

# The biology of the Alpine Accentor *Prunella collaris*. I. Behaviour: Principal component analyses of organization of activity clusters

M. JANIGA<sup>1</sup> and E. ROMANOVÁ<sup>2</sup>

<sup>1</sup>Research Coordination Centre of the Tatra National Park, 059 60 T. Lomnica, e-mail: janiga@tanap.ta3.sk, Slovak Republic

<sup>2</sup>Milcova 19, 010 01 Žilina, Slovak Republic

**Abstract.** The functional organization of behaviour of the Alpine Accentors, *Prunella collaris* (Scopoli 1769), was studied in a high altitude area in the High and Low Tatra mountains, West Carpathians. We found different behavioural schemes being used in an adaptive way to meet the circumstances of an ecological niche. The presence of a particular external situation elicited and oriented the appropriate behavioural groups. The number of birds in a flock and seasons were the most important factors which modified the qualitative and quantitative structure of clusters of behaviour. Some of the behavioural schemes also differed at different sites in the area and with respect to different weather conditions. In "anthropic" habitats with cottages, refuges, and hotels in the high altitude zone, the signs of "local endemism" in behaviour of accentors were significantly suppressed.

**Key words:** *Prunella collaris*, behavioural grouping, the Tatra mountains, local endemism

## Introduction

Many activities of birds tend to be grouped in time. For example, a hungry accentor performs a series of activities while searching for food and eating it, such as standing, waiting, preening. These activities tend to form a group which occurs for a given period of time and then ceases, to be replaced by a different group, perhaps sitting, sleeping, preening. In all animals some grouping of activities occurs. Difficulties are further compounded by the lack of exhaustive quantitative studies (Marler and Hamilton 1966). Moreover, very few studies (Beverige and Deag 1987) carried out under field or field-experimental conditions have controlled (either experimentally or statistically) for the effects of variables that potentially influence the behavioural schemes in birds (Elgar 1989, Saino 1994).

This study describes the general types of behaviour of Alpine Accentors, suggesting a multifactorial quantification and interpretation for the observed clusters of activities and for a general, hypothesized distinction between the clusters in natural and anthropic habitats. Moreover, we

analysed variation in the structure of clusters of activities in relation to flock size, weather conditions, year of observation, season, and locality. The schemes of behaviour of accentors in the presence of "anthropic" factors (mountain cottages, refuges, touristic paths) were compared with the schemes of apparently "undisturbed" birds.

## Material and methods

### Field observations

The field work was carried out from 1985 to 1993 in the High and Low Tatra National Parks, in north central Slovakia. The accentors prefer to live almost entirely on rocky mountain slopes between the tree limit and the snow line. Binoculars, of various powers, were of assistance. The notes were simply written or dictated onto tape. In particular, when many individuals had to be watched simultaneously (for example in autumn), birds were video-recorded, and the recordings were later analysed in the laboratory.

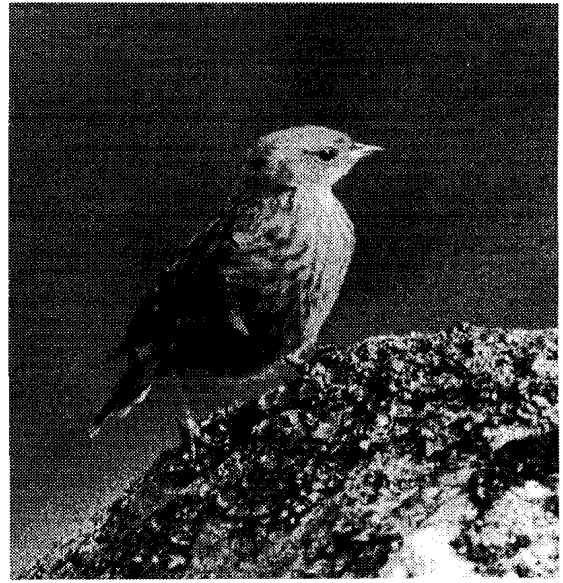
### Description and classification of behaviour

Persistent observation of individuals over a reasonably long period resulted in a preliminary picture of the life history of accentors. Then we concentrated on four basic categories of maintenance activities, differing in the complexity of integration of the temporal groups of behaviour involved. We recorded the following episodes: feeding, standing (sitting alert), sitting (drowsily), and preening. The categories were described in terms of some consequences of the muscular movements, and in general, all four categories are different examples of locomotion. The notion of general maintenance activity encompasses a wide variety of behaviour patterns (McFarland 1987).

