bird. Tichomír used to feed for a longer time than Jaromír. In 1999/2000 and 2000/2001, Jaromír arrived at the site with Radomír and Drahomír, but not Tichomír. In 2001/2002, there was one additional un-ringed bird with them (Fig. 2). Jaromír was the resident and dominant bird (Tables 1 and 2). Radomír and Drahomír were equal birds. They fed on biscuits and bread, as well as garbage left by hikers and skiers. The birds did not benefit much from the hotel's renovation; they lost their favorable resting and singing places. In 2001/2002, Jaromír, Radomír, Drahomír, and a fourth bird, Kazimír, appeared in the area, feeding on garbage left by skiers. In 2002/2003, only Jaromír showed up for the last time. As if to say goodbye to the area, he sat in a tree near the hotel, which had long since been rebuilt and was no longer suitable for birds to rest in. The birds were not seen again in the winters of 2003/2004, 2004/2005, and beyond.

Information transmission, role of young birds and residents

Of the 27 birds observed (Table 1), only 9 were birds that had resided at the site for at least two winter seasons (Table 2), in other words, birds that can be considered to have shown this wintering site to other individuals. Of these, Miroslav, Mojmír, Slavomír and Jaromír had learned to visit the wintering site from older individuals as young yearlings (Table 1). This was probably also the case with Vratislav, who was at the site in the 1986/87 season (he was ringed with metal rings at the time). Only four individuals (Vratislav, Miroslav, Slavomír and Jaromír – Table 2) seem to be key birds out of all 27 birds for transmission of information about the wintering site to other accentors. They first arrived at the site as young yearlings (Table 1), then adapted to the food resources of the site as residents for at least three years, and after some development at the wintering site became α-dominant individuals (Table 1) in the hierarchy of the wintering flock of accentors. These were demonstrably males.

Season	Stanislav - 10	Svätoslava - 6	Branislav - 7	Miloslav - 11	Dobroslav – 9	Víťazoslav - 3	Radoslav - 4	Jaroslav- 5	Vratislav - 8	Ladislav - 23	Bohuslav-25	Ľuboslava-24	Vladislav-TB	Levoslav-39	Kvetoslav-40	Miroslav-119	Bronislav-168	Drahoslav-169	Ľubomír-203	Vladimíra-212	Mojmír-210	Slavomír-211	Jaromír-230	Tichomír-247	Radomír-254	Drahomír-255	Kazimír-265
1987/88	*β	*	*	*	*α	*β	*	*	*α																		
1988/89				*	*		*		*β	*α	*β	*γ	*														
1989/90						*δ	*ε		*γ	*α	*γ			*δ	*β												
1990/91									*α	*α	*β					*γ											
1991/92								*γ	*α							*β	*	*δ									
1992/93																											
1993/94																*											
1994/95																*α			*β								
1995/96																*α				*β	*δ	*γ					
1996/97																*α					*γ	*β					
1997/98																					*α	*α	*β				
1998/99																							*α	*β			
1999/00																							*α		*β	*β	
2000/01																							*α		*β	*β	
2001/02																							*		*	*	*
2002/03																							*				
Sex		F	M	M	M		M	M	M	M	M	F			M	M	M	M		F	M	M	M	M	M	M	M

Table. 1. Identified Alpine Accentors presented at Malinô Brdo, the Great Fatra National Park, Slovakia. To enhance identification, each bird was assigned its own name, which is then paired with an identification number from the author's database. * - Presence of birds in the winter season at the site. Greek letters in the rows indicate the hierarchy between individuals in a particular winter season in the order of the Greek alphabet, - the strongest, dominant individual. Green - juveniles in the first year of life. M - males (identified and confirmed at the end of February, March, April - drilling), F - females. In some birds the sex could not be identified at 100% (mainly young birds).

