Oecologia Montana 2021, **30,** 85-99

Biology of alpine accentor (*Prunella collaris*) VI. Interspecific relationships among alpine accentors and other species of birds during winter

M. JANIGA
Institute of High Mountain Biology, Žilina University, Tatranská Javorina 7, SK-059 56, Slovak Republic; e-mail: janiga@uniza.sk

Abstract. Observations were carried out on winter aggregations of alpine accentors. This species of bird was more likely to feed at dawn and dusk. During winter, regular feeding groups of different species of birds congregating at the same time at feeding sites, were consistent in composition and space. Dominant hierarchies formed that were weight related. The following ranking orders of dominance were observed among different species of birds (> - indicates a higher position in the dominance ranking, = indicates an equal position): *Pica pica* > ***Prunella collaris*** > *Dendrocopus major* > *Chloris chloris* => *Fringilla coelebs* = *Emberiza citrinella* => *Parus major* > *Poecile montanus*, ***Prunella collaris*** > *Picus canus, Garrulus glandarius* > ***Prunella collaris***, *Corvus corax* > ***Prunella collaris***, *Nucifraga caryocatactes* > ***Prunella collaris***, *Turdus pilaris* > ***Prunella collaris***, *Turdus merula* > ***Prunella collaris*** =>< *Parus major* > *Periparus ater* > *Cyanictes caeruleus* > *Lophophanes cristatus*, ***Prunella collaris*** > *Sitta europaea* > *Periparus ater, Erithacus rubecula* > *Chloris chloris* => *Emberiza citrinella, Cocothraustes cocothraustes* > *Emberiza citrinella*. Additionally, the possible transmission of diseases between different bird species, within different ecosystems, and in the food chain between accentors and birds of prey during autumn is discussed.

Key words: alpine accentor, *Prunella collaris*, dominance and hierarchy among bird species, winter flocks, supplementary feeding

Introduction

Food availability is one of the most influential factors affecting bird subsistence and as a result many authors assume that supplementary feeding enhances survival and fitness in birds. However, the short-term effect of supplementary feeding may also correlate negatively with natural selection. Supplementary feeding can alter body condition, reproduction, survival, diseases prevalence, and migration in bird species (Plummer *et al.* 2015; Galbraith *et al.* 2017a). In addition, the practice of garden bird feeding often activates interspecific interactions between bird species that would normally not interact in the absence of contact at these supplementary bird feeders. Thus, the sites where birds are fed are not only the locale of their atypical concentration, but also the location for increased transmission of infectious diseases (Timko and Kmeť 2003; Novotný *et al.* 2007). Based on natural selection, such a locality may also impose a potential threat from unknown predators. The ecological effects of a dense concentration of birds at feeders remains poorly understood (Robb *et al.* 2008), though supplementary feeding has increased rapidly since the second half of the 20th century, and current estimates suggest that in some countries more than 50 % of households repeatedly feed wild birds (Cowie and Hinsley 1988).

The alpine accentor is a passerine species living in alpine regions. It is a trans-migratory and partially migratory species, making significant local migrations throughout winter. Adult males are commonly observed throughout the year near breeding sites, forming changing aggregations of one to three individuals. At lower elevations, several hundred kilometers from breeding sites, aggregations often involve more individuals. Birds forage mainly in rocky areas of the mountains, with larger groups also foraging in lower altitude pastures. Feeding on artificial resources within human proximity - at bird feeders or near settlements and winter resorts - usually represent only a small fraction of foraging time. At bird feeders, alpine accentors encounter various other species of birds and mammals, and these encounters are only possible during winter. This study presents a list of many species that accentors encountered over many years of research. In some cases, interactions are described in more detail, particularly in terms of dominance or daily behavioural cycles. Competitive interactions amongst many passerine and other bird species were recorded in order to verify the dominance hierarchy between alpine accentors and other bird species. The importance of body size as a determinant of rank in the hierarchy was also examined.

Material and Methods

This study describes how alpine accentors and other bird species compete for food during winter. Field work was conducted at two sites. At the first site, accentors were studied between 1984 and 2005 in the Great Fatra Mountains National Park, at the

Malinô Brdo ski resort. Birds were monitored from the beginning of November to the end of April. Details on the number of birds seen in respective years and the number of visits per year are presented in Janiga (2020). In the majority of years, the presence of birds was dependent on heavy snow and deep snow cover in the mountains, but in some years, birds had a continued presence at the resort on sunny days when snow cover disappeared in many areas. Accentors foraged near hotels, pensions and restaurants. Daily visits lasted a minimum of five hours, but many visits lasted from dawn till dusk. To study feeding preferences (Janiga and Novotná 2006), a feeder with several sections containing different dietary sources was positioned near the hotel where the birds also roosted, preened or rested. Supplementary food was provided ad libitum. Sections of different food in the feeder ensured that foraging behaviour was not influenced by the location of high and low value foods. 27 accentors were captured with a cheese/millet-baited falling trap. Each bird was individually marked with colour rings. The majority of birds were individually distinguished and re-sighted over the next years. Binoculars of various powers were of assistance for observation. Notes on behaviour were simply written or dictated onto tape. Competitive interactions and visits of accentors and other bird species were video recorded, and the recordings were later analysed in the laboratory.

At the second site, two wintering accentors were systematically monitored at the Spišská Magura, near the village of Ždiar (Antošovský hill). The presence of accentors was initially detected from footprints; the size and shape of which usually differed from other bird species. (Fig. 1).

Fig. 1. The footprints of alpine accentors are specific and different from those of many other bird species.