**Feeding.** If the main consequence of a particular pattern of muscular contractions was that food had been obtained then the pattern as a whole was described as "feeding". The category responses to appetitive behaviour, and includes all those activities that are involved in searching, obtaining, handling, and ingesting food. The term was applied to the active exploratory phase of behaviour that preceded the consumatory phase that a bird exhibited when it reached its diet. The category also included "hunting" (for example, the birds hunted butterflies in autumn). The "hunting" involved "cap-



**Fig. 1.** Feeding - exploratory phase (male), 2 July, 1989.



**Fig. 2.** Standing (juvenile), 7 August, 1986.



**Fig. 3.** Preening, 10 October, 1986.



**Fig. 4.** Resting (sitting drowsily), 16 March, 1985.

turing". The exploratory phase of feeding was often closely associated with "foraging" which was necessary mainly in autumn, when the food was not mobile. "Drinking" was also included in this category, although feeding was not always a direct stimulus for drinking. In the high altitude habitats, both food and water are usually readily available, and birds tended to eat and drink (or eat snow) in synchrony, but if access to food was restricted to certain parts of the day or season, the daily rhythm of drinking might continue.

*Standing.* The term was given to a somewhat heterogeneous group of behavioural patterns which all had something to do with *active immobility*. The category included the following behavioural patterns:

1. Watching the members of the family. The birds looked for the members of the family, and possibly benefited from watching their activities.

2. Standing on one leg, the active means by which the bird defended its body from physical factors, especially freezing.

3. Standing during feeding. Birds often had to be alert to the possibility of being surprised by predators. Mainly older birds looked up repeatedly while feeding.

4. Standing - alarm response. Accentors often remained motionless in a camouflaged position until detected by a predator (goshawk), and only then made their escape.

5. Standing before feeding. When accentors had access to abundant and predictable sources of food, they usually did not go to sources immediately after arrival, but stood on selected sites, very often without any movement. Sometimes after 1 h of standing, the birds became active, and moved to food sources.

6. Standing - intention movements. A bird standing on the ground was about to take off in flight, or to feed.

*Preening.* These activities all had something to do with body care, whether it was routine maintenance, as in the preening of birds or removal

of parasites. The category consists of perhaps 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 post-bathing preening, body shaking, wing whirring, oiling, scratching. The classes "sitting + preening" or "standing + preening" were always considered as equivalent to the class "preening". Preening was sometimes seen in conjunction with other comfort behaviour such as bathing, and sunning. The displacement preening was also included in this category.

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

*Classification.* We recorded the behaviour of accentor(s) once per minute. This was the shortest interval in which we were still able to record the behaviour in the field. Our description represents all categories which occurred in each designated minute. We classified the categories in such a way that the members of one class did not also occur in another class. Accentors were sometimes, for example both "standing" and "feeding" during a given minute. In this case, we separately scored the two categories in this minute (e.g. the third minute in Table 1).

Time	N	Variables			
		Feed.	Stand.	Rest.	Preen.
13:04	1	1			
13:07	1	1			
13:08	1	1	1		
13:09	5	3	2		
13:14	5	4	1		
13:15	5				
13:18	5	2	1	2	
13:19	5			5	2
<hr/>					
Ratio of totals at 13:00-14:00		12	5	7	2

**Table 1.** Mapping the activities of individual birds in a day at one locality. N represents the number of birds observed in a minute, one sample represents one minute of observation per one bird. Each ratio of totals at any hour had to contain, at least, ten samples (in this case - 26). Ratio is characterized by variables, i.e. relative amounts of minutes spent for each activity (in this case, 12 - feeding, 5 - standing, 7 - resting, and 2 - preening).

#### Measurements and statistics

*Samples.* The relative amounts of minutes spent for each category in a designed hour were used as variables for principal component analysis (PCA). An example is shown in Table 1. 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

number of samples of feeding per hour. The field work was carried out for so many years, until, at least, ten samples for each designed hour in a model of a day were collected.

*Ratio scale.* All arithmetical operations were carried out on ratio scales of the four defined categories. The ratio scale has all the 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 activity of birds was recorded between 1 May and 1 November. For each month, a model of a day was separately constructed. Each hour, from dawn to dusk, of the model had to contain approximately ten ratios from different sites (note that each of these ten ratios contained at least ten samples). An example of one ratio is given in Table 1. For May, we collected 192 ratios, June - 198, July - 195, August - 199, September - 171, and October - 150, for a total of 1,105 ratios. Number of ratios depended on the number of hours of daylight in a month. The equal distribution of data in the models of a day enabled us to exclude the effects of daily rhythms from the comparisons of behavioural schemes of accentors in different months. The ratios were also examined in relation to weather conditions, different localities, and years. The comparisons of the behavioural groups were also made between the birds living in "anthropic" and natural, undisturbed environment. From 1985 to 1993, we collected the following numbers of samples by month: 5,460 - May, 2,001 - June, 4,020 - July, 6,786 - August, 6,771 - September, and 7,468 - October.