Season	**Stanislav - 10**	**Svätoslava - 6**	**Branislav - 7**	**Miloslav - 11**	**Dobroslav – 9**	**Vítazoslav - 3**	**Radoslav - 4**	**Jaroslav- 5**	**Vratislav - 8**	**Ladislav - 23**	**Bohuslav-25**	**Ľuboslava-24**	**Vladislav-TB**	**Levoslav-39**	**Kvetoslav-40**	**Miroslav-119**	**Bronislav-168**	**Drahoslav-169**	**Ľubomír-203**	**Vladimíra-212**	**Mojmír-210**	**Slavomír-211**	**Jaromír-230**	**Tichomír-247**	**Radomír-254**	**Drahomír-255**	**Kazimír-265**
1987/88	C	ST	C	RS	RS	ST	C	R	**C**																		
1988/89				AT	AT		R		**RS**	RS	RS	R	R														
1989/90						ST	ST		**RS**	RS	RS			ST	ST												
1990/91									**RS**	RS	RS					**RS**											
1991/92								RS	**RS**							**RS**	ST	ST									
1992/93																											
1993/94																**RS**											
1994/95																**RS**			RS								
1995/96																**RS**				RS	RS	**RS**					
1996/97																**RS**					RS	**RS**					
1997/98																					RS	**RS**	**RS**				
1998/99																							**RS**	RS			
1999/00																							**RS**		RS	RS	
2000/01																							**RS**		RS	RS	
2001/02																							**RS**		RS	RS	RS
2002/03																							**RS**				
Sex		**F**	**M**	**M**	**M**		**M**	**M**	**M**	**M**	**M**	**F**			**M**	**M**	**M**	**M**		**F**	**M**	**M**	**M**	**M**	**M**	**M**	**M**

Table. 2. The affinity of Alpine Accentors to their wintering sites. ST - spring migrants, birds appearing in March, AT - autumn migrants, birds appearing only in November, R - rare occurrence, usually a few days in a winter month, C - common, birds appearing throughout the winter but only up to 50% of the time observed by the other individuals, RS - birds appearing permanently throughout the winter each year. Bold indicates birds that were key in providing wintering information.

Residents and transmigrants

Winter season 1991/92 (Fig.4) **seemed to be crucial for the transfer of information on wintering behavior from Vratislav to Miroslav.** Vratislav became a permanent resident (842 minutes of observation) and α -dominant at the site. Miroslav had already discovered the site in February 1990/91 in the flock of older birds (Table 1) as a very low-ranking yearling (Table 1). In 1991/92 he was not frequently observed at the site (282 minutes), but he was already present throughout the winter period with a β -position in the hierarchy of accentors. He was two years old, was very alert and had the opportunity to learn from at six-year-old birds like Jaroslav and especially Vratislav. Jaroslav knew the wintering place already from 1987/88, but this winter he appeared only for a few minutes. In his old age, during 1991/92, he started to use the wintering place for synanthropic feeding (observed for 664 minutes). Although he was an old resident, he was only the third γ -position in the flock. He behaved purposefully, showed little stress (alertness), but spent more time foraging than Vratislav, who had dominant access to food. Bronislav was a spring migrant (Table 2), who appeared at the wintering site with Drahoslav at the end of February and March. He was rarely present at the site (observed for only 93 minutes). Drahoslav, also a spring transmigrant (Table 2), had the lowest position in the flock (δ), but was frequently at the site in late February and March (369 minutes observed). He used the site mainly for foraging and feeding.

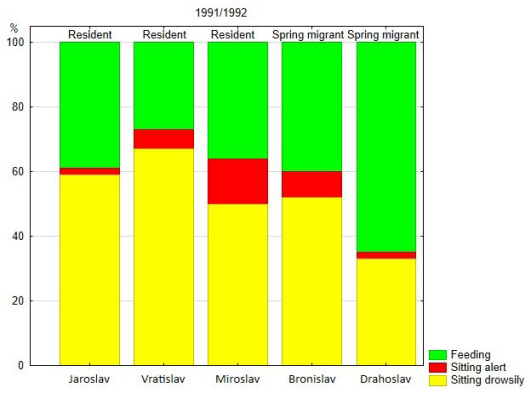

Fig. 4. A comparison of the behavior of residents and spring migrants during the 1991/92 winter season. Percentage of spent minutes.