Birds were also attracted to feeders by a large winter flock of yellowhammers (*Emberiza citrinella*). The period of observation lasted from the beginning of December to the end of March in winters 2018/2019 and 2019/2020. Four Bushnell Trophy Cameras were used to take pictures and continual video recordings (Fig. 2). Maintenance activities (feeding, resting, preening, interactions, etc.) of birds were recorded 24 hours per day over 80 days. Data collection took place each day (weather permitting). The two general forms of competition among different species of birds are interference competition and exploitation. Interference competition occurs when competing species confront directly (usually at bird feeders). Exploitation competition occurs when species use the same resources but do not inhibit each other. Both exploitation competition (e.g., Gustafsson 1987) and interference competition (Slagsvold 1975) seem to be common between different passerine bird species. Interference competition of accentors was recorded at the bird feeder. Both exploitation competition and more complex behaviours were recorded in an enclosed yard where accentors were provided with their favorite diet and were not disturbed by other bird species (Fig. 2). Aggressive interactions between birds can take several forms, but this study focussed on competitive interactions. This included subtle interaction, when one bird waited for another to finish feeding as well as displacement, when one bird suddenly arrived and frightened off other birds, or displaced or chased another from a perch at or near a bird feeder.

Results

Winter flocks are characteristically formed by the association of birds that nest separately, and thus often consist of several species. The results of this study, based on direct or recorded observations of interactions at bird feeders, demonstrate that body size differences amongst different species of birds significantly influence patterns of feeding behaviour and the ability to monopolise food resources. Accentors are a good example to illustrate this phenomenon.

Coal tit (Periparus ater) and crested tit (Lophophanes cristatus)

Although coal tit sometimes successfully managed to usurp food, successful takeovers were rare and were often associated with waiting or desertion of feeding opportunities. Accentors always gained the

Fig. 2. Experiments utilizing free feeding of accentors without the presence of other bird species. Trophy Cameras (left) and supplementary feeders (right) were used.

Fig. 3. Coal tit and alpine accentor at feeder with different kinds of food (left). Coal tit had precedence over crested tit (right).

best position when feeding. Fifteen interactions between accentors and coal tits were recorded. In eleven cases, the tits avoided accentors, while in three others they moved close to the accentors with a threat display but did not feed (Fig. 3). In one case the tit was driven away.

When a number of species join forces, there is usually a pecking order amongst them. This can be easily observed at bird feeders where the competition is high. Alpine accentor always maintained precedence over coal tit, while coal tit had precedence over crested tit. Coal tit avoided Eurasian nuthatch, while crested tit avoided alpine accentor.

Blue tit (Cyanictes caeruleus) and crested tit (Lophophanes cristatus)

Alpine accentor had precedence over blue tit at both sites (Malinô Brdo and Ždiar) in multiple years (Fig. 4). But the type dominance varied from day to day. Out of 18 recorded interactions, the tit flew away five times and waited 10 times at a short distance. In three cases, when the tit distinguished no danger from the accentor, it gradually began to feed alongside this bigger species. In general, dominance rank is determined by body mass across species, and heavier species monopolise access to food. However, in contrast to this general theory, some individuals of lighter species may be seen feeding with larger birds (Fig. 5). The strategy of mutual feeding between two bird species of different size is based on experience. These findings suggest that a species' position within the bird hierarchy can influence its experience, and thus this factor must be taken into account in studies on social hierarchy in birds. It was also observed that the accentor learned to respond to the alarm call of the blue tit.

Fig. 4. Blue tit usually waited at the distance 10 – 20 cm until the accentor was fed.

Fig. 5. The blue tit fed only when the alpine accentor was no longer interested in the food source. After tits experienced non-antagonistic accentor behaviour, both species fed together.

Blue tit always exhibited precedence over crested tit. Crested tit avoided more aggressive blue tit or waited some distance from the feeder until the blue tit fed (Fig. 6). When closely related species have similarities in foraging preferences, it is highly probable that dominance hierarchy between these species is a result of evolutionary history. Blue tit always avoided great tit.

Willow tit (Poecile montanus)

The Willow tit is a relatively aggressive species and can actively chase smaller species of birds. The tit avoided accentors, but usually only from a short distance (Fig. 7). At the feeder, however, the Willow tits always avoided great tits, and avoided but sometimes also defended against yellowhammers or European greenfinches.

Great tit (Parus major)

At both field sites, a total of 68 interspecific interactions between great tits and accentors were recorded at supplementary feeders. In general, it was confirmed that dominance is determined by body mass between these two species. Tits tended to avoid accentors, particularly at the second locality (Ždiar), where they flew away or waited several metres away (35 observed interactions, Fig. 8). At the first site (Malinô Brdo), heavier accentors also frequently monopolised access to the food source (7 interactions, Fig. 8 – right). However, on occasion, lighter great tits were able to defend their food (Fig. 9), particularly when subordinate accentor specimens (in the hierarchy of a flock of accentors) chose to feed on a food source preferred by tit. Although body size is an important factor in food availability, this may not be true if the

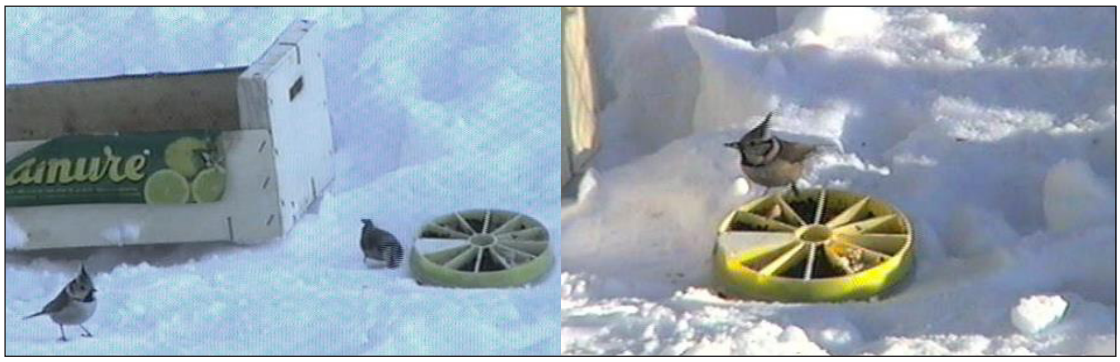

Fig. 6. The crested tit avoided blue tit and waited until there was free access to the feeder.

