# The biology of the Alpine accentor *Prunella collaris.* IV. Maintenance activities and their clusters from late autumn to early spring. 20 year observation

M. JANIGA

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

**Abstract.** The maintenance activities and seasonal rhythms in behaviour and behavioural clusters of Alpine accentor (*Prunella collaris*) were studied between 1984 to 2003 at Malinô Brdo, Great Fatra NP, a ski resort in the West Carpathians, Slovakia. The following episodes of behaviour were recorded: feeding, standing (sitting alert), sitting (drowsily), preening, flights, calls and songs.

Notes on behaviour were simply written or dictated onto tape. One minute of an activity of one bird constituted one field sample. In total, 21 282 samples of feeding, 1699 of preening, 18 411 of seating, 2417 of standing, 3775 of songs or calls, and 1630 of flights (longer than 100 metres) were collected. Daily activity of accentors ranged from 8 hours per day in late December to approximately 11 hours per day in April. During November, daily feeding schedules were bipolar, with peaks in early morning and at two o´ clock p.m. Rest periods rapidly increased during December. Resting was accompanied by the disappearence of vocalisation and a rapid reduction in preening. In January, the accentors exhibited a series of activities comparable to the structure of behaviour in November. The increased length of daylight in February likely induced hormonal activity in birds, and the amount of time devoted to singing rapidly increased. Subsongs often alternated with preening. In March, throughhout a day, birds displayed a mixture of many different kinds of activities including singing, preening, short flights, and standing alert. In April, accentors exhibited a series of activities that corresponded to pre – mating behaviour. Generally, birds were more stressed during feeding on cloudy than sunny days. The association between flocking and resting without additional activity, such as preening, supports the notion of a link between flocking and an efficient use of energy during winter.

*Key words:* Alpine accentor, behaviour, maintenance activities, winter ecology

## Introduction

In general, maintenance mechanisms in animals are designed to enable them to behave in the most profitable manner, without an undue waste in energy. At the same time, animals must contend with a number of potential hazards and dangers. Many species follow specific routines, based on their internal clock. The time of day and season can be important stimuli for appetite, rest or preening.

Seasonal rhythms in maintenance activities of Alpine accentors wintering in a ski resort in the Western Carpathians (Slovakia) are the subject of this study. Alpine accentors vary in their wintering strategies. Mainly older males are resident, engaging in only local movements (Martín-Vivaldi *et al.* 1995; Heer 1996; Heer and Fraenkl 1999). Migratory birds usually include a large proportion of females and yearlings (Nakamura *et al.* 1996; Nakamura and Nishiumi 2000; Henry 2011). Extreme changes in climatic factors, such as temperature, light intensity, winds, and snow cover, affect accentors directly. However, indirect climate effects are also a factor, including fluctuations in food availability, numbers of predators, etc. Seasonal and circadian rhythms enable accentors to anticipate changes in environmental conditions (Janiga and Romanová 1997). Such mechanisms facilitate the accurate timing of specific types of behaviour or events, especially under winter conditions. Many events tend to be grouped in time. For example, a hungry accentor performs a series of maintenance activities while searching for food, such as standing, waiting or calling. These activities tend to form a group or a cluster of activities that occur for a given period of time and then cease, to be replaced by a different group; perhaps sitting, sleeping, and preening (Janiga and Romanová 1996). Clusters of activities may be effectively differentiated by multivariate statistics when a suitable amount of quantitative data exists. In this study, the general types of behaviour of wintering Alpine accentors are described. The variation in the structure of clusters was analysed in relation to different variables such as month or flock size. Of particular interest are seasonal variations in maintenance activities.

## Material and Methods

*Data collection in field*

The field work was conducted between 1984 and

| Year | 84/85 | 85/86 | 86/87 | 87/88 | 88/89 | 89/90 | 90/91 | 91/92 | 92/93 | 93/94 | 94/95 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **No. of birds** | 10 | 9 | 8 | 7 | 4 | 7 | 4 | 4 | 2 | 1 | 2 |
| **No. of visits** | 15 | 18 | 24 | 13 | 25 | 10 | 9 | 19 | 5 | 5 | 4 |
| **Year** | 95/96 | 96/97 | 97/98 | 98/99 | 99/00 | 00/01 | 01/02 | 02/03 | 03/04 | 04/05 | |
| **No. of birds** | 2 | 3 | 5 | 3 | 3 | 4 | 4 | 1 | 0 | 0 | |
| **No. of visits** | 12 | 9 | 11 | 7 | 9 | 10 | 5 | 3 | 5 | 5 | |

**Table 1.** Maximum number of birds seen in one day during the winter period at Malinô Brdo.

2005 in the Great Fatra Mountains National Park, at the Malinô Brdo ski resort (Table 1). Generally, birds were monitored from the beginning of November to the end of April. Details on maximum number of birds seen in respective years and the number of visits per year are presented in Table 1. 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, they also stayed in the resort on sunny days when snow cover disappeared in many patches. Thus, the presence of a bird in the wintering area was often individually motivated, and often the occurrence of accentors was dependent on the type of food offered by tourists, hotel managers or skiers. The survey area was restricted to the ski resort, approximately 1 km long and 2 kms wide, where accentors fooraged near hotels, pensions or restaurants. Daily visits lasted a minimum of five hours, but many visits lasted from dusk till dawn. 27 birds were captured with a cheese/millet-baited fallingtrap. Each bird was individually marked with colourings and measured. The majority of birds were individually distinguished and resighted over the next years. Binoculars of various powers were of assistance for observation. Notes on behaviour were simply written or dictated onto tape. During simultaneous observation of multiple birds, individuals were videorecorded, and the recordings were later analysed in the laboratory.

*Description and classification of behaviour*

Detailed classification of behaviours was described in studies by Janiga and Romanová (1996, 1997). The following episodes were recorded: feeding, standing (sitting alert), sitting (drowsily), preening, flights, calls and songs. The notion of general maintenance activities usually encompasses a wide variety of behaviour patterns (McFarland 1987).

*Feeding (Fig. 1)*

This category encompasses appetitive behaviour, and includes activities involved in searching, obtaining, handling, and ingesting food. This category also included "hunting" (for example, the birds hunted flies in sunny March and April days near the windows and roof of the hotel). "Hunting" also involved the activity of "capturing". The exploratory phase of feeding was often associated with "foraging". "Drinking" was also included in this category, although feeding was not always a direct stimulus for drinking. In winter, birds tended to eat and drink in synchrony by consuming snow.