Hierarchy and different seasons

Vladimír (observed for 52 minutes), Mojmír (observed for 73 minutes), and Slavomír (observed for 42 minutes) were yearlings and residents (Fig.5). However, their behavior was only monitored from the day of their capture in January or February of 1996. Nevertheless, they were less abundant at the site than the adult resident, Miroslav, who was observed for 300 minutes and exhibited stable behavior with a high percentage of resting. The young birds were merely familiarizing themselves with the site by feeding. Mojmír and Slavomír visited the site until winter 1997/98, when they arrived with a group of five birds, including yearling Jaromír (observed for 90 minutes). Slavomír's behavior stabilized at the site; he spent more time resting and was at the site more often (514 minutes observed) than Mojmír (218 minutes). During this period, Slavomír was the true transmitter of wintering site information, having received it from Miroslav as a yearling in the winter of 1995/1996 and transferred it to Jaromír in 1997/1998 (see Tables 1 and 2).

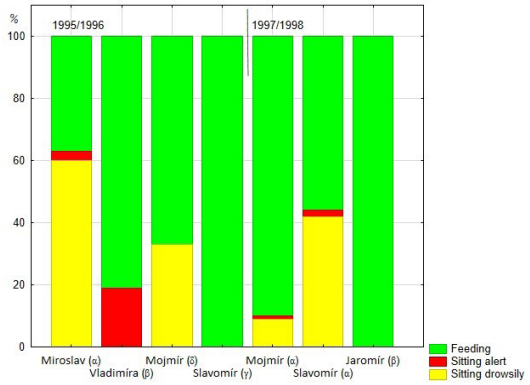

Fig. 5. Changes in the behavior of individual birds over the course of two winter seasons: 1995/96 and 1997/98. Percentage of spent minutes.

Behaviour – individual differences of birds responsible for transmission of information

Vratislav, Miroslav, Slavomír and Jaromír were the main transmitters of information about the wintering site. The behaviour of Slavomír is presented in Fig. 5. Vratislav (Fig. 6) was observed in the winters of 88/89, 89/90, 90/91, and 91/92 for 774, 142, 333, and 842 minutes, respectively. When he was recorded, he was usually in a group of three to six birds that rotated at the site. In 1989/90, when he was low in the hierarchy of wintering birds (Table 1), he spent much more time sitting alert. Vratislav waited for the opportunity to access food sources where dominant individuals were feeding. Vratislav was a key bird that transmitted information about the wintering site to birds arriving in subsequent years (Table 2).

Miroslav (Fig.7) was a key bird for information about the wintering place of other Alpine Accentors. In winter 1993/94 he was alone at the site, in 1994/95 Ľubomír was with him, but **winter 1995/96 turned out to be the key winter**, when three yearlings, including Mojmír and Slavomír, arrived with him as founders of a new wintering **"-mír dynasty"** (Table 1). Miroslav first arrived at the site as a yearling in the winter of 1990/91, at which time he was very low in the flock hierarchy (Table 1, 155 minutes observed). From winter 1991/92 to winter 1996/97 he was resident throughout the winter. The only exception was winter 1992/93, a snow-free winter, when Alpine Accentors were almost absent from the site, appearing only for a very brief period in February. As a yearling, the individual had low alertness, which increases in young, strong adults in the second year of life (Fig. 7). When he was four years old, Miroslav was alone at the site, which increased the need for alertness, he could

not use the social effect of observing danger. From the fifth to the seventh year of life he took the position of α - dominant individual. He was familiar with the site and the offered food sources and was experienced and able to feed quickly at the presumed food source, which allowed him as a dominant individual to spend significantly more time resting (sitting drowsily). In 1991/92, 1993/94, 1994/95, 1995/96 and 1996/97 he was observed with behavioral records of 282, 138, 97, 300 and 860 minutes respectively.

