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Feeding preferences and foraging behaviour in the Alpine Accentor *Prunella collaris*

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In flocks of Alpine Accentors (*Prunella collaris*), we observed the foraging behaviour of birds when they were foraging on a grid containing clumps of seeds. We measured the feeding rate, diet diversity, individual and seasonal feeding preferences and dominance in birds. Producing and scrounging were frequently observed and they often involved aggressive interactions. Most birds used both tactics to obtain food. We found that foraging method was not related to dominance. No significant differences in feeding rate and diet diversity were detected between dominant and subordinate birds. The Alpine Accentors showed a strong degree of heterogenity in their food specialisations in different seasons. Calculations of nutritive values of diet showed that birds received relatively more carbohydrates in the autumn than in spring or winter. In the "snowy" seasons, the diet contained a relatively high number of lipids. Birds also had significant individual food preferences.

1. Introduction

There can be considerable variation in a population in the way individuals exploit food resources. There are several possible mechanisms which may be responsible for individual differences in the feeding behaviour of birds. Foraging producer-scrounger systems have been described in many bird species (Barnard & Sibley 1981, Giraldeau & Lefebvre 1986, Giraldeau *et al.* 1994). The systems assume that an individual is either engaged in searching for its own food (producer) or searching for joining opportunities (scrounger). Scroungers in a population can specialize on parasitizing the food discoveries of producers (Giraldeau & Lefebvre 1986, Flynn & Giraldeau 2001). The producer-scrounger relationships are not fixed and may mainly be a result of individual differences in learning ability (Durell 2000), individual food preferences, physiology of a bird (Moon & Ziegler 1979) and dominance (Flynn & Giraldeau 2001, Johnson *et al*. 2001, Liker & Barta 2001, 2002).

Because the roles of producers and scroungers may be exchangeable as a function of food types (Giraldeau & Lefebvre 1986), it seems crucial to consider that individual birds are plastic in their feeding preferences (Cueto *et al.* 2001). Different food types may be preferred by different individuals in a flock of birds (Brown 1969, Giraldeau & Lefebvre 1985). The existence of individual variability in the selection of food type in birds may significantly influence the choice of individuals to be producers or scroungers.

Dominance relationships also influence the use of social foraging tactics (Giraldeau & Beauchamp 1999). Individuals in many species often behave aggressively during feeding and may form dominance hierarchies within foraging flocks. Because the dominance rank of an individual may crucially affect its success in competition for food, social status may influence an individual's "decision" to play producer or scrounger in ringed individuals in a foraging group of birds (Barta & Giraldeau 1998). Dominant individuals can displace subordinates, which gives them priority in accessing food sources, so they mainly play scrounger. Subordinates mostly use producer tactics.

Besides the phenotypic differences of individual birds, the use of alternative foraging tactics, producer or scrounger, depends on environmental spatio-temporal conditions, for example time of day (Barta & Giraldeau 2000) or season (Greenberg 1987). Because producer-scrounger models can successfully predict the use of foraging tactics in some ground feeding birds (Johnston & Janiga 1995, Giraldeau & Caraco 2000, Mottley & Giraldeau 2000, Coolen *et al.* 2001), we used the Alpine Accentor (*Prunella collaris* Scop.) to investigate whether individual differences in food preferences and social hierarchy are related to the producing-scrounging game in a species living in extreme conditions variable over time.

The Alpine Accentor lives in mountainous regions from western Europe through central Asia to Japan, typically breeding well above the treeline at heights of 1,800–4,000 m a.s.l., but even higher in the Himalayas where it has been seen at nearly 8,000 m on Mount Everest (Cramp 1988, Dyrcz & Janiga 1997). It is a non-migratory species but it can make considerable local movements during winter. Some birds remain in breeding areas in winter whereas others become altitudinal migrants feeding near buildings. Birds use different behavioural schemes in different seasons which may differ among sites and with respect to weather conditions (Janiga & Romanová 1996, 1997). They breed in polygynandrous groups whose size is influenced by the temporal availability of fertile females (Davies *et al.* 1995, Heer 1996). In spring, autumn and winter they forage socially and exhibit a dominance hierarchy in which birds compete aggressively for food and have been shown to use producer-scrounger tactics (Glutz Von Blotzheim & Bauer 1985).

