

The biology of the Alpine Accentor *Prunella collaris*. II. Behaviour: Rhythmic aspects of maintenance activities

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Abstract. Daily routines of behaviour of the Alpine Accentors had comparable structure in the late spring (May) and in the autumn. Summer structure of daily behaviour did not correspond to the autumn daily routine. In summer, the amount of time devoted to flights and maintenance activities increased, while the level of food intake was lower than in spring or autumn. In the late summer, the feeding rhythms showed at least two peaks. The daily activity of accentors ranged from 11 hours in October to 17 hours in July.

Key words: *Prunella collaris*, daily and seasonal rhythms, the Tatra mountains,

Introduction

Seasonal and circadian rhythms enable Alpine Accentors to anticipate changes in environmental conditions. Such a mechanism facilitates the accurate timing of events, especially under alpine conditions where climatic factors may vary from day to day. Extreme changes in climatic factors, such as temperature, light intensity, winds, and snow cover, affect accentors directly, but there are also indirect effects of climate, such as fluctuations in food availability, numbers of predators, etc.

The seasonal and daily rhythms of accentors living in the High and Low Tatra mountains are the subject of this study. Of particular interest are: (1) seasonal variations in maintenance activities; (2) periodicity of fundamental rhythms; (3) daily variations in the maintenance activities.

Material and methods

The study area, field methods, and four basic categories of maintenance activities, feeding, standing (sitting alert), sitting (drowsily), and preening have been described in detail by Janiga and Romanová (1996). But in the present study, the next two categories, *sounds* and *flights* were added to determine the rhythms in behaviour. They can be used by birds in a number of behavioural contexts, and they give harmful information to researchers.

All types of flight (McFarland 1987) were accu-

mulated to the category of flight. Category sounds consists from all manners of sounds, for example calls of adults, silent calls of females and young, and songs of males and females.

The classes "sitting + preening" or "standing + preening" were always considered as equivalent to the class "preening". The same payed, for example, for "sitting + song" or "calls + flight". Preening was sometimes seen in conjunction with other comfort behaviour such as bathing, and sunning. The displacement preening was also included in this category.

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. This is the reason that cumulative relative numbers may be higher than 100 % (for example in Fig. 2.)

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 activity of birds was recorded between 1 May and 1 November. For the six categories, we collected the following numbers of samples by month:

Hour	May	June	July	Aug.	Sept.	Oct.
6.00	-	-	135	554	461	77
7.00	37	37	459	761	249	219
8.00	159	45	413	240	560	712
9.00	280	58	274	209	305	575
10.00	453	239	356	128	367	748
11.00	955	191	120	514	642	884
12.00	475	174	347	406	1006	728
13.00	565	97	215	433	611	793
14.00	788	108	223	210	497	519
15.00	556	389	187	243	310	669
16.00	715	126	340	124	310	897
17.00	43	57	151	557	327	311
18.00	97	21	54	608	212	110
19.00	22	94	50	396	-	-
20.00	-	78	71	55	-	-
21.00	-	33	-	-	-	-

Table 1. Amounts of minutes (per a bird) used for the computation of relative hourly activity budgets (Fig.1.).