*Standing (Fig. 2)*

The term was given to a somewhat heterogeneous group of behavioural patterns which all had something to do with active immobility. The category included: *Watching* the members of the family. The birds looked for the members of a wintering group, and possibly benefited from watching their activities. *Standing* on one leg – whereby the birds preserved body heat. *Standing* alert during feeding. Birds had to be alert to the possibility of being surprised by predators, particularly domestic cats. Standing before feeding when accentors had access to abundant and predictable sources of food (bird feeder). Generally, during the early morning, following arrival at the ski resort, birds did not immediately seek food sources, but stood, very often without any movement in selected sites beneath the roof of the hotel. *Standing - intention* movements - a bird standing on the ground was about to take off in fllght, or to feed.
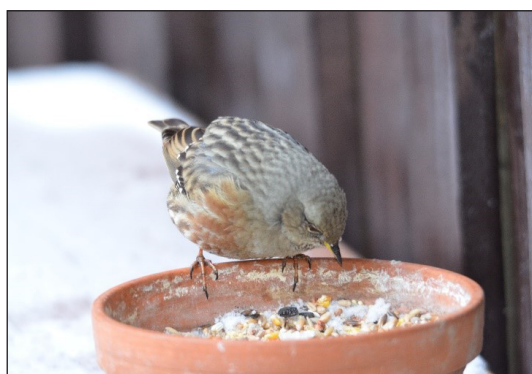


**Fig. 1.** Feeding (Photo: Marián Janiga).



**Fig. 2.** Standing (Photo: Marián Janiga).

*Preening (Fig. 3)*

These activities all had something to do with body care, whether it was routine maintenance, as in the preening of birds or rernoval of parasites. The category consists of pethaps twenty different activities, the most of them were active means by which the bird defended its integuments against attack from biological factors, specifically ectoparasites. "Preening" included postbathing preening, body shaking, wing whirring, oiling, and scratching. The behaviours of "sitting + preening" or "standing + preening" were always considered equivalent to simply, "preening". Displacement preening was also included in this category.



**Fig. 3.** Preening (Photo: Marián Janiga).

*Resting (sitting drowsily; Fig. 4)*

Accentors often rest during a day. Resting is most commonly associated with sessions lasting many minutes, during which a bird sits and remains immobile, sometimes moving only its head. During the daylight, the category was often associated with active (not quiet) sleep.



**Fig. 4.** Resting or sitting (Photo: Marián Janiga).

*Flights*

Usually short flights from one site to a second site. Flights can be used by birds in a number of behavioural contexts, and may be misleading to researchers. All types of flight (McFarland 1987) were included in the category of flight.

*Calls and songs*

Category consists from all manners of sounds, for example calls of adults during depart. Calls and songs. This category consists of all manner of sounds. Examples include the calls of adults during departure from the locality or long continual subsongs during sunny days in early spring. The "sitting + song" or "calls + flight" were considered equivalent.

*Classification of activity budgets - months, decades and hours*

I recorded the behaviour of accentor(s) once per minute. This was the shortest interval in which I was still able to record the behaviour in the field. The description represents all categories which occurred in each designated minute. Categories were designed in such a way that the members of one class did not also occur in another class. For example, accentors somtimes were observed "sitting" and "preening" during a given minute. In this case, I separately scored the two categories in this minute. One minute of an activity per one bird was a field sample. If ten birds were seen in a minute, then ten samples were collected. So, the variable "feeding" in a hour means the number of samples of feeding per hour. The activity of birds was recorded between November 1st and April 30th. The following number of samples was collected per month (Table 2).

| Hour | Nov. | Dec. | Jan. | Febr. | March | April |
|---|---|---|---|---|---|---|
| 6.00 | | | | | 222 | 439 |
| 7.00 | 235 | 5 | 109 | 1311 | 1553 | 287 |
| 8.00 | 669 | 314 | 1589 | 2222 | 1206 | 239 |
| 9.00 | 134 | 544 | 907 | 1276 | 1432 | 101 |
| 10.00 | 93 | 299 | 567 | 976 | 798 | 211 |
| 11.00 | 134 | 467 | 488 | 1280 | 1008 | 235 |
| 12.00 | 231 | 380 | 435 | 694 | 1533 | 338 |
| 13.00 | 214 | 715 | 562 | 671 | 919 | 404 |
| 14.00 | 495 | 392 | 127 | 1858 | 477 | 300 |
| 15.00 | 776 | 641 | 1350 | 1732 | 1676 | 267 |
| 16.00 | 494 | 849 | 1134 | 1450 | 1592 | 758 |
| 17.00 | 6 | 4 | 63 | 741 | 953 | 291 |
| 18.00 | | | | 6 | 125 | 239 |
| 19.00 | | | | | | 12 |

**Table 2.** Amounts of samples (one minute per a bird equals one sample) used for the computation of relative hourly activity budgets. Eastern European Time.

In total, 21 282 samples of feeding, 1699 of preening, 18 411 of seating, 2417 of standing, 3775 of songs or calls, and 1630 of flights (longer than 100 metres) were collected. For each month, a model of a day was separately constructed.

*Classification of activity clusters and statistics*

*Ratio scale*

Hourly sums of the minutes of observations of four bird activities - sitting (resting), standing (siting alert and watching), feeding and preening composed their ratio. For example: 10 : 2 : 25 : 3 means 10 minutes of sitting, 2 of standing, 25 of feeding, and 3 of preening in a hour (e.g. between 10:00 and 11:00). As mentioned above, one minute of observation of one bird equaled one sample, so if more birds were watched in a minute, more samples in a minute were obtained. All arithmetical operations dealing with activity clusters were carried out in these hourly ratio scales. The ratio scale has all characteristics of an interval scale, the unit of measurement is equal in all four classes of activities, and scaling is independent of the observer 's viewpoint. The internal structure of ratios was examined in relation to weather conditions, flock size observed in the field, and calendary months.