Principal components 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 elements (Jolicoeur 1963, Lawley and Maxwell 1971). The designed ratios were the fundamental inputs to the data matrix for PCA. Principal components were computed from correlation matrix of variables (Table 1), 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 scores (Sommers 1986). The signs of the elements define the schemes (groups) of behaviour. The calculations were carried out using the statistical package STATGRAPHICS 5.

## Results

### "Feeding + standing" behavioural group

The first principal component (PC1) shows the activities which were most often observed - feeding and standing. The component is partially an indication of observer error, because the correlations on PC1 are of the same sign (Table 2). Note that preening and resting have relatively low values of component weights. The component weights indicate the tempo of increase of the samples in the observers' notebooks. Although the accentors spent much time by feeding and standing, the data were influenced by ability of observers to find and watch

the birds. This was a reason why this group of behaviour was not more detailed analysed. The next principal components (PC2, PC3, PC4) are statistically independent of the first one.

Variable	PC1	PC2	PC3	PC4
Resting	0.16	0.78	-0.42	0.43
Standing	0.72	0.06	-0.26	-0.64
Feeding	0.66	-0.38	0.18	0.62
Preening	0.16	0.49	0.85	-0.12
% variance	28.6	26.4	24.5	20.6

**Table 2.** Structure (component weights) of behavioural groups in Alpine Accentors.

*"Resting and preening versus feeding" behavioural group*

Another information on behavioural group structure is present in PC2, which shows a sharp contrast between resting and feeding. This cluster of behaviour may be called a "real rest", resting is accompanied by preening. The rate at which accentors foraged in their territory mainly increased with the number of birds in a family or aggregation (Table 3, Fig. 5a). Feeding also increased in windy weather (Fig. 5c). Also, there was a significant difference in the structure of the behavioural group in different months of a year. The rate of eating increased in late spring and autumn, and declined in summer (Fig. 5b) Fig. 5d shows that this behavioural scheme is very sensitive to different environmental conditions, and may change from a year to year. The rate of resting mainly increased in the years 1986, 1989, 1990.

Factor		PC2	PC3	PC4
Weather	F	2.38	0.66	2.67
	P	0.02	0.70	0.01
Months	F	8.49	4.35	3.48
	P	0.000	0.0006	0.004
Year	F	4.38	0.62	3.5
	P	0.0001	0.74	0.01
Locality	F	2.81	1.45	2.01
	P	0.001	0.15	0.03
Flock size	F	16.09	23.45	35.71
	P	0.000	0.000	0.000

**Table 3.** Effects of weather, months, years, locality, and number of birds in a flock on the behavioural schemes of Alpine Accentors. One-way ANOVAs (F) and their significance levels (P) refer to comparisons of principal component scores. Mean values of principal component scores with 95% confidence intervals are shown in Figs. 5, 6, and 7.

*"Preening versus resting" behavioural group*

This type of behavioural group is represented by the third principal component (Table 2). The component

accounts for 24.5% of total variation in the data. It is important to note that this temporal group of behaviour may occur independently of the previous "resting + preening" group. This type may be called "active preening" because preening is positively associated with feeding, and negatively with resting. Although the group structure was similar throughout the accentors' distribution, there was variation in the group structure on a seasonal and a bird number basis (Table 3). In this cluster, the active preening increases progressively in spring and mainly in autumn (Fig. 6a) when the birds move in aggregations of families (Fig. 6b). The preening declined during the breeding season, when the accentors move solitary or in smaller groups. Seasonal and locality comparisons made on this structure of behavioural group showed no statistically significant differences (Table 3). "Preening - resting" scheme is apparently affected by different (endogenous ?) processes than those that determine "resting - feeding" behavioural group.