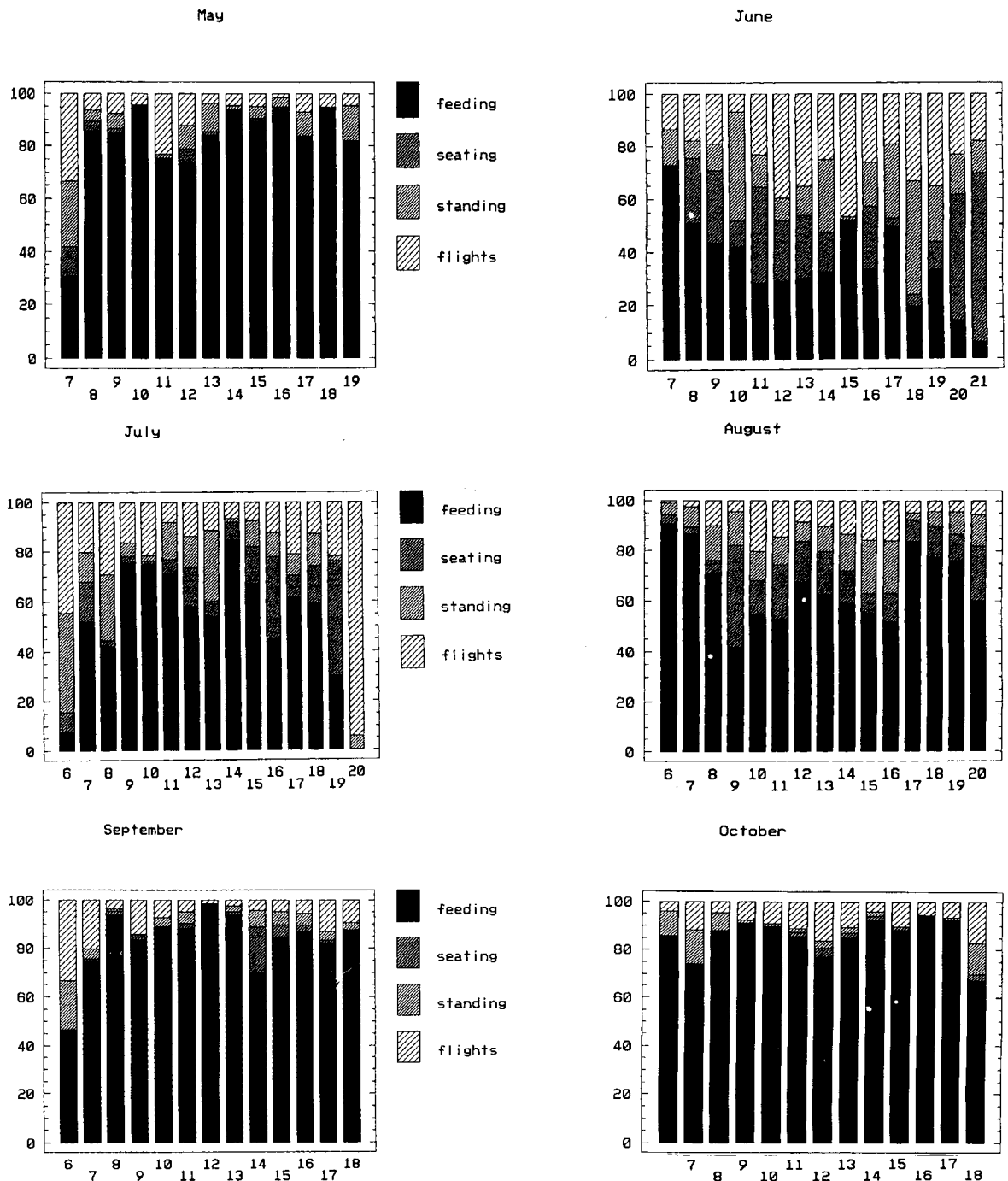


Fig. 1. Hourly activity budgets for the Alpine Accentors from May to October (% of minutes of observation per one bird). For the amounts of samples see Table 1.

6,209 - May, 2,737 - June, 5,192 - July, 8,380 - August, 7,885 - September, and 8,406 - October. Because of limited data from early and late hours in a day, the reduced amounts of samples were used for the calculation of hourly activity budgets. The amounts of minutes are presented in Table 1.

Results

Daily routine. The Alpine Accentors are active throughout the day. The daily routine of accentor behaviour more or less did not differ between late spring (May) and autumn (September, October). In these seasons, feeding was the most important component of the schedule of behaviour (Fig. 1). Amounts of minutes devoted to feeding rapidly de-

clined at the beginning of June. In June, the accentors exhibited a series of breeding activities that corresponded to the change in the structure of daily scheme of behaviour (Fig. 1). In the spring and autumn, birds mainly foraged in the middle of a day, while in June, accentors looked for the diet in the early morning, and throughout a day they displayed many different kinds of breeding activities. In July, and especially in August, the rhythms of feeding had at least two peaks, one in the morning, and the second by the evening.