Principal component analysis is a multivariate technique that may be used for summarizing data sets combining large numbers of variables The importance of principal components can be judged from the amount of variance associated with them, and from the signs of their weight (coordinates) elements (Jolicoeur 1963; Lawley and Maxwell 1971) The designed ratios were the fundamental inputs to the data matrix for PCA. Principal components (factors) were computed from correlation matrix of variables (Table 3), i.e. relative amounts of minutes spent for each category in a ratio. Analysis of variance was used to test for effects of the different factors on principal component coordinates of cases (Sommers 1986). The calculations were carried out using the statistitical package STATISTICA 12.

## Results

*Daily routine*

The daily routine of wintering accentors differs in different months and also in different hours of a month. On the basis of direct observations in the field, Alpine accentors arrived to the ski resort approximately fifteen minutes after dawn and departed from fifteen to twenty minutes before dusk. The daily activity of accentors ranged from 8 hours per day in late December to approximate-

ly 11 hours per day in April (Table 4). During November, the scheme of daily feeding in birds was bipolar with peaks in early morning and around two o´clock p.m. (Fig. 5a). Birds mainly rested from 10 to 11 o´clock with increased amounts of time devoted to postbreeding preening (Fig. 5b).
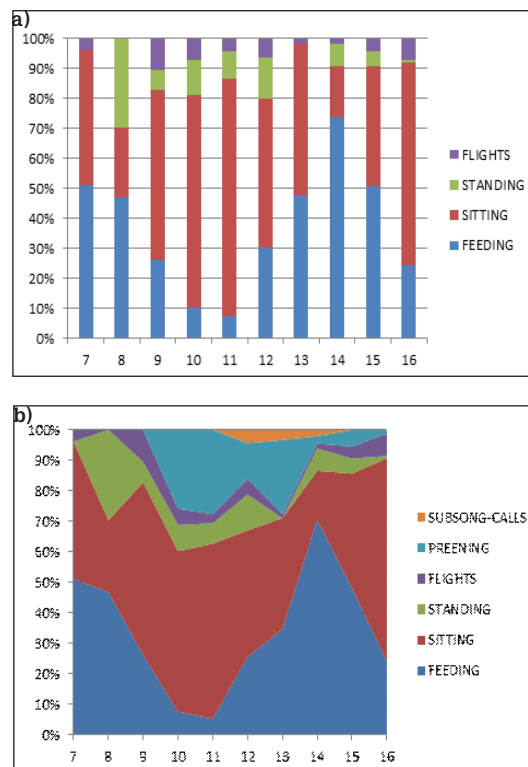


**Fig. 5.** Hourly activity budgets of wintering Alpine accentors in November. **a)** Structure of four most important maintenance activities. **b)** Maintenance activities accompanied with preening and vocalisation.

Amounts of minutes devoted to resting (sitting, sitting drowsily) rapidly increased in December (Fig. 6a). Birds more or less foraged for the duration of the day. Resting in December was accompanied with the disappearence of vocalisation and a rapid reduction of preening in comparison to the behavioural scheme from November. Mobility of birds in the area during a day was also reduced (Fig. 6b).

In January, accentors exhibited a series of activities comparable to the structure of behaviour in

| Variable | PC1 | PC2 | PC3 | PC4 |
|---|---|---|---|---|
| Sitting | -0.855532 | **0.267957** | -0.149336 | **0.417088** |
| Standig | -0.626596 | **-0.449398** | **0.636626** | 0.011238 |
| Feeding | -0.619934 | **-0.577808** | **-0.509397** | -0.149446 |
| Preening | -0.759451 | **0.540585** | 0.058789 | **-0.357136** |
| Variance in % | 52 | 22 | 17 | 8 |

**Table 3.** Factor coordinates of included variables into principal component analysis. Structure of fundamental behavioural groups in Alpine accentors in winter. Numbers, which denote the main behavioural schemes are in bold.

| Date | Arrival (EET) | Departure (EET) | Month/Activity length | Dawn | Dusk |
|---|---|---|---|---|---|
| Nov. 7th | 16:10 | | | | |
| Nov. 20th | 17:07 | | | | |
| Nov. 20th | 17:10 | | | | 17:25 |
| Nov. 22nd | 16:54 | | | | 17:15 |
| Nov. 23rd | 7:43 | | | | |
| Nov. 23rd | 7:48 | | | | |
| | | | End of November app. 9 hrs. 15 min | | |
| Dec. 8th | 7:58 | | | | |
| Dec. 9th | 8:05 | | | | |
| Dec. 10th | | 17:01 | | | |
| Dec. 17th | 8:12 | | | | |
| Dec. 21th | 8:05 | | | | |
| Dec. 22nd | 8:05 | | | 7:55 | |
| Dec. 26th | | 16:46 | | | |
| Dec. 28th | | 15:40 | | | |
| Dec. 29th | 8:29 | | | 8:10 | |
| | | | End of December app. 8 hrs. 15 min | | |
| Jan. 1st | | 16:44 | | | |
| Jan. 2nd | 8:2 | | | 8:00 | |
| Jan. 4th | | 17:16 | | | 17:30 |
| Jan. 7th | | 16:38 | | | |
| Jan. 8th | 8:12 | 17:20 | | | |
| Jan. 8th | | 16:50 | | | |
| Jan. 15th | | 16:55 | | | |
| Jan. 15th | | 17:15 | | | |
| Jan. 23rd | | 17:00 | | | |
| Jan. 24th | 8:05 | | | | |
| Jan. 25th | 8:10 | | | | |
| Jan. 27th | | 17:46 | | | |
| Jan. 29th | 7:55 | | | | |
| Jan. 29th | 8:05 | | | | |
| Jan. 30th | | 17:07 | | | |
| | | | End of January app. 9 hrs. | | |
| Febr. 1st | 8:00 | | | | |
| Febr. 2nd | 7:50 | | | | |
| Febr. 5th | | 16:40 | | | |
| Febr. 6th | | 16:59 | | | |
| Febr. 7th | 7:59 | | | | |
| Febr. 8th | 8:10 | | | | |
| Febr. 10th | 7:40 | | | | |
| Febr. 11th | 7:28 | | | 7:28 | |
| Febr. 11th | 7:42 | | | | |
| Febr. 12th | | 16:37 | | | |
| Febr. 15th | | 17:23 | | | |

| | | | |
|---|---|---|---|
| Febr. 18th | | 18:00 | |
| Febr. 19th | 7:20 | | 7:00 |
| Febr. 19th | | 18:01 | |
| Febr. 20th | 7:10 | | |
| Febr. 21th | 7:55 | | |
| Febr. 22nd | | 16:57 | |
| Febr. 23rd | | 16:10 | |
| Febr. 24th | | 17:10 | |
| Febr. 27th | | 17:44 | |
| | | End of February 9 hrs. 30 min | |
| March 1st | | 17:30 | |
| March 1st | | 18:16 | |
| March 1st | 7:25 | | |
| March 2nd | | 18:06 | |
| March 3rd | 7:15 | | 7:00 |
| March 3rd | | 18:18 | |
| March 4th | 7:00 | | |
| March 6th | 7:30 | | 6:50 |
| March 7th | | 17:50 | |
| March 26th | 7:21 | 18:24 | 6:20 |
| | | End of March app. 10 hrs. 30 min | |
| April 3rd | | 18:48 | |
| April 4th | | 18:13 | |
| April 15th | | 18:35 | |
| April 15th | | 19:05 | |
| April 15th | | 19:15 | |
| | | April – app. 11 hrs. and more | |