Fig. 7. Examination of interactions around species' ranks suggests that Willow tit are considerably more dominant than expected given their body mass. In the figure on the left, the tit attacks the yellowhammer, while accentors continually maintained precedence over tits (right).

Fig. 8. Interactions between alpine accentors often depend on individual birds. At the second experimental field site, both male and female tits avoided accentors. At the first experimental site, female tits usually waited near the feeder for the accentor to feed (right).

Fig. 9. Interactions between different species of birds is dependant on individual birds. Through agonistic threat displays (above – right and left) smaller species or some individuals of smaller species may gain control of limited resources (right bottom). Sometimes two accentors recognized this position and accepted it (left bottom).

food source is limited. In this case, some individuals - even from smaller species – are able to defend their food source against a larger species. This study suggests that these differences in body mass often result in the creation of an interspecies dominance hierarchy, granting the heaviest species the greatest control of feeding sites. However, in select cases, smaller species have been shown to gain control of limited resources through agonistic interactions, including threat displays (Fig. 9) or physical combat. Six interactions were recorded when great tits exhibited precedence over alpine accentors. In 20 cases, tits and accentors behaved neutrally, feeding without evidence of dominance between individual birds.

In this relationship between accentors and great tits, the tits tend to find new food sources earlier and faster than accentors. During early morning, tits arrived earlier and often scattered food around the feeder, while accentors usually arrived later in the day and first collected scattered millet before utilizing the feeder. While scavenging, they mirrored the feeding pattern of tits.

Eurasian nuthatch (Sitta europaea), Eurasian blackbird (Turdus merula) and fieldfare (Turdus pilaris)

Nuthatch spent less time feeding at the supplementary feeder during each visit than accentors, as they had to spend more time waiting in close proximity to feeding sites until feeding opportunities arose. Dominance in interactions often depended on individual birds. 13 interactions were recorded. The accentors actively pushed the nuthatch twice. When less food was available, stress was higher and direct aggressive contact between these two species was more likely to occur. The nuthatch avoided the accentor six times, while accentors ran and flew away from nuthatches twice, and three other interactions were neutral (Fig. 10). However, accentors consistently avoided blackbirds (three interactions observed, Fig. 11) and fieldfares (two interactions observed).

Fig. 10. Nuthatch may benefit from feeding quickly; reducing the amount of time spent on feeders to avoid costly interactions with dominant accentors.

Fig. 11. Consistent with expectations, the dominant blackbirds were more likely to be observed utilising supplementary diets than less dominant accentors.

Yellowhammer (Emberiza citrinella)

The bird feeder in Ždiar is used every winter by a flock of more than one hundred yellowhammers. Thousands of photo-trap records were obtained. Some specimens were found to feed very close to accentors, but accentors can usually reach the food source first due to their greater size and more dominant behaviour (Fig. 12).

The usual pattern for wintering birds is for submissive individuals to stand just out of range of a feeding neighbour´ s attack, as a method of avoidance behaviour. For individual yellowhammers, this minimum closure distance tends to be more consistent, resulting in the yellowhammers encircling the accentors, whereby movement of the circle is dependent on movement of the accentors (Fig. 13).

European greenfinch (Chloris chloris) and common chaffinch (Fringilla coelebs)

There was considerably less inter-species competition directly below the feeder, where food was scattered by both birds and the elements. This allowed subordinate species, like greenfinch to gain greater access to the food source during winter, and subordinate species like chaffinch to gain greater access to food during the early spring (Fig. 14). Both species avoided accentors. At the feeders, greenfinch had a slight precedence over yellowhammer and great tits. However, this relationship was more dependent on individuals than on species. In such a feeding aggregation, each individual has its own place in the flock and accepts that it must give way to more dominant species both within and outside of its position at the feeding site. In many cases, greenfinches, tits or yellowhammers fed together. (Fig. 15). Further more, a bird´ s dominance over another might alter from day to day.

Crows and woodpeckers

A species' position within the hierarchy of a flock can influence food choice and foraging tactics. At the feeders found at both experimental sites, common raven (*Corvus corax*), spotted nutcracker (*Nucifraga caryocatactes*), Eurasian jay (*Garrulus glandarius*) and magpie (*Pica pica*) were significantly more likely to use the feeders or feeding grounds, compared to less dominant accentors. Encounters were rare (ravens – two times, nutcrackers – five times, jays – two times, and magpies – six times), and accentors always avoided the larger species. Crows can always reach the food source first due to their large body size and domineering behaviour, which can consequently deter other bird species (Fig. 16). This is the way pecking orders or dominance hierarchies are developed, and following the initial jostling for power, these relationships become fairly stable. However, while this tendency may reduce the risk of aggression between individuals, it can also be detrimental to lower-ranking species. Dominance rank was not found to be significantly positively associated with body mass be-

Fig. 12. Dominant, heavier accentors exert greater control over natural foraging sites than subordinate, lighter yellowhammers (left). However, the relationship between some individuals may be more neutral, allowing some yellowhammers to feed very near to accentors (right).

Fig. 13. Yellowhammers create circles around heavier and dominant accentors.

Fig. 14. The relationship of greenfinches (left, right) or chaffinches (right) to accentors was most commonly a consequence of body size. Both species avoided accentors.

Fig. 15. Joint feeding of greenfinches and great tits (left) and yellowhammers and great tits (right).

tween woodpeckers and accentors. Great spotted woodpecker (*Dendrocopos major*) avoided accentors and other birds in large interspecific flocks (yellowhammers, greenfinches), and a grey-headed woodpecker (*Picus canus*) was chased away by an accentor defending access to the feeder with an upraised wing.