On the basis of direct observations in the field, alpine accentors were found to be active from half a hour after the dawn to ten or twenty minutes before the dusk (Table 2). The daily activity in accentors ranged from 11 hours in the late October

Month - decade	CW	Start (EET)	N	CW	End (EET)	N	Dawn	Dusk	Activity length (hrs)
May - 1				W	20.00-20.43	2			
May - 2	W	6.05-6.07	2						14.5
June - 1,2	C	5.20	1	W	20.14-21.30	3			16
June - 3	C	5.00	1	W	21.30	1			16.5
July - 1	C	4.30	2	C	21.01-21.30	3			17
July - 2	CW	4.28-4.45	2	CW	20.45-20.55	2	3.15	21.15	16.5
July - 3	W	4.40	1	W	20.23-20.30	3	3.40	21.15	16
August - 1	C	4.55	1	W	19.55-20.20	2	4.30		15.5
August - 2	W	5.30	1	W	20.00-20.45	2			15
August - 3	W	5.30	1	W	19.55	1			14.5
September - 2C		5.38-5.50	2	CW	19.00-19.20	2		19.35	13.5
September - 3CW		5.50-6.13	4	W	18.25-18.55	3	5.20	19.05	13
October - 1 W		6.40-6.45	2	W	19.01	1	5.20		12.5
October - 2 C		6.40-7.00	3	W	18.04-18.54	2			12
October - 3 C		7.15	1	W	18.15-18.22	2			11

Table 2. Seasonal variation in the length of daily activity of Alpine Accentors in the High and Low Tatra Mountains. C - calls, W - watched birds, N - number of days of observations, EET - Eastern European Time.

to 17 hours in July.

Seasonal rhythms. In late spring, accentors spent most of their time, about 90 %, feeding. Behavioural structure in May clearly characterizes mating and prenesting period. By early summer birds had decreased time spent foraging and feeding (Fig. 2.) Accentors increased the time they spent singing, resting. Birds also increased time spent in flight. June is the most important month of nesting in the Accentors, especially in the Low Tatra Mountains. Compared to early summer, in middle and late summer, birds spent more time feeding than in June, but there were no significant changes in the structure of time budgets. From July to August, fledglings usually follow their mother or a group of Alpine Accentors. Time budgets in this season indicate the postfledging care. By the end of August and beginning of September, accentors molt. In the late spring (May) and in the autumn, time spent in flight, singing, and mainly feeding was equally divided. In the autumn, increased time spent feeding enables to accumulate body reserves for winter.

Discussion

Early summer (June) brought great changes in the time budgets of Alpine Accentors (Fig. 3.). The pronounced decrease in the proportion of time spent feeding probably also reflects the longer period of daylight (Table 2) as well as a reduced energy-demand for maintenance due rising temperature. Similar changes in time budgets have also been reported for other passerines (Pinkowski 1979, Enoksson 1990). Interaction between day length and a rhythmicity may prove to be the critical factor here. In birds, the endogenous circadian rhythm may contribute to photoperiodic responses in a very positive way (Marler and Hamilton 1966). In accentors, the onset of development of adult protuberance occurs in the late May (Nakamura 1990, Nakamura and Matsuzaki 1995) when the period of daily activity lasts approximately 14.5 hours (Table 2). In summer months, accentors devoted more time to resting,

preening, singing and most importantly, to breeding activities (Drškoňová and Janiga 1989). In Karkonosze mountain, Dyrz (1976) described the daily activity of birds in the middle of June, birds began to call approximately 30 minutes earlier than in the Tatras.

Alpine Accentors breed in polygynandrous groups in which two or more unrelated males share for two or more females (Davies *et al.* 1995, Nakamura 1995,