**Table 4.** Seasonal variation in the length of daily activity of Alpine accentors in the wintering area, Malinô Brdo, NP Great Fatra mountains, Slovakia. EET – East European Time.
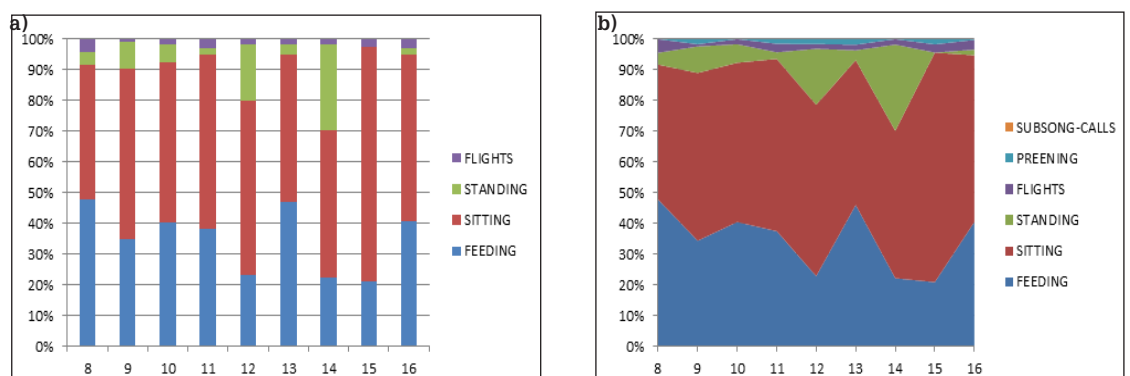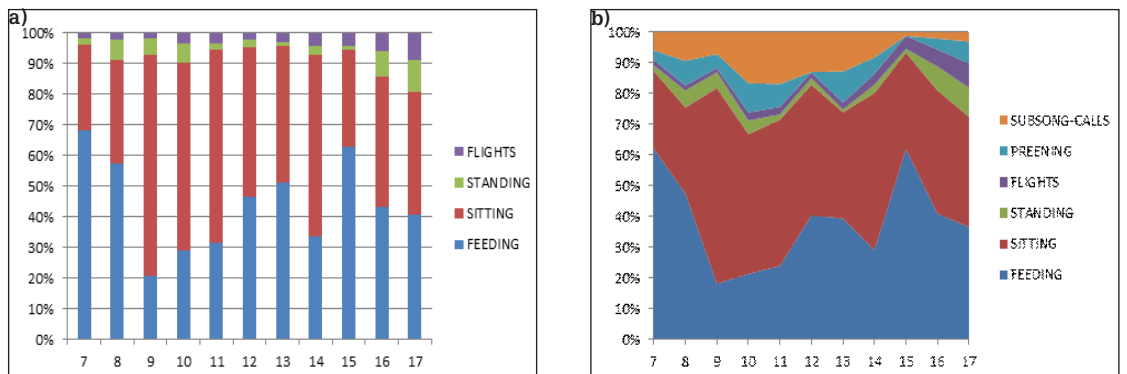


**Fig. 6.** Hourly activity budgets of wintering Alpine accentors in December. **a)** Structure of four most important maintenance activities. **b)** Maintenance activities accompanied with preening and vocalisation.

November. In deep winter they usually started to feed immediately after arrival. In the mornings, they spent approximately 80 per cent of their time feeding (Fig. 7a). After 10 o´clok birds usually started to rest (sitting) and the second smaller peak of feeding occurred one hour before departure (Fig. 7b).

In February, accentors foraged in the early morning as well as in the afternoon, from one to two hours before departure (Fig. 8a). The length of daylight during February is probably sufficient to activate hormonal activity in birds, and the amount of time devoted to singing rapidly increased. Singing often alternated with preening (Fig. 8b).
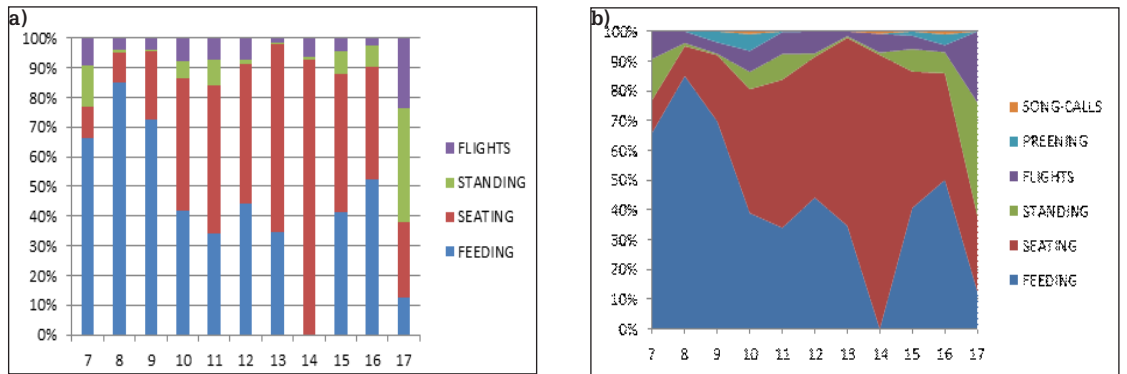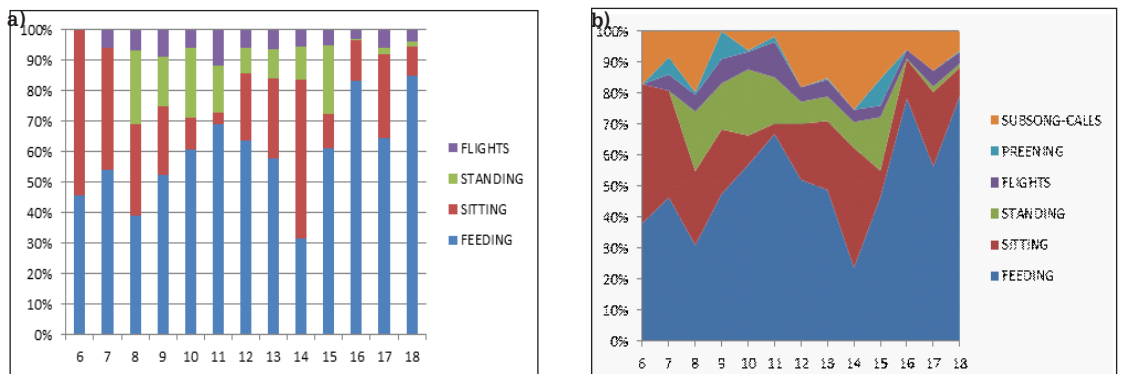
**Fig. 7.** Hourly activity budgets of wintering Alpine accentors in January. **a)** Structure of four most important maintenance activities. **b)** Maintenance activities accompanied with preening and vocalisation.