Other songbirds

The interaction of accentors with other songbirds that occurred in the experimental plot were never observed or recorded by cameras, because at this time, accentors were no longer present in the plot. The European robin

Fig. 16. Magpies (left) and great spotted woodpeckers (right) frequented the same feeding site as accentors.

(*Erithacus rubecula*), hawfinch (*Cocothraustes cocothraustes*), Eurasian tree sparrow (*Passer montanus*) and bullfinch (*Pyrhulla pyrhulla*) that hold territory in early spring may join up with the flocks of yellowhamers as they pass through. Aggregations of different species at the same feeding site in winter or spring can have serious epidemiological implications. Birds originate or migrate from very different ecological conditions and feeding sites may serve as a source of potential viral and bacterial disease transmission. At the plots, droppings are often mixed with seeds from supplementary food. Robins had precedence over yellowhammers and greenfinches, and yellowhammers avoided hawfinch (Fig. 17). Dominance rank was not found between tree sparrows and yellowhammers or bullfinches and yellowhammers (Fig. 18).

Birds of prey and mammals

Flocks may reduce the chance of attack by predators, and in many groups of birds there seems to be interspecific recognition of alarm calls; at least between blue tits, coal tits and accentors. On the other hand, flocks draw attention to themselves, and it is often easy for a predator to target one atypical bird from of a flock of yellowhammers. Moreover, accentors seem to be less adapted to more unknown predators in forest environments. While yellowhammers or tits quickly fly up into the trees at the alarm call, the response of accentors was often delayed. On occasion, an accentor remained standing alone in the snow. Birds are not primarily adapted to domestic cats, dogs, or fox. Cats in particular can effectively hunt songbirds under feeders. In February 1992, a cat killed one accentor specimen this way. The birds reacted most effectively

Fig. 17. Yellowhammers and greenfinches created distant circles around robins; robins had precedence over them (left); yellowhammers also avoided hawfinch (right).

Fig. 18. Eurasian tree sparrows (left) and bullfinches were also rare visitors to the feeding site (right).

to attacks by common kestrel (*Falco tinnunculus*) and managed to fly away. Conversely, if they saw the silhouette of a Northern goshawk (*Accipiter gentilis*), they remained motionless. The sites below the feeders were also sporadically frequented by European pine marten (*Martes martes*), least weasel (*Mustela nivalis*), and short-tailed weasel (*Mustela erminea*), but there is no evidence of accentors being caught by these predators during winter.

Information transfer and learning

Feeding advantages of group foraging lie in the number of trained eyes employed in seeking food. Some species are more skilled at foraging than others, and those less skilled often take advantage of what the former have found. In some cases, when a new food source became available at a feeding site, alpine accentors responded, and other present bird species (great tits, woodpeckers) learnt of the new feeding prospect from their behaviour. Conversely, the opposite occurred, wherein flocks of yellowhammers helped accentors find food (Fig. 19).

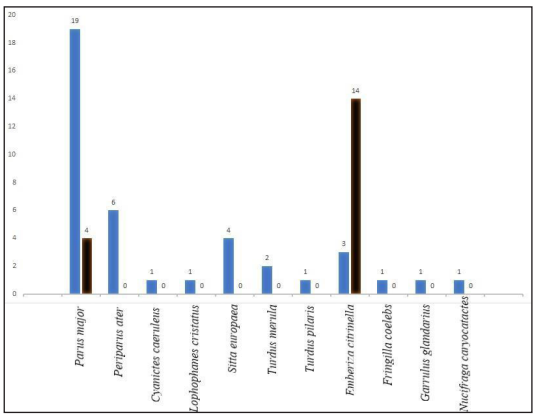

Fig. 19. Recorded number of observations of transmission of information on feeding sites. The left histograms (numbers for each species) show that when a food source becomes available at a feeding site, accentors respond, and some other bird species may learn of the feeding prospect from the behaviour of accentors. Usually these were species exhibiting solitary behaviour during winter. The early morning feeding area likely represented the primary center for directed information transfer. On the contrary, wintering yellowhammers undertake foraging, flight and roosting in aggregations of flocks. It likely that a yellowhammer in a flock not only "feels" safer but actually is safer from most forms of predation in winter. When yellowhammers (*E. citrinella*) located food and started eating, they were quickly joined by accentors (right histograms).

Factors of weather in winter

Alpine accentors were significantly more likely to seek out food immediately after sunrise and before sunset. Because it requires a relatively short handling time, supplementary diets enable birds to gain a greater energetic benefit at a lower foraging cost. This is the reason accentors place particular emphasis on foraging for valuable foods in the early morning or just before darkness. During winter, birds are likely to experience higher thermoregulatory costs overnight due to decreased ambient temperatures. In addition to

Fig. 20. Snowing and windy. During snowstorms (left), the accentors would arrive at the feeding sites early in the morning and rest or feed there all day (right).

Fig. 21. Snow cover. Accentors can accurately locate snow-covered food sources (left). At that time they usually arrive at early dawn (right). It is evident that this adaptation helps them to survive in high-altitude alpine ecosystems.

low temperatures, accentor flights from higher altitudes are caused by snowfall, strong winds and thickness of snow cover (Figs. 20, 21, 22 and 23). Figs. 24 and 25 show that when these factors act together, the probability of accentors arriving at feeders is very high.

Fig. 22. Snow cover and drinking. Accentors use snow as a water source in winter. Feeding on snow allows them to save energy in freezing periods, as they do not have to search for water sources.

Fig. 23. Temperature. During frosts, accentors can ruffle up their feathers very quickly. It takes them about ten seconds to increase the volume and achieve a suitable "spherical" shape to provide sufficient insulation.