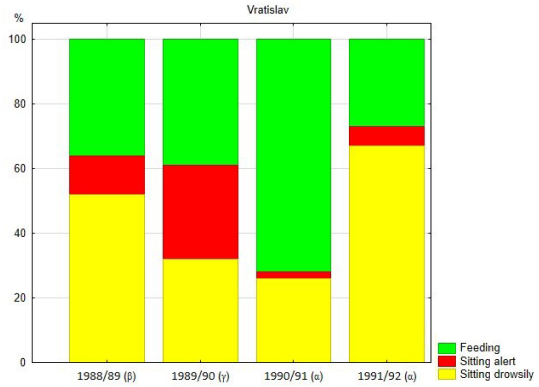

Fig. 6. Vratislav's behavior in different winter seasons depended on its position in the flock's hierarchy. The Greek letters indicate the position in the hierarchy of the wintering flock. α indicates the strongest, dominant birds. Percentage of spent minutes.

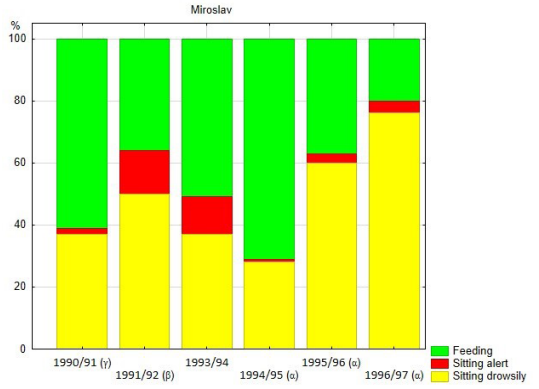

Fig. 7. Behavior of Miroslav as the next transmitter of information on wintering site. Percentage of spent minutes.

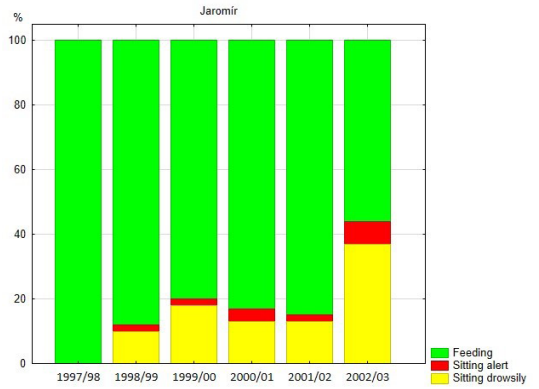

Fig. 8. Behavior of Jaromír as the last transmitter of information on wintering site. Percentage of spent minutes.

Jaromír (Fig. 8) appeared as a young bird in the winter of 1997/98. His behavior and feeding, was observed for 90 minutes, and became the resident bird with a β -position along with the two older adult birds (Table 1). In the following years he always occupied the resident α -position at the site in a group of three to four birds (Table 2). The birds were mainly observed feeding, and during this time the hotel was rebuilt, (i.e. the site of roosting and sleepy or drowsy sitting disappeared for them). In the last winter season, 2002/2003, when Jaromír was alone at the site, he rested more on selected places on the ground or on the roof of the local cafeteria, which was not covered from above and therefore did not provide shelter from predators even in bad weather. This was the last year that Alpine Accentors were present at the site. Since then, the site has been monitored for many years, but no accentors have been observed, and the overwintering site has disappeared. From 1998/99 to 2002/03, the time of observation of the behavior of Jaromír was 427, 788, 332, 126 and 409 minutes, respectively.