**Fig. 8.** Hourly activity budgets of wintering Alpine accentors in February. **a)** Structure of four most important maintenance activities. **b)** Maintenance activities accompanied with preening and vocalisation.
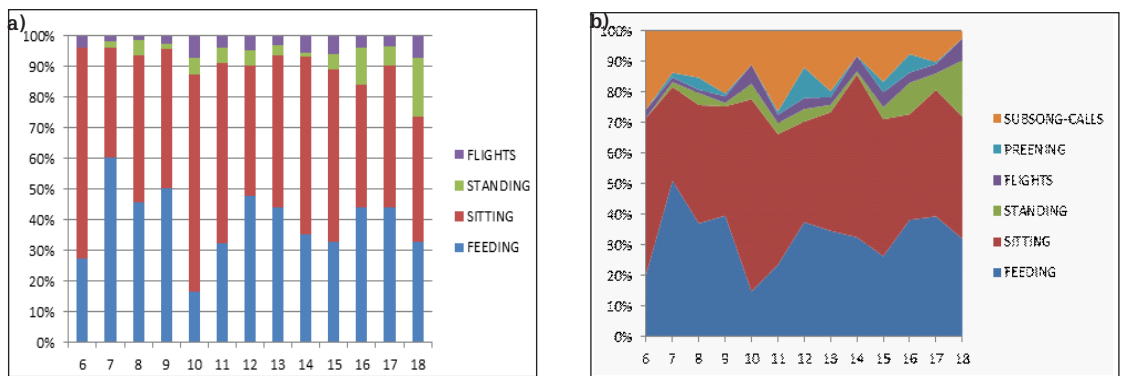


**Fig. 9.** Hourly activity budgets of wintering Alpine accentors in March. **a)** Structure of four most important maintenance activities. **b)** Maintenance activities accompanied with preening and vocalisation.
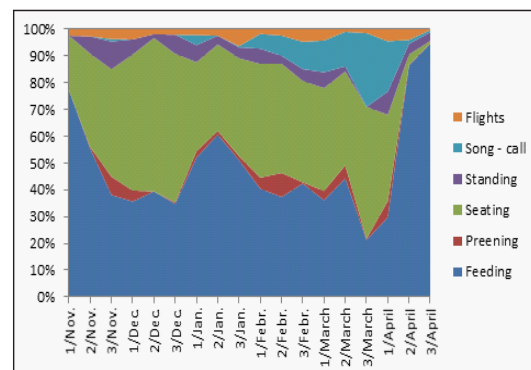


**Fig. 10.** Hourly activity budgets of wintering Alpine accentors in April. **a)** Structure of four most important maintenance activities. **b)** Maintenance activities accompanied with preening and vocalisation.

In March, the structure of daily behaviour rapidly changed in comparison to February. Birds foraged throughout the day but foraging decreased to 30 - 40 % of hourly behavioural budgets (Fig. 9a). Throughout a day birds displayed a mixture of many different kinds of activities including singing (Fig. 9b).

During April, the number of minutes devoted to feeding rapidly declined in the early morning and significantly increased in the late afternoon (Fig. 10a). Birds often started to forage in open grassy areas. During a day, accentors exhibited a series of activities that corresponded to pre – mating behaviour. The amount of time devoted to short distance flights, standing alert and singing increased (Fig. 10b), especially mid-day during sunny days. The rhythm of intensive feeding usually began in the late evening, from one to two hours prior to daily departure.
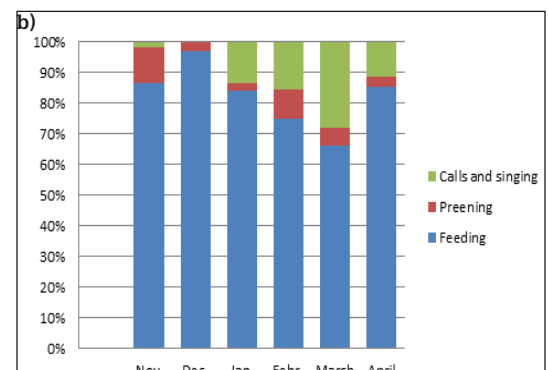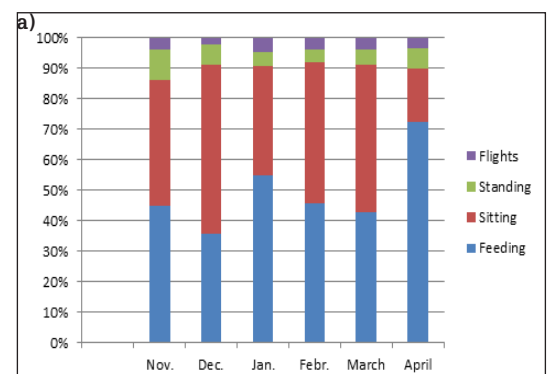
*Seasonal routine*