Discussion

Rank orders in winter. When a number of species commonly join forces and hunt together in mixed flocks, there may be a pecking order between them (Popp *et al.* 1990). This can be easily observed in bird tables where competition for available food may be high (Woodrey 1990; Galbraith *et al.* 2017b). In many bird species, a highly significant positive association between dominance rank and body mass across species suggests that the hierarchy is largely driven by variation in body mass or size (Alatalo and Moreno 1987; Cowie and Hinsley 1988; *Galbraith et al.* 2017b). Inter-species interactions at supplemental feeding sites in this study confirmed that birds with greater body mass were more dominant than smaller species. The alpine accentor is the largest species in the family Prunellidae, and also lives at extremely high elevations in the mountains. This alone guarantees non-aggressive accentors a dominant position at feeding sites in winter, when they encounter smaller songbird species. Experimental video-recordings suggest that differences in body mass may lead to the formation of dominance hierarchies between species, leaving the heaviest species in the greatest control of higher value foods at supplemental feeding stations. Lower-ranking species move quickly to avoid dominant birds, and their foraging tactics may allow them to avoid engaging in costly interactions with dominant birds (Birkhead 2008; Zeng and Lu 2009; Miller *et al.* 2017). However, in other situations, these foraging strategies may impact fitness, as smaller species may be at greater risk of predation than larger more dominant species. The following dominance rank orders were observed among different species of birds (> - indicates a higher position in the dominance ranking, = indicates an equal position): *Pica pica* > ***Prunella collaris*** > *Dendrocopus major* > *Chloris chloris* => *Fringilla coelebs* = *Emberiza citrinella* => *Parus major* > *Poecile montanus*, ***Prunella collaris*** > *Picus canus, Garrulus glandarius* > ***Prunella collaris***, *Corvus corax* > ***Prunella collaris***, *Nucifraga caryocatactes* > ***Prunella collaris***, *Turdus pilaris* > ***Prunella collaris***, *Turdus merula* > ***Prunella collaris*** =>< *Parus major* > *Periparus ater* > *Cyanictes caeruleus* > *Lophophanes cristatus*, ***Prunella collaris*** > Sitta europaea > *Periparus ater, Erithacus rubecula* > *Chloris chloris* => *Emberiza citrinella, Cocothraustes cocothraustes* > *Emberiza citrinella*. Competitive interactions, where one individual is consistently successful, can lead to the formation of a system in which each animal is either dominant or subordinate to another. Accentors required a relatively short handling time to gain a

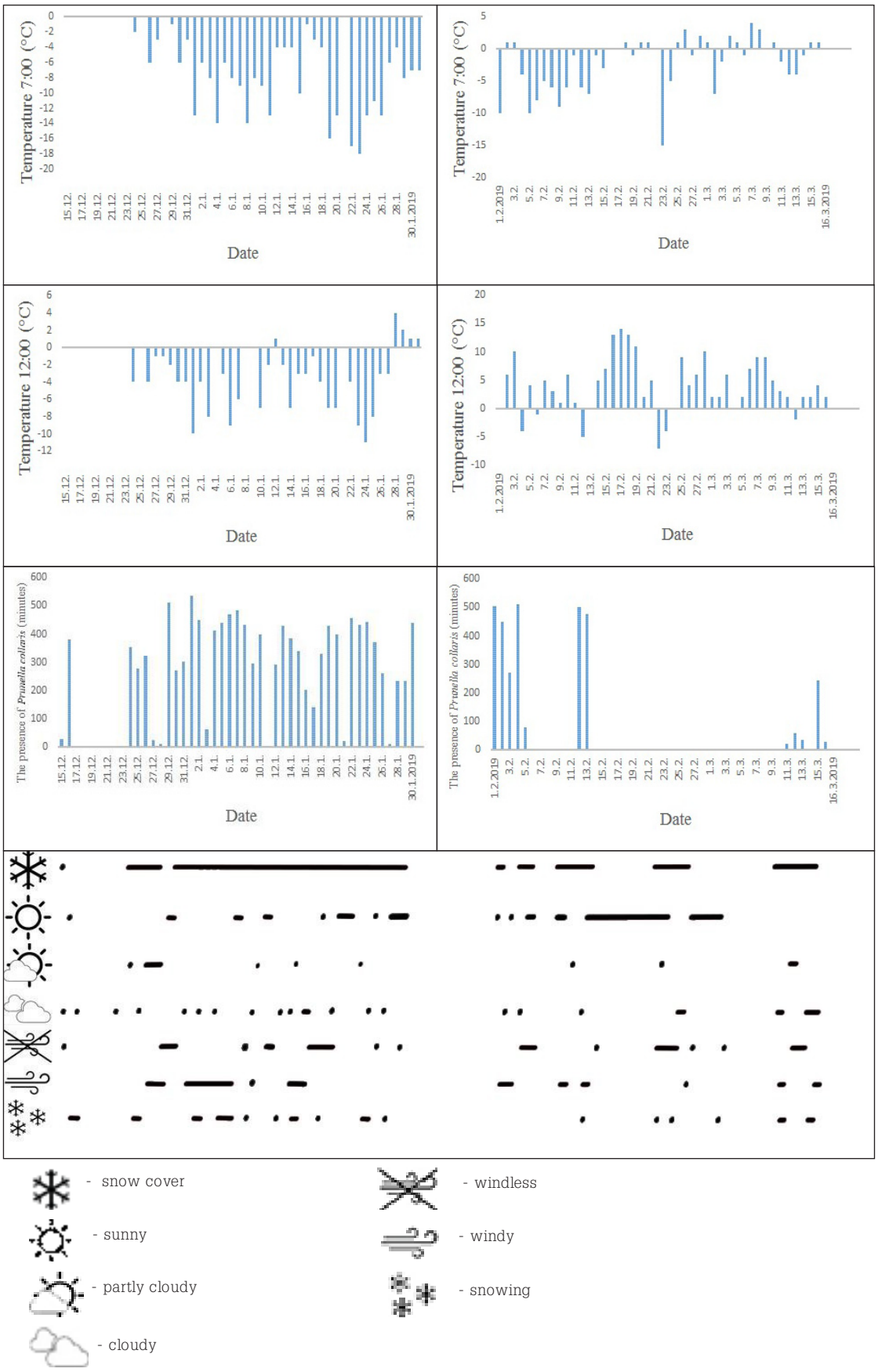

Fig. 24. Occurrence of alpine accentors at the feeding site depending on the most important factors of weather in winter 2018/2019 (Spišská Magura).