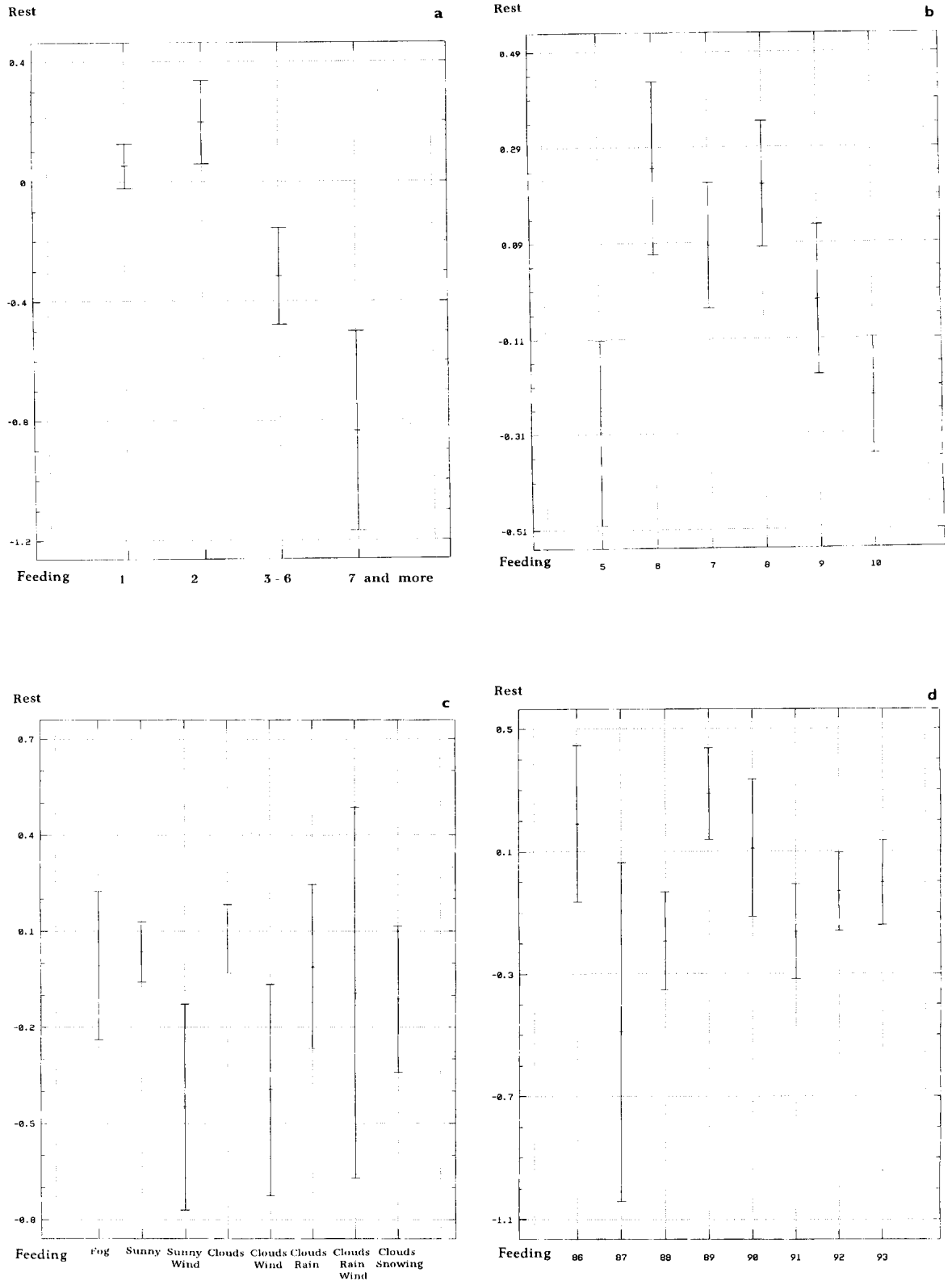
*"Feeding versus standing" behavioural group*

This cluster is an evidence that some activities are not restricted to one type of behavioural grouping. Feeding is repeated in several groups of activities (PC1, PC2, and PC4), but the temporal groups differ in structure. The rate of standing increased in solitary birds (Table 3, Fig. 7a), while the tendency to feeding was more socially stimulated. The rate of feeding increased in windy days without rain (Fig. 7b), and mainly in the years 1986 and 1987 (Fig. 7c). The structure of this cluster of activities also differed between the Low and High Tatra natural habitats (Fig. 7d). In the Low Tatras (northern slopes), the rate of feeding increased while in the High Tatras (southern slopes and valleys), the rate decreased. In "anthropic" habitats with cottages, refuges, and hotels in the high altitude zone, the signs of "local endemism" in behaviour of accentors were significantly suppressed (Fig. 7d). Changes in the structure of the behavioural group depended on weather conditions in the Low Tatra mountains (F = 4.68, P = 0.001). In the High Tatra mountains, the weather conditions did not significantly influence the structure of the behavioural group (F = 1.01, P = 0.42). In both mountains, the scheme of behaviour of accentors differ between natural and "anthropic" sites (the Low Tatras - F = 6.7, P = 0.009, the High Tatras - F = 4.6, P = 0.03).