In late autumn, birds foraged during the early morning, immediately after arrival. In November, Alpine accentors could find food in rocky parts of the resort and wind-blown patches where the soil remained free of snow. In this late post-breeding period, before real winter, their diet consisted of vegetable matter. However, following the first heavy snows, which could occur as early as November, the moutain hotel and restaurants attracted several accentors. In addition to a feeder, the birds found scraps on the terraces of restaurants. When they

found good foraging sites with predictable diet, their behaviour strategy changed. From the beginning to the end of November, the daily time budgeted for feeding activity decreased from 70 to 40 per cent and the time devoted to seating (resting) rapidly increased (Fig. 11). Having a predictable site for feeding, accentors effectively saved energy, particularly in December. The daily budget for feeding decreased to 30 percent, and more than 50 % of daily time was devoted to resting (Fig. 12a). Vocalisation, preening or watching in alert (standing) was reduced to the minimum value (Fig. 12b). In birds, the gonads are mainly photo-stimulated and short periods of daylight in December likely contributes to the inactivity of accentors. Thus, December is probably the only month of the year when birds survive winter with minimal energy expenditure. The increased amount of daylight in January and





**Fig. 11.** Relative seasonal variation in the main activities of Alpine accentors in winter. Each month is divided into decades. For number of samples see Table 2.

**Fig. 12. a)** Relative montly variation in main maintenance activities of wintering Alpine acctentors in the Great Fatra NP, West Carpathians. **b)** Feeding activity of accentors in winter related to preening and vocalisation. For number of samples see Table 2.

| Factor | Exploratory versus resting activity clusters - PC2 (feed+stand versus sit+preen) | Alarm behaviour during feeding - PC3 (feed or stand and watch) | Sit and preen or sit and rest – PC4 |
|---|---|---|---|
| Weather | F (4,118)=1.65, P=0.16, NS | **F (4,118)=4.1, P=0.004\*\*** | F (4,118)=1.9, P=0.1, NS |
| Month | **F (5,131)=2.78, P=0.02\*** | F (5,131)=0.9, P=0.48, NS | F (5,131)=1.5, P=0.2, NS |
| Flock size | F (3,133)=2.18, P=0.09, NS | F (3,133)=0.86, P=0.46, NS | **F (3,133)=2.7, P=0.048\*** |

**Table 5**. Effects of weather, months (season) and number of birds in a flock on the behavioural schemes of Alpine accentors in winter. One - way ANOVAs (F) and their significance levels (P) refer to comparisons of pricipal component coordinates of cases (hourly observations of bird behaviour in field). The significant differences in some groups are shown in bold and in Figs. 13, 14, and 15.
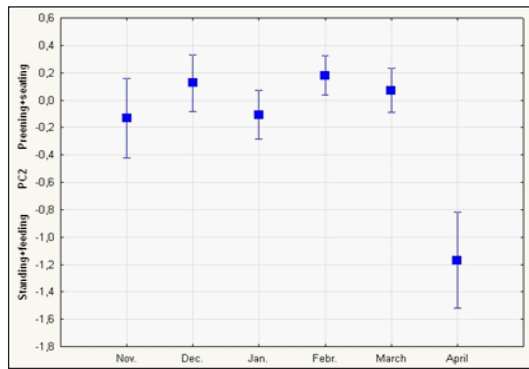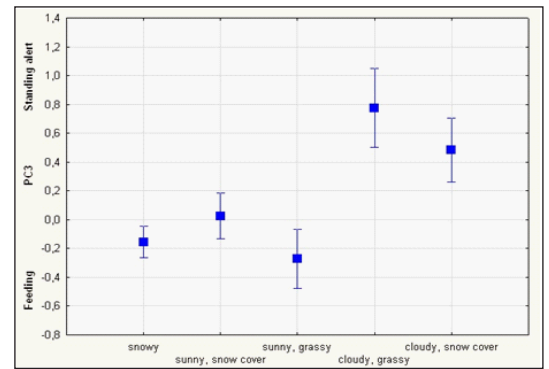
**Fig. 13.** Mean values of principal coordinates of cases on PC2 Vertical bars denote +/- standard errors. From November to March, Alpine accentors devoted more time to preening and sitting (resting) and less to feeding and standing alert than in April. In April, the exploratory activies (see Table 5) proportionally increased to resting activities.
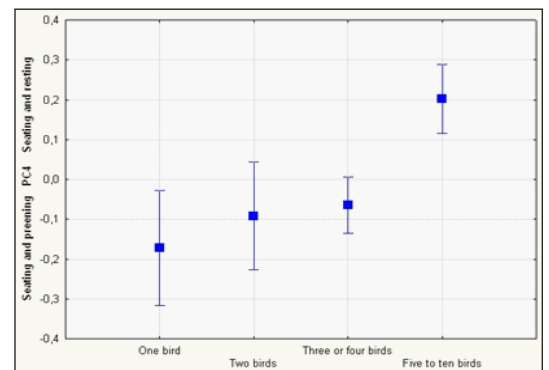


**Fig. 14.** Mean values of principal coordinates of cases on PC3 Vertical bars denote +/- standard errors. In cloudy weather, the accentors devoted proportionally more time to watching surroundings during feeding than in the sunny winter days or during snowfall.

February activate hormonal cycles. Alpine accentors often warbled subsong when resting under the roof of mountain hotel. Subsong activity increased toward March (Figs. 11, 12 b.) Subsongs were most intense on sunny mid-days. Several birds could be seen singing at a distance of one meter under the same roof. In early spring, during April, accentors changed their scheme of behaviour. Birds increased the time spent foraging, and feed mainly on open patches of grassy areas exposed by snow melt. Starting in March, accentors were seen catching dipterous near the windows and under the roof of hotels and collecting arthropods on the snow. Birds evidently started to look for animal proteins which enable quick body restoration following winter. By the end of April birds spent more time feeding than in winter months (Figs. 11, 12a).

*Activity clusters*

As mentioned in the Introduction, many activties of animals tend to be grouped by time and by basic maintenance activity. For example, feeding, may be a member of different behavioural clusters. A hungry accentor performs a series of activities while searching for food and eating it, such as standing or calling. These activities form a group which occurs for a given period of time and concrete space and then ceases, to be replaced by a different group; perhaps feeding, sitting and preening. For the analysis of behavioural clusters principal component analysis was used. The first principal component (Table 3) is an indication of researcher activity, and the correlations on PC 1 are of the same sign. The variation of data in PC1 refers to the ability of the observer to find and watch the birds. This was a reason why this component was not analysed in more detail. The next principal components (PC2, PC3, PC4, Table 3) are statistically independent of the first and decribe real clusters of accentor behaviour.