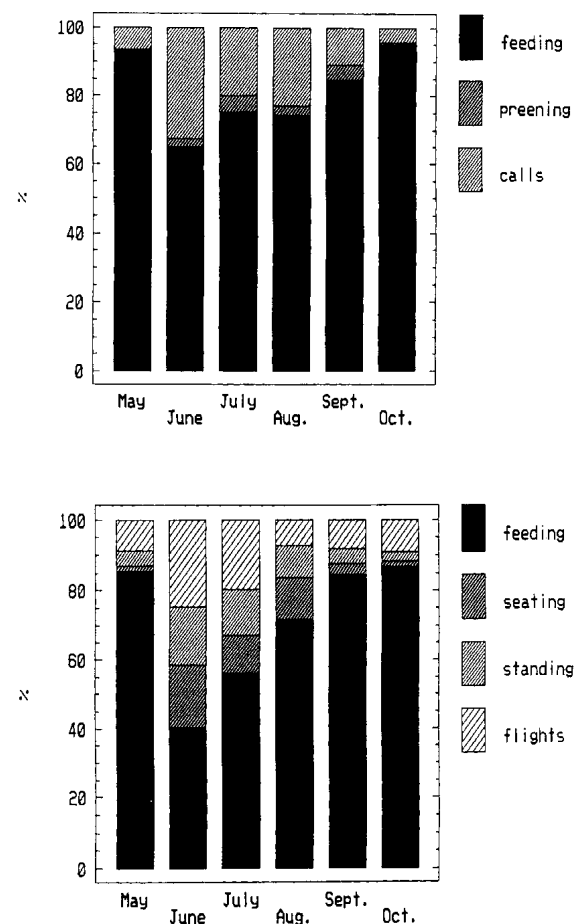


Fig. 2. Seasonal variation (in %) in the main activities of Alpine Accentors in the Tatra Mountains. For the sample numbers see Material and Methods.

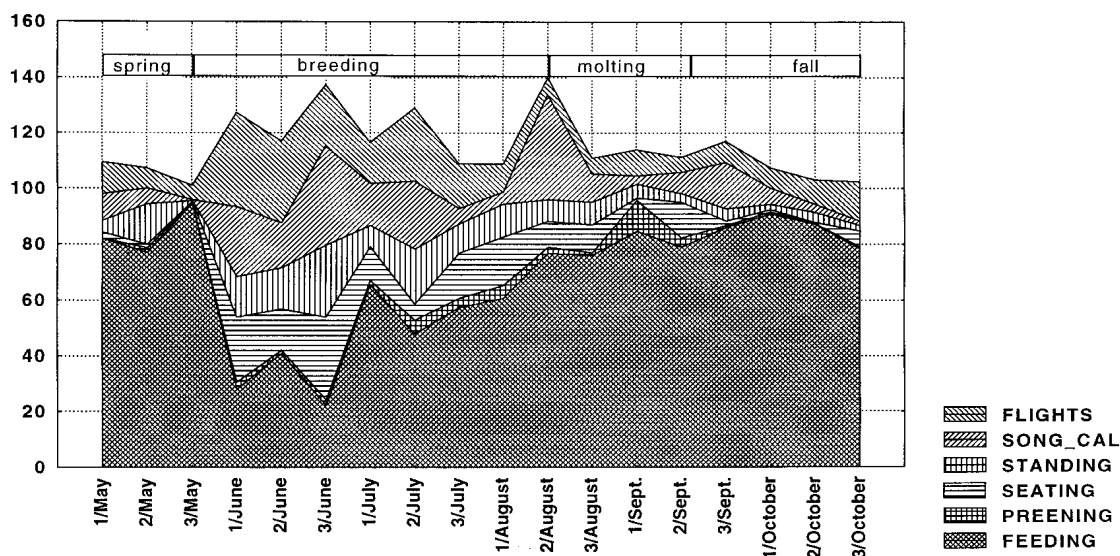


Fig. 3. Seasonal variation (in %) in the main activities of Alpine Accentors in the Tatra Mountains. Each month is divided into decades.

Heer 1996). As the breeding season progresses, individual birds spend more of their time alone (Nakamura 1995). Increase in the proportion of time spent feeding in August probably reflected more solitary behaviour.

Late August and September brought again great changes in the time budgets. The daily routine of behaviour was comparable to the time budgets from May. Daily activity in birds approximately lasted 14.5 hours. The scheme of behaviour in autumn surely indicates so-called refractory period which follows the breeding season in many birds. In this period, the Accentors molt (Fig. 3). This period must be completed before day length changes elicit another cycle (Marler and Hamilton 1966). In Accentors, molt takes place on or close to the breeding grounds at the end of the breeding season (Glutz von Blotzheim 1985). Feeding in September was accompanied by the increased time of preening (Fig. 3). An early timing of molt may lower the profitability of starting the second breeding (Svensson and Nilsson 1997). Low proportions of second broods in the Tatra Mountains could be a direct result of early timing of adult molt, making females less willing to initiate the second clutches. In October, birds very actively forage and feed in big aggregations. In early November, the majority of birds leave the breeding area (Maruyama *et al.* 1972).

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