## Discussion

Each species is adapted to a specific set of factors in its environment which it needs for its maintenance, growth, reproduction, etc. Adaptation encompasses not only the morpho-physiologic mechanisms of an animal, but also its behaviour. This implies that behaviour can only be fully understood with respect to the ecological niche of the species.

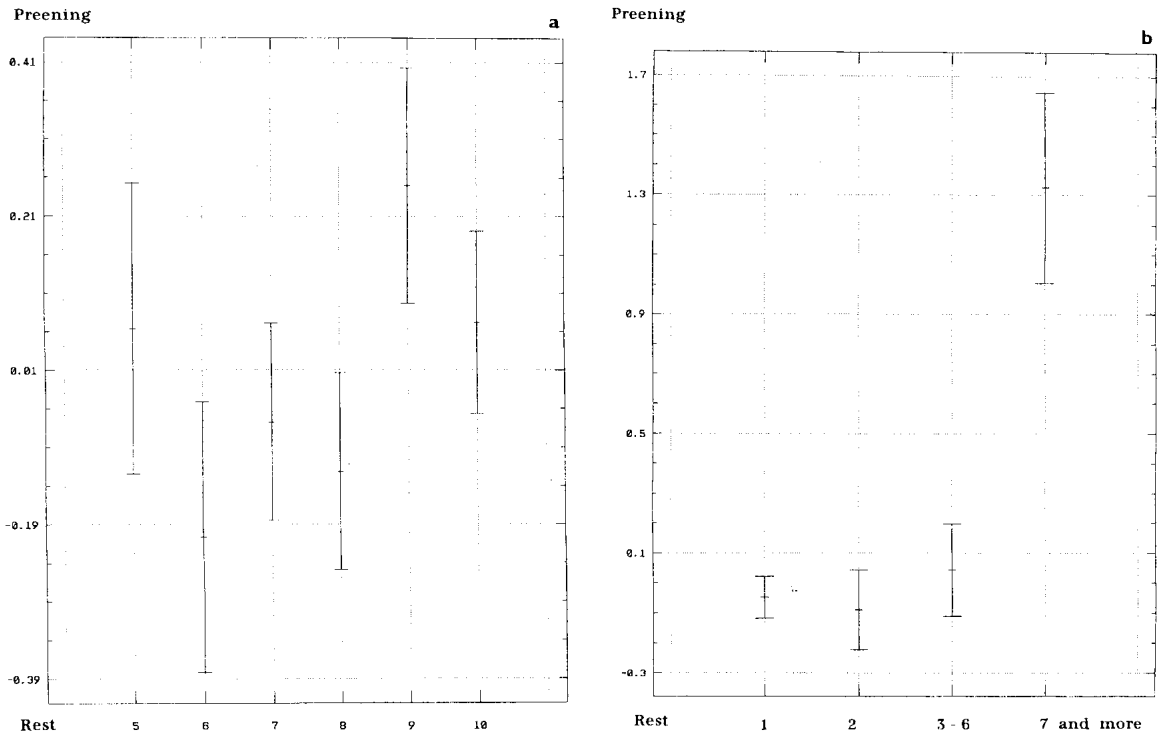
We showed that the Alpine Accentor has at its disposal a repertoire of schemes - behavioural groups of different orders. The appropriate usage of the groups helps the bird to adapt itself to its environment. The different number of birds in a company of accentors was probably the most important factor which influenced the structure of their behavioural



**Fig. 5.** Mean values of principal component scores (PC2 - "resting versus feeding" behavioural group) with 95% confidence intervals related to (a) different number of birds in a flock, (b) months in a year, (c) weather, and (d) years of observation. One-way ANOVAs (F) and their significance levels (P) are shown in Table 3.

schemes. Social behaviour makes it possible for the individuals of a bird species to compromise between the antagonistic tendencies to cluster and to disperse in a way which best suits their needs. If birds' essential resources are distributed over a large area, at least during a sufficiently long period of the year

to encompass the reproductive period, we are likely to find that the species has a territorial society. Alpine accentors breed in polygynadrous groups, group size is influenced by the temporal availability of fertile females (Davies *et al.* 1995). During the prebreeding season, the members of a group usually



**Fig. 6.** Mean values of principal component scores (PC3 - "preening versus resting" behavioural group) with 95% confidence intervals related to (a) different months in a year, and (b) different number of birds in a flock. One-way ANOVAs ( $F$ ) and their significance levels ( $P$ ) are shown in Table 3.