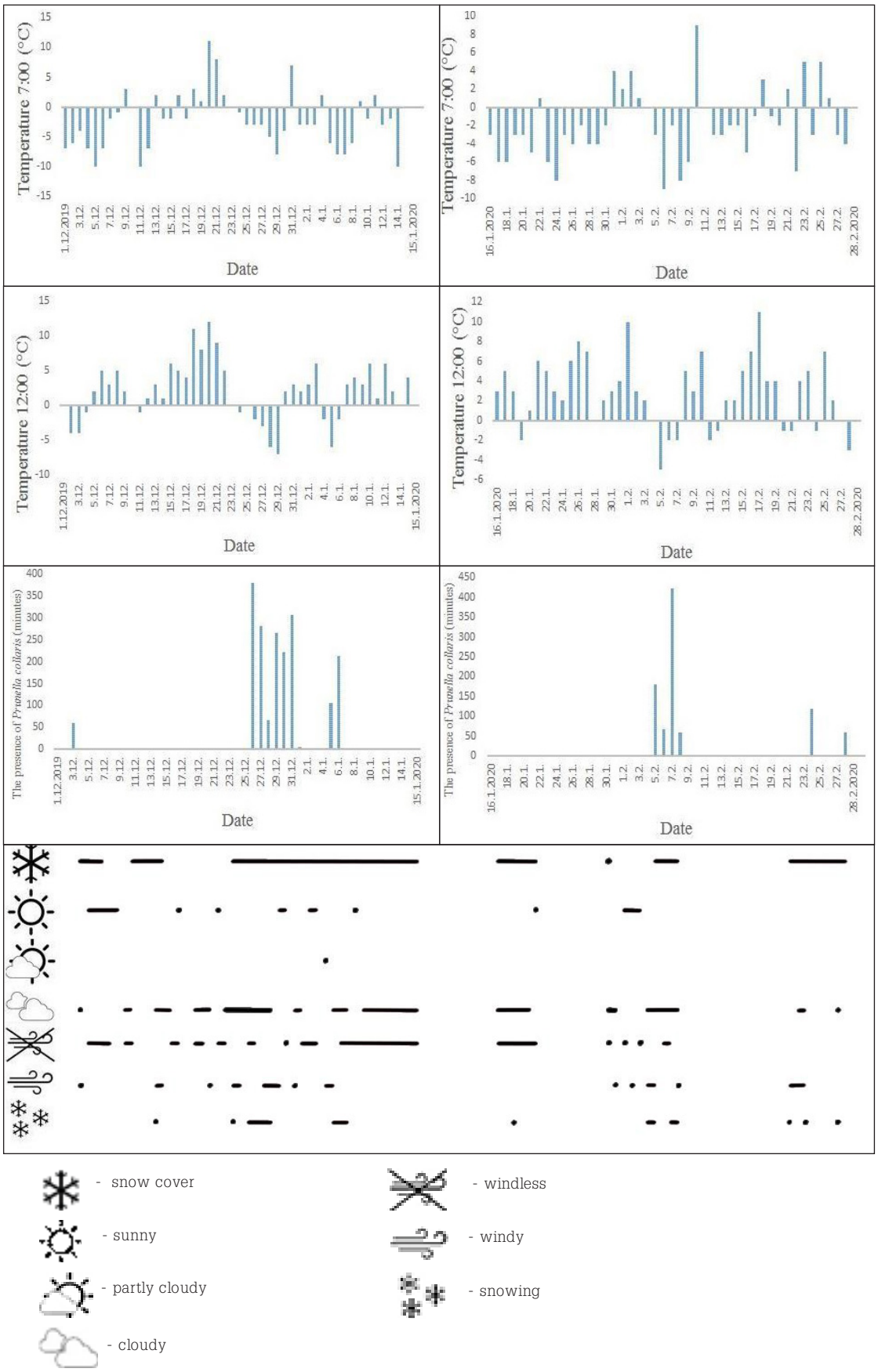

Fig. 25. Occurrence of alpine accentors at the feeding site depending on the most important factors of weather in winter 2019/2020 (Spišská Magura).

greater energetic benefit at a lower foraging cost. During winter, birds are likely to experience higher thermoregulatory costs overnight or during snow flurries during the day, due to decreased ambient temperatures (Olsson *et al.* 2000). Therefore, they place particular emphasis on foraging for high value foods in the hours near dawn or just before darkness. This allows accentors to establish themselves effectively in a hierarchy of multi-species bird aggregation. Hierarchy can decrease the number of aggressive interactions. The structure of such inter and intraspecific hierarchies can be determined by many factors, including; sex, age, previous experience, aggressive nature, and body mass. Species with greater body mass had increased competitive success and often displaced smaller species from food sources. However, the relative aggressiveness of some smaller species (e.g., the great tit) allowed them to defend food sources from bigger species; most notably accentors. The same behaviour was observed among dunnocks (*Prunella modularis*) in the High Tatras, where one individual dunnock was able to drive more than ten accentors away from the food source during an April snowfall.