Discussion

Season

The social behaviour of Alpine Accentors in winter is thought to be important both in transfer of information about good foraging sites (Nakamura *et al.* 1996) and in assisting in the finding of food at such sites (Janiga 2021). Successful individuals that foraged well the previous day ("producers") may attract followers ("scroungers;" - Giraldeau and Lefebvre 1986) as they leave roosting sites for the first daily feeding. The physical comportment of successful individuals is likely to signal their intent to forage (Janiga 2021). After leaving the nest, the young learn to recognize different types of food from their mother while she feeds them. Later, when they become independent, they follow adult birds from their family. They observe feeding sites, but they largely rely on individual trial and error to find food (novel food finding). Generally, in the second half of August and September, young birds are more likely to learn from individuals who can access the same feeding stations as them than from mismatched birds with whom they are socially associated. This illustrates preferential learning from individuals who regularly provide relevant information (Firth *et al.* 2016). From this perspective, it is clear why Alpine Accentors do not maintain their breeding flock from September to October. As this study has shown, when discovering places with sufficient food sources, inexperienced birds learn from adult birds present there, which are relatively old (confer Nakamura *et al.* 1996). This is important for young individuals because, starting in September and especially in October, accentors display a mix of individual and social behavior. Polygynandry breaks down at the end of July and in August (Heer 1996), but it can still be seen rarely at the beginning of September in the Tatras, when some females are feeding fledglings. These young birds can fly and follow males from their original family. The behav-

ior of adult individuals in September and later in October is also related to changes in metabolic processes during molting. During this time, females exhibit the molting pattern of migrants, while males exhibit the molting pattern of residents (Korec and Janiga 2024). Young individuals must therefore be flexibly prepared for either individual survival or existence within a social group during winter. Alpine Accentors form large feeding aggregations in autumn, especially in October. In the Tatra and Low Tatra mountains, the first aggregations of 20–30 individuals may form in late August or September. In October, these aggregations grow to include 40–60 individuals. These are relatively large numbers, considering that only about 550 adult accentors live in the entire Western Carpathians in spring (Janiga 2024). Although their numbers may increase with young birds in autumn, October is undoubtedly an important period for large aggregations where independent young learn information transmission with many individuals from different families. In the southern foothills of Italy (Val Seriana, Lombardy), such autumn aggregations consist of 100–150 individuals (Facoetti 1992). Post-breeding migration lasts from mid-October (Desfayes 1952; Nakamura 1998a) to mid-November (Christen 1984; Cramp 1988; present study). Migrants reach their wintering grounds from late October to mid-November (Christen 1984; Schmidt 1985; Cramp 1988; Lukač *et al.* 2016; present study). The large October aggregations usually split into smaller groups before leaving the high mountains. From the high parts of the Western Carpathians, they preferentially migrate to the more southerly limestone hills of Slovakia and Hungary. In their intensive study of *Prunella collaris* during the winter in Hungary from 1917 to 2022, Bozó and Csörgő (2024) noted only two observations involving 18 birds, both of which occurred in February, (i.e., the middle of winter). Most observations in Hungary involved one to four individuals. According to the authors, the birds begin to appear in their wintering grounds in late October and November. This process also occurred in our experimental area (Janiga 2020). The birds are primarily stimulated to leave their nesting sites by the first snowfall in the mountains, as reported throughout the species' range, including in the Alps (Glutz von Blotzheim and Bauer 1985; Heer and Fraenkl 1999; Närmann and Himmel 2017), the Caucasus (Beme 1926; Lyaister and Sosnin 1942; Tkatchenko 1966), Central Asia (Kozlova-Pushkareva 1933), the Balkans (Matvejev 1976), and the West Carpathians (Ferianc 1979).