move together within the home range. The high altitude areas are divided into territories, each in principle occupied by a family of accentors. As the breeding season progresses, the birds tend to be more solitary (Maruyama *et al.* 1972, Talposh 1977, Nakamura 1995). In late autumn, defence against predators and the detection of food are promoted by the formation of larger aggregations of families, sometimes with up to 100 birds recorded together in late autumn (Glutz von Blotzheim 1985, Cramp 1988). In this study we showed that in spring and autumn, the similar structure of behaviour existed in the Alpine Accentors. The environmentally induced (PC2 and PC4) behavioural schemes correlated with ecological situation and partially faced similar ecological problems. If birds live in different niches, then the possible schemes in behaviour may be variously deployed (the Low and High Tatra mountains).

The principal component analysis also enabled to distinguish the endogenous features in the structure of accentor behaviour. Preening (loaded on PC3) is an essential behaviour for maintaining the body and feathers in the proper condition. It is not surprising that this behavioural group is less dependent on environmental factors.

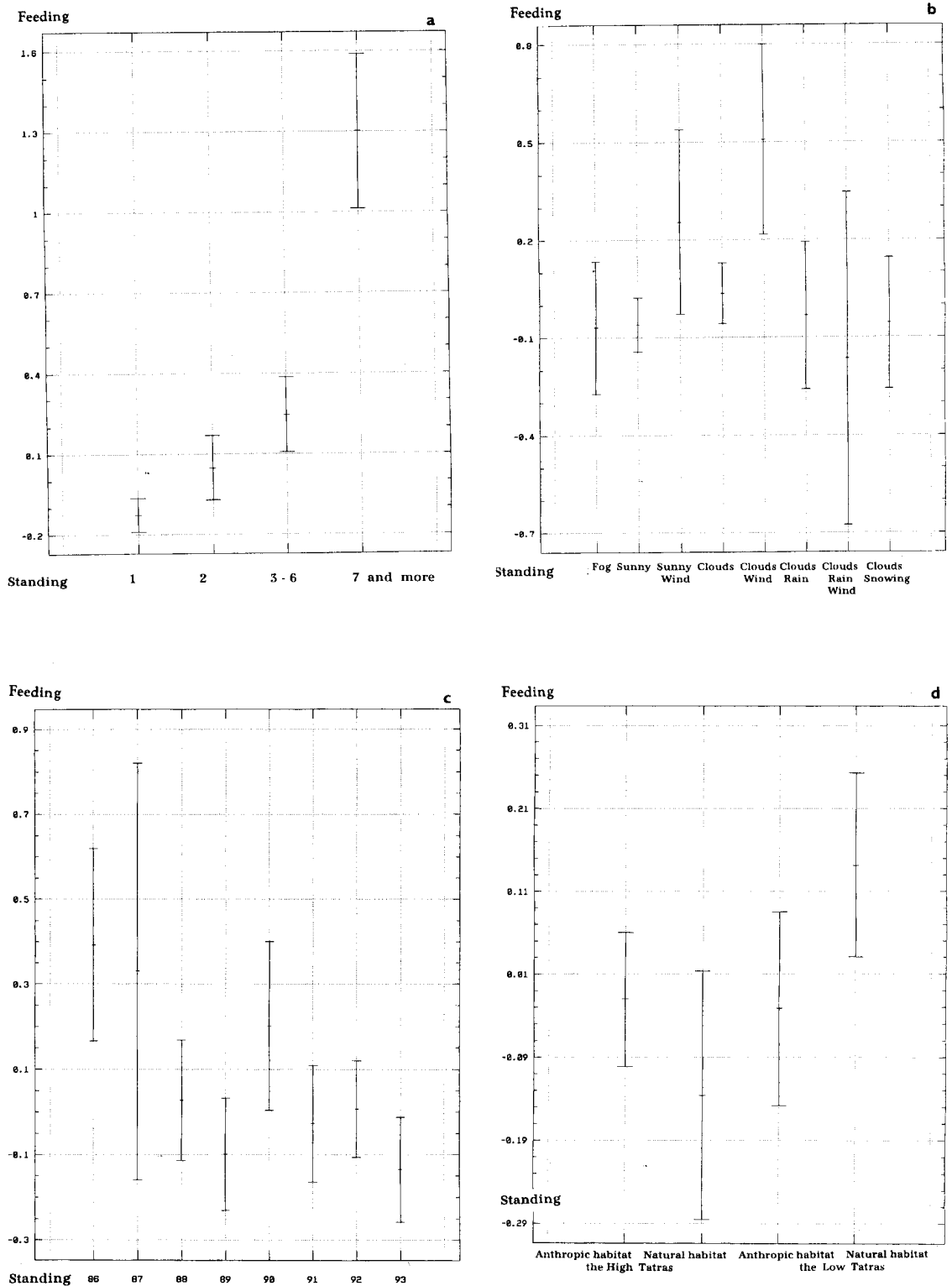
The basic behaviour patterns are usually not restricted to one type of behavioural group. We showed that, for example, "feeding" acts occurred in many different groups of behaviour. It is clear that the subject of the behavioural grouping of action patterns is complex. Our calculations as well as direct observations of food-searching birds showed that the different acts in the behaviour of birds appeared not in a random sequence but in definite