Diseases, hygiene and conservation. Individual birds and species that make frequent use of feeders are more likely to experience both the benefits and detrimental impacts of provided food. For example, supplementary feeding can influence disease transmission rates and disease dynamics in birds (Wilcoxen *et al.* 2015; Galbraith *et al.* 2017a), while winter flocks comprised of different species may draw the attention of additional predators (Orros and Fellowes 2015), and feeding in gardens may drive evolutionary change in bird migrants (Plummer *et al.* 2015). The positive effects of supplementary feeding in some species include: a reduction in individual stress; an increase in immune defense; faster feather growth; and improved body condition. On the other hand, some individuals exhibit symptoms of conjunctivitis, pox, dermal disease or cloacal disease (Wilcoxen *et al.* 2015). The risk of infections increases in late winter and early spring (Kocianová *et al.* 1985; Janiga 1991; Janiga *et al.* 2007; Kisková *et al.* 2011) when migratory and wintering birds meet at feeding sites. The most important genera of bacteria identified in faecal, cloacal, and pharyngeal samples of alpine accentors during this period are *Klebsiella, Yersinia* and *Staphylococcus* (Janiga *et al.* 2007). Intermixing of droppings and seeds from feeders (Fig. 26) can be a significant source of disease transmission between birds during different seasons and between differing ecosystems, as well as throughout the food chain between predator and prey. Autumn is the second-most important period for the occurrence of these different genera of bacteria in birds (Janiga 1991; Janiga *et al.* 2007). At this time of year, accentors are most frequently caught by birds of prey and other predators.

Interspecific interactions - from late spring to autumn, birds of prey, songbirds, other vertebrates

The alpine accentor is the subject of a long-term study by the Institute of High Mountain Biology. The first data on this bird species was systematically collected in 1984, and a multitude of research has been collected in the interim. In addition to this systemic data collection, many other phenomena in the life of this species were observed. The findings of this study are some of the first to shed light on how alpine accentors compete for access to food in winter. In recent decades, bird feeding has become an increasingly popular activity throughout the world, but its ecological impacts are still poorly understood (Robb *et al.* 2008). Although there are

Fig. 26. A mixture of scattered seeds and droppings (top left) under the feeder (top right) can be a source of disease transmission in birds. An accentor found a seed lying near the droppings (bottom left) and then ate it (bottom right).

many experimental supplementary feeding studies in both captive and natural settings, few studies discuss the wider impacts of supplementary winter feeding on bird life throughout the seasons. Accentors are a food source for some birds of prey and mammalian predators, particularly in autumn. Although some species of falcon are known as predators of accentors, the Northern goshawk (*Accipiter gentilis*) and the Eurasian sparrowhawk (*Accipiter nisus*) are likely the most common Eurasian bird predators of alpine accentors. In the Alps, accentors may compose a large percentage of the diet of some hawks in winter as well as in summer. In samples of the prey of a pair of sparrowhawks nesting in the Western Alps on the upper treeline, 156 samples of different animals were found over three years, 72 of which were alpine accentors (Glutz von Blotzheim and Bauer 1988). During research conducted through this study in the West Carpathians, nine direct interactions between hawks and accentors were recorded. One of these occurred in May, but the others took place during September and October, when hawks fly into the alpine zone to hunt migratory birds. Accentors, upon observing hawks, always flew sharply into the mountain cauldrons, and often did not return. On two occasions, remnants of accentor feathers were found and identified as caught by hawks. Falcons, such as the Eurasian hobby (*Falco subbuteo*) use a similar strategy to hunt migratory songbirds travelling over high mountains in autumn. In September, such an attack on accentors was recorded. In this case the accentor spotted the hobby, and quickly flew down into the valley. Another species of falcons, the kestrel (*Falco tinnunculus*), is dangerous to fledglings of accentors in summer (Dyrcz 1976; Heer 1998). Adult male and female alpine accentors utilize loud alarm calls when these predators appear, then systematically attack and drive it away. Several such interactions were observed in July.

Songbirds. Adult accentors were also found to attack some species of songbirds, such as the Northern wheatear (*Oenanthe oenanthe*). In the West Carpathians, accentors generally avoid common ravens (*Corvus corax*), though some interactions were observed near summits during the month of September. During this same timeframe, accentors were observed to avoid alpine clough (*Pyrrhocorax graculus*) in the Tian Shan. During autumn in the Tian Shan, alpine accentors responded to alarm calls of cloughs and plain mountain finches (*Leucosticte nemoricola*). Accentors were recorded foraging with the mountain finches, but the tfinches had precedence over the accentors. In Kyrgyzstan, interactions between accentors and wallcreeper (*Tichodroma muraria*) were also observed. Between these two species, the stronger and more aggressive appears to be the wallcreeper. During five observed attacks, a wallcreeper demonstrated precedence over an accentor four times, with the accentor claiming victory once. Between spring and autumn, accentors often come into contact with water pipits (*Anthus spinoletta*). Interactions between these species in the West Carpathians mainly occurs between July and September. In most cases, accentors chase pipits away from food, with only the occasional instance of the inverse. Inexperienced juvenile accentors sometimes form small flocks with juvenile pipits in summer (seen in July), but in other circumstances a 19-day-old accentor was observed to attack a water pipit (Glutz von Blotzheim and Bauer 1988). In a cage, an accentor can chase away a red crossbill (*Loxia curvirostra*) (Glutz von Blotzheim and Bauer 1988).

The Eurasian ermine (*Mustela erminea*) is a very dangerous mammalian predator of accentor nestlings during summer. The presence of ermine during this period always results in strong anti-predation behaviour by adult birds, whereby accentors will cooperatively attack ermines and aggressively defend nests. Sometimes higher vigilance to predation pressure can also be achieved through breeding aggregation with other species (Heer 1998). In autumn, when an accentor sees an ermine, it stands and does not move. In one case, a chamois (*Rupicapra rupicapra*) was observed to walk half a metre alongside an accentor that did not react at all. The common European viper (*Vipera berus*) can also be very dangerous for accentors during nesting. In the Pyrenees, 18 percent of broods were preyed on after hatching, and predators included both mustelids and the common viper (del Hoyo *et al.* 2005).