Exploratory versus resting activity clusters (PC2, Table 5, Fig. 13). This type may be called „resting versus exploratory" because sitting is positively associated with preening, and negatively with feeding and standing alert (Table 3). This activity does

not relate to different weather conditions, nor to the size of the wintering flock. However, in this cluster, the exploratory activities – feeding and standing alert – significantly increased in April in comparison to winter months. In winter, birds spent proportionally more time resting and preening than feeding or standing (Table 5, Fig. 13).

Watching and alarm responses during feeding (PC3, Table 5, Fig. 14). If an accentor senses a sign of danger, it stands alert, watching surroundings or members of the group. In PC3, this activity was negatively correlated with feeding. Birds were more stressed during feeding on cloudy than sunny days (Fig. 14). On cloudy days they spent more time standing alert than during snowfall. Cloudy days with fog probably mean less visibility for birds.

Type of a rest (PC4, Table 5, Fig. 15). In winter, birds can simply sit and rest or sit and preen. More birds in a flock, less preening and more simple resting. Individual birds spent proportionally more time preening when sitting (Table 5, Fig. 15). Visual responses are commonly found in birds that live in enlarged groups. In winter, accentors show more variation int he amount of flocking from place to place. Flocking usually correlates with the pres-



**Fig. 15.** Mean values of principal coordinates of cases on PC4 (for significancy see Table 5). Vertical bars denote +/- standard errors. Larger flocks tend to spend more time for simple resting and preen less during resting than smaller flocks or single individuals. Singles and small flocks preened more during sitting and resting.

ence or absence of environmental factors. In wintering accentors, the association between flocking and resting without additional activities like preening supports the notion of a link between flocking and the efficiemt use of energy in winter.

## Discussion

During wintertime, Alpine accentors forage within their summer territories, in surrounding mountain regions, roofs of mountain hotels and restaurants or fly down to lower-located areas (e.g. Praz 1976; Schmidt 1985; Cramp 1988; Martí *et al.* 1989; Martín-Vivaldi *et al.* 1995; Heer 1996; Heer and Fraenkl 1999; Henry 2011; Lukac *et al.* 2016). Ringed animals from the Tatra mountains show us that some birds extend their range considerably; as far as Hungary, for example. The wintering ecology of these migrants is poorly known. Wintering Alpine accentors at Malinô Brdo were probably first recorded in the 1970s (Hudec 1983). Hotel Malina and cable car were built during the 1960s. Accentors have been contributing to knowledge about this wintering ground for more than 30 years. Rapid change occurred after the political break in 1989. The ski resort was drastically enlarged and the hotel reconstructed in a way that was no longer suitable for perching of birds, and the amount of people visiting the site increased exponentially. These changes were accompanied by acoustic and artificial light smog. Behaviour in the last of the specimens was observed in 2003, when the birds largely disappeared from the site. These winter aggregations of birds were studied in detail between winter 1984/85 and winter 2002/2003 (Table 1).

In Europe, November brings great changes to time budgets of Alpine accentors. In the Slovakian Tatra mountains post-breeding migration starts at the beginning of November (cf. Maruyama *et al.* 1972), and migrants reach their wintering ground by mid-November. Once settled at their wintering site some birds may be sedentary, while some individuals may exploit feeding sites a few kilometres away. Some birds, usually dominant males, commute between their breeding territories on sunny days and feeding sites in the surrounding villages during snowfall or heavy freezing periods. Most birds descend below the snowline or seek snow-free patches during winter. Continuous snow cover means a fundamental change in maintenance activity time budgets in November, and the amount of time spent foraging and feeding decreases, while the amount of time spent resting and saving energy increases.

Diet, and the interaction between day-length and circadian rhythm in birds may be critical factors for change in bird behaviour in November. Photoperiodic regulation of migration is also achieved by the appropriate phasing of endogenous circadian and circaannual rhythms of endocrine function and of tissue sensitivity (Follett 1973). Thus, in accentors, the mediation of migration in November and the definite reduction of reproductive behaviour in December and January must be considered in terms of circadian and circannual periodicities whose phase relationships are an adaptive func-

tion of the environmental photoperiod. Distribution and an increased amount of light pulses (Lofts and Lam 1973) during daytime are probably the most important in stimulating photoinduced subsongs of accentors in February. At this time, the daily activity of accentors lasts approximately 9 hours and 30 minutes and daylight lasts approximately 10 hours. The amount of subsong increases in March and the beginning of April (Figs. 11 and 12b). Subsong activity may thus last for three months, increases toward spring, and is most intense on sunny days. At feeding sites, subsong does not cause overt agression and several males may be seen singing close to one another. Males switch from subsong to full song approximately one month before the beginning of the breeding season, usually at the end of April (Heer 1994) and in the beginning of May. The onset of developmet of adult protuberances occurs in the late May (Nakamura 1990; Nakamura and Matsuzaki 1995) when the period of daily activity lasts approximately 14.5 hours (Janiga and Romanová 1997).

In mid- winter (December), reduced time budget for feeding and increased time spent resting probably reflect the shortest period of daylight as well as an increased energy demand for maintenance due to low and freezing temperatures. In late autumn (November), and in February and March, accentors devoted more time to preening. Many passerine birds show an increase in infestation by ectoparasites during winter months (for example, Hamstra and Badayev 2009). The most favourable period for feather eating lice is winter. At this time, the number of lice increases (Janiga and Kubašková 2000), and the size of adult lice is largest, possibly due to a decrease in preening-mediated selection in December. In October and November, Alpine accentors compose feeding aggregations that can include hundreds of birds. Their body mass can increase from 40 to more than 50 grams (Janiga pers. obs.), and they have new plumage. The few individuals of lice that survive moult may trigger an increase that leads to larger infestations of lice in winter. Wintering birds in December spend most of the short daylight period feeding and resting without preening. Less frequent preening, reduced daylight in December, and relatively new plumage provides the lice with a very favourable environment. Mid - winter is an excellent period for the growth and development of Ischnoceran lice (Janiga 2018). The ratio of male to female lice does not differ except during spring, but during most seasons lice in females is more prevalent (Janiga and Mičková 2004). We can hypothesize that preening played the most iportant role in this louse reduction during early spring. Moreover, from February through March, the fat stores of birds are quickly reduced (Heer 1998), reflecting changes in their behaviour and physiology. The lice found on the bodies of birds were smaller in the spring than in winter but nymphs were found, indicating an occurrence of a new parasite generation (Janiga 2018)