temporal schemes.

In addition to the above mentioned more or less realistic simplifications, a whole range of additional factors can affect the correct interpretation of the structure of behavioural groups. They include variables such as sex, age and past experience that can influence the behaviour of the Alpine Accentor (Davies *et al.* 1995, Hartley *et al.* 1995, Nakamura 1995). More than 300 accentors were captured and individually colour ringed in the Tatra mountains, and an influence of those factors on the behaviour of accentors will be the subject of our future studies on this fascinating bird.

Mixed behavioural strategies, especially those which contain feeding, are exhibited by the majority of bird species (e.g. Klima 1966, Widén 1984, Swihart and Johnson 1986, Hobson and Sealy 1987, Enoçsson 1988, Kacelnik and Cuthill 1990, Székely and Moskát 1991, Black *et al.* 1992). Alpine-nesting birds have been very useful in predicting how organisms in climatically unstable environment may change their behavioural strategies (Hendricks 1987a,b, Norvell and Creighton 1990, Frey-Roos *et al.* 1995). In this study, we also showed that the behavioural schemes of accentors may very rapidly change, and they clearly reflected the strong structural and abiotic constraints imposed by the alpine environmental conditions.

*Conservation issues.* Our study also allows some conclusions that are relevant for conservation issues. In two different areas, the Low and High Tatras, the birds tended to have their own schemes of the behaviour (behavioural endemism). The schemes were used in an adaptive way to meet the circum-



**Fig. 7.** Mean values of principal component scores (PC4 - "feeding versus standing" behavioural group) with 95% confidence intervals related to (a) different number of birds in a flock, (b) weather, (c) years of observation, and (d) different localities. One-way ANOVAs (F) and their significance levels (P) are shown in Table 3.

stances of an ecological niche. But accentors also adapted to the touristically devastated parts of the mountains. Organized group sight-seeing, hiking, ski-touring, downhill skiing, mountaineering bring garbage to the mountains. Tourist refuse has become a serious problem in the Tatra mountains (Stone

1992, Janiga *et al.* 1993). This study shows that the present-day impact of tourism has probably weakened the regional features in the structure of behaviour of accentors. Moreover, negative physiologic responses to feeding on garbage may be awaited.

## Acknowledgments

Our thanks to Martin Novacký for his comments on this paper, and James Petch for editing the manuscript. We are also grateful to Bohumil Murin, Monika Bobalová, Gabriela Ďurčová, Zuzana Janigová, Jozef Radúch for assisting in the field data collection.