Acknowledgements

My thanks to Martin Janiga for his technical support in figure preparation. I also thank the volunteers and students who accompanied and assisted my work in the winter resort Malinô Brdo.

References

Alatalo, R.V. and Moreno, J. 1987: Body size, interspecific interactions, and use of foraging sites in tits (Paridae). *Ecology*, **68**: 1773-1777.

Birkhead, M.E. 2008: The social behaviour of the Dunnock *Prunella modularis*. *Ibis*, **123**: 75-84.

Cowie, R.J. and Hinsley, S.A. 1988: The provision of food and the use of bird feeders in suburban gardens. *Bird Study*, **35**: 163-168.

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.

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

Galbraith, J.A., Jones, D.N., Beggs, J.R., Parry, K. and Stanley, M.C. 2017b: Urban bird feeders dominated by a few species and individuals. *Front. Ecol. Evol.*, **5**: 81.

Galbraith, J.A., Stanley, M. C., Jones, D. N., and Beggs, J. R. 2017a: Experimental feeding regime influences urban bird disease dynamics. *J. Avian Biol.*, **48**:700-713.

Glutz von Blotzheim, U.N. and Bauer, K.M. (eds.) 1988: Handbuch der Vögel Mitteleuropas. Band 11.II. Aula-Verlag, Wiesbaden.

Gustafsson, L. 1987: Interspecific competition lowers fitness in Collared Flycatchers *Ficedula albicollis*: an experimental demonstration. *Ecology*, **68**: 291-296.

Heer, L. 1998: The polygynandrous mating system of the alpine accentor *Prunella collaris*, individual reproductive tactics, breeding adaptations on high mountain conditions and winter ecology. Ph.D. Thesis, Zoological Institute, University of Bern, Bern.

Janiga, M. 1991: The study of plumage polymorphism and ornithosis in feral pigeons (*Columba livia*). In: *Nestling mortality of granivorous birds due to microorganisms* and toxic substances (eds. J. Pinowski, B.P. Kavanagh

and W. Górski), pp. 33-44. Polish Ecol. Publ., Warsaw.

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

Janiga, M., Sedlárová, A., Rigg, R. and Novotná, M. 2007: Patterns of prevalence among bacterial communities of alpine accentors (*Prunella collaris*) in the Tatra Mountains. *J. Ornithol.,* **148**: 135-143.

Kisková, J., Hrehová, Z., Janiga, M., Lukáň, M., Haas, M. and Jurčovičová, M. 2011: *Yersinia* species in the Dunnock (*Prunella modularis*) in the sub-alpine habitats of the Western Carpathians. *Pol. J. Microbiol.*, **60**: 79-83.

Kocianová, E., Řeháček, J., Janiga, M. and Lisák, V. 1985: Infestation of the twon population of pigeons (*Columba livia* f. *domestica*) by *Coxiella burnetti* and *Chlamydia psittaci* in Bratislava. In: *Zoocenózy urbánnych a suburbánnych celkov so zvláštnym akcentom na podmienky Bratislavy* (eds. Z. Feriancová-Masárová and J. Halgoš). Slovak Zoological Society, Bratislava.

Miller, E.T., Bonter, D.N., Eldermire, C., Freeman, B.G., Greig E.I., Harmon, L., Lisle, C.R. and Hochachka, W.M. 2017: Fighting over food unites the birds of North America in a continental dominance hierarchy. *Behav. Ecol.*, **28**: 1454-1463.

Novotný, M., Fečková, M., Janiga, M., Lukáň, M., Novotná, M. and Kovalčíková, Z. 2007: High incidence of *Yersinia enterocolitica* (Enterobacteriaceae) in alpine accentor *Prunella collaris* of the Tatra Mountains. *Acta Ornithol.*, **42**: 137-143.

Orros, M.E., and Fellowes, M.D.E. 2015: Widespread supplementary feeding in domestic gardens explains the return of reintroduced red kites *Milvus milvus* to an urban area. *Ibis*, **157**: 230-238.

Olsson, O., Wiktander, U. and Nilsson, S. 2000: Daily foraging routines and feeding effort of a small bird feeding on a predictable resource. *Proc. R. Soc. B: Biol. Sci.*, **267**: 1457-1461.

Plummer, K.E., Siriwardena, G.M., Conway, G.J., Risely, K. and Toms, M.P. 2015: Is supplementary feeding in gardens a driver of evolutionary change in a migratory bird species? *Glob. Change Biol.*, **21**: 4353-4363.

Popp, J.W., Ficken, M.S. and Weise, C.M. 1990: How are agonistic encounters among black-capped chickadees resolved? *Anim. Behav.*, **39**: 980-986.

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.

Slagsvold T. 1975: Competition between the Great Tit *Parus major* and the Pied Flycatcher *Ficedula hypoleuca* in the breeding season. *Ornis Scand.*, **6**: 179-190.

Timko J. and Kmeť V. 2003: Susceptibility of Enterobacteriaceae from the alpine accentor *Prunella collaris*. *Acta Vet. Brno*, **72**: 285-288.

Wilcoxen, T.E., Horn, D.J., Hogan, B.M., Hubble, C.N., Huber, S.J., Flamm, J., Knott, M., Lundstrom, L., Salik F., Wassenhove, S.J. and Wrobel, E.R. 2015: Effects of bird-feeding activities on the health of wild birds. *Conserv. Physiol.*, **3**: cov058.

Woodrey, M.S. 1990: Economics of caching versus immediate consumption by white-breasted nuthatches: the effect of handling time. *The Condor*, **92**: 621-624.

Zeng, X. and Lu, X. 2009: Interspecific dominance and asymmetric competition with respect to nesting habitats between two snowfinch species in a high-altitude extreme environment. *Ecol. Res.*, **24**: 607-616.

Received 7 August 2021; accepted 3 November 2021.