In addition to the above-mentioned factors, a range of additional effects can influence the correct interpretation of the structure of Alpine accentor behaviour in winter. They include exo- and endogenous variables such as local weather or ag-

gregation (flock) size. The winter habitat feature of the accentors is a predictably unfavourable climate. During the winter season, mean daily temperatures may be very low. In late autumn and early spring, the amount of precipitation may be high. In this study it was confirmed that cloudy days with fog could cause devation from normal behaviors for several days, as experienced ornithologists know that birds see very poorly in the fog. In cloudy and foggy days, accentors devoted more time to standing alert and less to feeding. Behaviour of birds may also depend on the size of their flock. Autumn and winter flocking in accentors is associated with diet. At this time, the species eats seeds, and granivorous birds are more likely to show flocking behaviour compared to birds that eat mainly animal matter, including insects. In passerine birds, in addition to synchrony of movements, other behaviural patterns such as feeding or sleeping show a strong tendency to be synchronous within a flock. For example, when one or two individuals start sleeping or resting, the others rapidly follow suit. Flock synchrony is based on visual signals or on contact calls (McFarland 1987). In wintering accentors, the association between flocking and resting (without preening) supports the notion of a link between flocking and energy preservation in winter.

## Acknowledgements

## References

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

Follett, B.K. 1973: Circadian rhythms and photoperiodic time measurement in birds. *J. Reprod. Fert. Suppl.*, **19**: 5-18.

Hamstra, T.L. and Badayev, A.V. 2009: Comprehensive investigation of ectoparasite community and abundance across life history stages of avian host. *J. Zool.*, **278**: 91-99.

Heer, L. 1994: Zur sozialen Organisation und Brutbiologie der Alpenbraunelle MSc. Thesis, Institute of Zoology, University of Bern, Bern.

Heer, L. 1996: Cooperative breeding by Alpine accentor *Prunella collaris*: polygynandry, territoriality and multiple parternity. *J. Ornithol.*, **137**: 35-51.

Heer, L. 1998: The polygandrous mating system of the Alpine accentor *Prunella collaris*, individual reproductive tactics, breeding adaptations on high mountain conditions and winter ecology. PhD Thesis, Institute of Zoology, University of Bern, Bern.

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

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

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

Janiga, M. 2018: Adaptive placticity in insect parasites – *Philopterus* lice and their accentor passerine hosts. *Pol. J. Ecol.*, **66**: 395-406.

Janiga, M. and Kubašková, L. 2000: The biology of the Alpine accentor *Prunella collaris* III. The coevolution of Alpine accentors and lice (Phthiraptera). *Oecologia Montana*, **9**: 24-28.

Janiga, M. and Mičková, A. 2004: The biology of the Alpine accentor *Prunella collaris* V. The sex ratio and transmission of lice *Philopterus emiliae. Oecologia Montana*, **13**: 17-22.

Janiga, M. and Romanová, E. 1996: The biology of the Alpine accentor *Prunella collaris*. I. Behaviour: Principal component aualyses of orgauization of activity clusters. *Oecologia Montana*, **5**: 71-78.

Janiga, M. and Romanová, E. 1997: The biology of the Alpine accentor *Prunella collaris*. II. Behaviour: Rhythmic aspects of maintenance activities. *Oecologia Montana*, **6**: 45-48.

Jolicoeur, P. 1963: Note: the multivariate generalization of the allometry equation. *Biometrics*, **19**: 497-499.

Lawley, D.N and Maxwell, A.E. 1971: Factor analysis as a statistical method Butterworths, London.

Lofts, B. and Lam, W.L. 1973: Circadian regulation of gonadotropin secretion. *J. Reprod. Fert. Suppl.*, **19**: 19-34.

Lukač, G., Vujčič-Karlo, S., Milovac, M. and Adžič, I. 2016: Breeding and winter distribution of Alpine accentor (*Prunella collaris*) on the Eastern coast of Adriatic sea. *Larus*, **51**: 7-16.

Martí, R., Gómez-Manzaneque, A. and Perales, J.A. 1989: Diferencias segun edad y sexo en los movimientos dispersivos de una población de acentor alpino (*Prunella collaris*) en Espana central. *Ardeola,* **36**: 224-226.

Martín-Vivaldi, M., Marín, J.M. and Villar, M. 1995: Selección de habitat, tamano de bando y movimientos locales del acentor alpíno (*Prunella collaris*) en Sierra Nevada (SE de Espana). *Ardeola*, **42**: 11-20.

Maruyama, N., Kawano, M., Atsumi, H, Ueki, K. and Nezu, W. 1972: The social organization and the distribution of the Alpine accetttor, *Prunella collaris*, at the Kubiki and Togakushi mountain range. *Tori*, **27**: 325-338.

McFarland, D. 1987: The Oxford companiou to animal behaviour. Oxford University Press, New York.

Nakamura, M. 1990: Cloacal protuberance and copulatory behavior of the Alpine accentor (*Prunella collaris*). The *Auk*, **107**: 284-295.

Nakamura, M. and Matsuzaki, Y. 1995: Sex detetmination based on cloacal plotubetances in the Japanese Accentor *Prunella rubida. J. Yamashina Insf. Ornithol.*, **27**: 78-88.

Nakamura, M., Matsuzaki, Y. and Ootaka, H. 1996. Social unit of the Alpine accentor *Prunella collaris* in the non-breeding season. *Jpn. J. Ornithol.*, **45**: 71-82.

Nakamura, M. and Nishiumi, I. 2000. Large variation in the sex ratio of winter fl ocks of the Alpine accentors *Prunella collaris. Jpn. J. Ornithol.*, **49**: 145-150.

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

Schmidt, E. 1985. IX. A Havasi Szurkebegy (*Prunella collaris*) Magyarországon. *Aquila*, **92**: 105-111.

Sommers, K.M. 1986: Multvariate allometry and removal of size wrth principal component analysis. *Systematic Zoology*, **35**: 359-368.