## References

- Beveridge, F. M. and Deag, J. M. 1987: The effects of sex, temperature and companions on looking up and feeding in single and mixed species flocks of house sparrows (*Passer domesticus*), chaffinches (*Fringilla coelebs*) and starlings (*Sturnus vulgaris*). *Behaviour*, **100**: 303-320.
- Black, J.M., Carbone, Ch., Wells, R.L. and Owen, M. 1992: Foraging dynamics in goose flocks: the cost of living on the edge. *Anim. Behav.* **44**: 41-50.
- Cramp, S. (ed.) 1988: Handbook of the Birds of Europe the Middle East and North Africa. The Birds of the Western Palearctic. Vol. V - Tyrant Flycatchers to Thrushes. Oxford Univ. Press, Oxford, New York.
- Davies, N.B., Hartley, I.R., Hatchwell, B.J., Desrochers, A., Skeer, J. and Nebel, D. 1995: The polygynandrous mating system of the alpine accentor, *Prunella collaris*. I. Ecological causes and reproductive conflicts. *Anim. Behav.*, **49**: 769-788.
- Elgar, M.A. 1989: Predator vigilance and group size in mammals and birds: a critical review of the empirical evidence. *Biol. Rev.*, **64**: 13-33.
- Enoksson, B. 1988: Age- and sex-related differences in dominance and foraging behaviour of nuthatches *Sitta europaea*. *Anim. Behav.*, **36**: 231-238.
- Frey-Roos, F., Brodmann, P.A. and Reyer, H.-U. 1995: Relationships between food resources, foraging patterns, and reproductive success in the water pipit, *Anthus sp. spinoletta*. *Behav. Ecol.*, **6**: 287-295.
- Glutz von Blotzheim, U.N. (ed.) 1985: Handbuch der Vögel Mitteleuropas, 10. AULA-Verlag, Wiesbaden.
- Hartley, I.R., Davies, N.B., Hatchwell, B.J., Desrochers, A., Nebel, D., Skeer, J. and Burke, T. 1995: The polygynandrous mating system of the alpine accentor *Prunella collaris* II. Multiple paternity and parental effort. *Anim. Behav.*, **49**: 789-803.
- Hendricks, P. 1987a: Foraging patterns of Water Pipits (*Anthus spinoletta*) with nestlings. *Can. J. Zool.*, **65**: 1522-1529.
- Hendricks, P. 1987b: Habitat use by nesting Water Pipits (*Anthus spinoletta*): A test of the snowfield hypothesis. *Arctic and Alpine Research*, **19**: 313-320.
- Hobson, K.A. and Sealy, S.G. 1987: Foraging, scavenging, and other behavior of swallows on the ground. *Wilson Bull.*, **99**: 111-116.
- Janiga, M., Marenčák, M., Šoltéssová, A., Šoltés, R. and Kyselová, Z. 1993: A study on the preservation of the Tatras region and plans to hold the 2002 Winter Olympics in northern Slovakia. *Oecologia Montana*, **2**: 31-45.
- Jolicoeur, P. 1963: The multivariate generalization of the allometry equation. *Biometrics*, **19**: 497-499.
- Kacelnik, A. and Cuthill, I. 1990: Central place foraging in starlings (*Sturnus vulgaris*) II. Food allocation to chicks. *Journal of Animal Ecology*, **59**: 65-674.
- Klima, M. 1966: A study on diurnal activity rhythm in the European Pochard, *Aythya ferina* (L.) in nature. *Zoologické listy*, **15**: 317-332.
- Lawley, D.N. and Maxwell, A.E. 1971: Factor analysis as a statistical method. Butterworths, London.
- Marler, P. and Hamilton III, W.J. 1966: Mechanisms of animal behavior. Wiley and Sons, New York.
- Maruyama, N., Kawano, M., Atsumi, H., Ueki, K. and Nezu, W. 1972: The social organization and the distribution of the Alpine Accentor, *Prunella collaris*, at the Kubiki and Togakushi mountain range. *Tori*, **21**: 325-338.
- McFarland, D. 1987: The Oxford companion to animal behaviour. Oxford University Press, New York.
- Nakamura, M. 1995: Territory and group living in the polygynandrous Alpine Accentor *Prunella collaris*. *Ibis*, **137**: 477-483.
- Norvell, J.R. and Creighton, P.D. 1990: Foraging of horned larks and water pipits in alpine communities. *J. Field Ornithol.*, **61**: 434-440.
- Saino, N. 1994: Time budget variation in relation to flock size in carrion crows, *Corvus corone corone*. *Anim. Behav.*, **47**: 1189-1196.
- Somers, K.M. 1986: Multivariate allometry and removal of size with principal component analysis. *Systematic Zoology*, **35**: 359-368.
- Stone, P.B. (ed.) 1992: The state of the world's mountains. A global report. Zed Books Ltd, London, New Jersey.
- Swihart, R.K. and Johnson, S.G. 1986: Foraging decisions of American robins: somatic and reproductive tradeoffs. *Behav. Ecol. Sociobiol.*, **19**: 275-282.
- Székely, T. and Moskát, C. 1991: Guild structure and seasonal changes in foraging behaviour of birds in a Central-European oak forest. *Ornis Hungarica*, **1**: 10-28.
- Talpoš, V.S. 1977. O biologiji razmnozheniya evropeiskoi alpiiskoi zavorushki v SSSR. *Nauchnye doklady vysšei shkoly, biologicheskie nauky - zoologiya*, **9**: 54-59.
- Widén, P. 1984: Activity patterns and time-budget in the Goshawk *Accipiter gentilis* in a boreal forest area in Sweden. *Ornis Fennica*, **61**: 109-112.

Received 23 November 1995; revised 15 April 1996;  
accepted 2 September 1996