Once settled at the wintering site, some individuals are sedentary, performing only local altitudinal movements (Kovshar 1966; Tkatchenko 1966; Praz 1976; Martí *et al.* 1989; Martín-Vivaldi *et al.* 1995; Nakamura *et al.* 1996; Heer and Fraenkl 1999; Bezzel *et al.* 2005; Berezovikov *et al.* 2008; Bauer *et al.* 2012). These individuals, usually males, live in relatively small groups of one to three individuals (Janiga 2021), and on nice days during winter they also fly to snow-covered peaks, as evidenced by many photographs of winter hikers. Other individuals exploit feeding sites only a few kilometers apart (Cramp 1988; Martí *et al.* 1988; Gstader and Tschaikner 1991; Grošelj 1994; Davies *et al.* 1995; Heer and Fraenkl 1999; Ruiz 2000; Fosse 2001). Some individuals migrate up to 250 km to lowlands (Bulgarini *et al.* 1966; Molamusov 1967; Kutchin 1982; Nakamura et al. 1996; Shitikov *et al.* 2001; Misiuna 2002; at least 170 km in this study). In Switzerland, wintering grounds are mainly in the southwestern Swiss Jura (Christen 1984). There are also birds that migrate relatively far—300 km or even more than 1000 km—to Scandinavia, Britain, Russia, Poland, Belgium, the Netherlands, Malta, and the Canary Islands (Portenko 1960; Glutz von Blotzheim 1964; Dick and Holupirek 1978; Wojciechowski 1979; Cramp 1988; Jacob 1996; Naylor 2025; Birdforum 2025). A similar situation exists in the Pyrenees in Spain (Martí *et al.* 1988; Martín-Vivaldi *et al.* 1995). Birds often roost in castles with good views and suitable rocks. During the winter, meadows with flattened grass or areas near trees or buildings where snow melts faster are important (Heer and Fraenkl 1999). The size of the aggregation usually increases with decreasing altitude. Below 2,000 meters, the average is four to six individuals (Desfayes 1952; Dementiev *et al.* 1954). Above 2,000 meters, one to three individuals can be found in winter (Heer and Fraenkl 1999). In the Western Carpathians, these groups are smaller. In the alpine environment at lower altitudes, larger aggregations of 40 to 80 birds occur, even in winter (Praz 1976; Wartmann 1977). Such large aggregations are not seen in Slovakia, Hungary, or Poland in winter. This is partly because only up to 550 individuals nest in the entire Western Carpathians (Janiga 2024). In winter, they roost on rocks and in niches but not in crevices. Old castles and churches with recesses can be important roosting sites where individuals from different directions can gather (Heer and Fraenkl 1999). Departure from wintering grounds starts in February (Schmidt 1985, this study). Prebreeding migration peaks in early April, with the latest records from May (Christen 1984; Schmidt 1985; Cramp 1988). During this period, they begin appearing at their nesting sites, even in large numbers (Kovshar 1988; Janiga 2024). However, in April and May, many birds roam the ridges of the surrounding smaller mountain ranges (Kupcová 1981; Clesse 1996). Some of them become year-round non-breeding vagrants. The winter ecology of Alpine Accentors is poorly understood (Marti *et al.* 1988, 1989; Heer 1999), and the role of non-breeding vagrants in the survival of Alpine Accentors remains largely unknown (Topercer 1997). These are likely individuals discovering new potential nesting sites and wintering grounds. From this perspective, Hellmann's (2009) long-term work appears to be significant. His series of records of this mountain bird on the Harz peak in the Harz National Park has been almost unbroken for years. The granite environment of Harz National Park (1,140 m) is a place where Alpine Accentors fly through in spring and autumn but do not stay in during the winter. It is a stopover site in spring and autumn, just as Malinô Brdo was for many individuals. In March and April, Alpine Accentors fly through Harz, and one or two individuals were present here at the beginning of June. The treeless, widely visible peak of the Brocken likely attracts Alpine Accentors that have flown far north. The Harz is the northernmost German mountain range, and for accentors that have flown this far, it is the last suitable mountain

peak in terms of altitude and habitat before the flat North German lowlands. All the birds that could be observed closely were adults. In April and May, they were scattered throughout the site. By the end of May, five birds were seen, but they split into two groups. Two of the birds stayed longer as if showing the location to the others. The birds were also observed in October and November. The author assumes that these are often the same birds that pass on information about the transmigration site from year to year. They stayed at the site for up to 45 days. There were years when Alpine Accentors were not present at the site, which suggests that new generations may also find it suitable for transmigration. In June and July, the birds were probably non-breeders, showing no signs of nesting behavior. The site is very popular with tourists. Some individuals return to the same wintering or migration sites every year, as evidenced by studies of the Harz National Park and Veľká Fatra, among others. (cf. Nakamura *et al.* 1996; Henry 2011).

Wintering and individual characteristics

Alpine Accentors exhibit a complex pattern when visiting several possible foraging sites each day. The birds may use different sites at different times of day. The number of birds at a site varies from one day to the next and at different times (Janiga 2021). Therefore, individual accentors engage in complex monitoring of known food sources. They know from experience that the amount of food present, varies. Results from this study reveal differences in migration and wintering strategies between sexes and age classes. Adult males tend to stay closer to the breeding grounds than yearlings do. Typically, fewer than 10 percent of young birds remain at their nesting sites during the winter (Heer and Fraenkl 1999). According to observations in the Tatra Mountains, these birds are often yearlings from late broods. Due to the relatively large dispersal of young birds during the summer and fall, a large proportion of future yearlings leave their nesting sites earlier than adult birds, primarily adult males (Henry 2011). However, our findings clearly show that young birds arrive at the site at the same time as adults when traveling from farther distances. Young birds learn from adults how to find wintering sites and how to find food. Food limitations affect yearlings more than older individuals (Nakamura 1995a, b), which is why young birds must forage more and learn from older birds that rest more due to their dominance and age (see Figures 6 and 7). This study demonstrates the importance of yearlings developing an affinity for their wintering grounds. Once this occurs, the young birds become residents and pass on information about the wintering site to others (see Tables 1 and 2). The most important residents of the concrete site are those who have been present since their first year of life. Migratory accentors are largely faithful to their wintering grounds (Nakamura *et al.* 1996), but only a few individuals have historically been responsible for transmitting information about these grounds. At Malinô Brdo, four out of 27 birds became familiar with the site as yearlings. The closer the wintering site is to the nesting site, the greater the number of males in the wintering flock (Aichhorn 1969; Martí *et al.* 1989; Martín-Vivaldi *et al.* 1995; Heer 1996), so it is not surprising that young males remain closer to the nesting sites. This is also the case at Malinô Brdo, which is located about 150–170 km from the breeding habitats. Migratory birds that travel longer distances include a large proportion of females (Nakamura and Nishumi 2000). Approximately the same number of yearlings migrate with the females, who remain at the wintering grounds longer than the males (Henry 2011). Large flocks of females are expected to have established wintering grounds, while males tend to stay near their nesting sites. One of the mechanisms that likely drives differential migration is dominance avoidance, whereby males remain close to their nesting sites to protect their nesting territory in early spring (Heer and Fraenkl 1999). Males' early arrival at breeding grounds increases mating opportunities. Dominant males are indeed "reluctant" to leave their nesting territory. In males, dominance rank is a very important determinant of mating strategy and reproductive success.

A dominance hierarchy is a major social feature of Alpine Accentors. Males dominate females, and older individuals dominate yearlings (see Tables 1 and 2). A 10-year long-term study by Nakamura (1998b) showed that males moved up in social rank with increasing age, yet 79% of males remained subordinate because alpha males occupied the top rank for much of their lifetime. Females over five years old occupied a low status. In both males and females, dominance increases linearly with age (Davies *et al.* 1995; Heer 1998, 2013), and a long-term study at Malinô Brdo shows that most adult males maintain their status in the flock (Table 1). Status may also change slightly during the nesting period (Nakamura 1998b), as after two years, yearlings appeared in a different position at the wintering site. Positions, therefore, change even during nesting, but since the winter flock is a completely different social unit from the summer polygynandrous family, the hierarchy also changes during wintering, which was also observed at Malinô Brdo. With flocks which are organised as are these accentors, it becomes difficult from one year to the next to decide which birds stand higher in the social order if they are not marked. The phenomenon of peck dominance (i.e. an individual's social position in the social structure) may change in subsequent years.

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