The aim of this study was to study how the producer-scrounger system results from conflict-cooperation among individuals and whether ecological conditions on mountain tops play a part in determining the outcome. We also investigated whether individual feeding preferences and exploration of potential food (feeding rate) are related to the species' tactic use. In this paper we further present field evidence of strong individual and seasonal differences in the diversity of diet of group-feeding Alpine Accentors.

2. Methods

2.1. Locality

We investigated the feeding preferences of Alpine Accentors during the winter (January–February, wintering birds), spring (March–April, spring arrival in the mountains) and autumn (September–October, moulting, adult and fledged juvenile aggregations). The study areas were located in the Tatra and Great Fatra National Parks in the Western Carpathians, Slovakia, ranging from 900 m a.s.l.(Great Fatra, Malino Brdo ski resort, 960 m a.s.l, 49°18'N, 19°18'E; wintering area) to 1,700–2,500 m a.s.l. (High Tatra mountain peaks and valleys: Skalnate lake 1,778 m a.s.l., 49°11'N, 20°14'E; Solisko peak 1,840 m a.s.l., 49°08'N, 20°02'E; Tery Cottage 2,015 m a.s.l., 49°10'N, 20°13'E; Krivan peak 2,494 m a.s.l., 49°09'N, 20°00'E; Rysy peak 2,503 m a.s.l., 49°11'N, 20°05'E). Field observations and experiments were done in the years 1997, 1999, 2000 and 2003. The birds live on mountain tops, well above the treeline, in a habitat of steep cliffs and grassy meadows strewn with rocks. Over 90% of the summit area is covered with deep snow in winter and early spring. The region has the typical climate of high mountain regions: substantial daily changes in temperature and precipitation in spring and early summer. Snowfall occurs even in June and July.

2.2. Birds

Birds were mist-netted or caught with food traps. Adult birds were sexed by the shape of the cloacal protuberance (Nakamura 1990, for more details see e.g. Janiga 1992). One-year-old birds were aged by the colouring of the middle and greater wing-coverts. The minimum age of some birds was calculated from the day of ringing. Feeding preferences and diversity of diet were studied in 33 birds. The individuals were also checked in detail by video-taping (individual features in the plumage colour and pattern, mainly of throat, primaries, tertials and head, individual characteristics in behaviour). The roles of producer or scrounger were indentified in 24 birds (4 individuals in 1997, 10 in 1999, 2 in 2000, and 8 in 2003). The number of birds studied corresponded to the flock sizes used in this type of behavioural studies on sparrows (max. 20 birds for producer-scrounger system, Barta & Giraldeau 1998) and pigeons (Brown 1969, Giraldeau & Lefebvre 1985).

Birds were video-taped from distances of ca. 2–3 m, usually from the side. Head position was visible in every case. Food searching and feeding were monitored with a portable video camera system (Panasonic S-VHS.NV MS4). Interrupted video observations lasted from 30 minutes to 10 hours. The number of visits made by each individual and the time it stayed at the feeder were analysed later in the laboratory.

2.3. Behavioural data collection

One artificial feeding ground (plastic dish of 15 cm diameter and 2 cm depth) was placed in a randomly chosen feeding area. Each of the dish's 11 segments were filled with ca. 20 g of a diet item, a different item in each segment. Individuals were observed in random order during each day (Liker & Barta 2002). The birds normally arrived to feed within 5–20 minutes of the dish being placed on the ground. Every feeding bird was filmed throughout the course of its trial. Trials were run in quick succession and we filmed from 3 to 35 trials per day (minimally one, and maximally 17 trials per bird), in total 167 trials. Trials were often interrupted by changing weather at the tops of mountain peaks. They were separated by a few minutes, during which we restocked the dish. A trial started when the focal individual started to feed and ended when the bird stopped to feed and usually left the dish. The average trial lasted 62 seconds. From the video tapes, the following variables were measured for each feeding trial: (1) individual feeding preferences in food selection, (2) the ability to find and change to new food sources in successive trials, (3) dominance status (by recording two or more individuals, see below) (4) diversity of diet (according to feeding pecks) and (5) feeding rate as the number of pecks divided by time spent on the grid (Liker & Barta 2002).

2.4. Diet

The species prefers insects in spring and summer whereas in autumn it eats seeds of alpine grasses. Wintering birds often eat garbage in ski areas (Cramp 1988). In our experiments we used seeds of the following herbaceous species: white millet (husked) and panicum millet (unhusked) *Panicum miliaceum*, poppy seed *Papaver somniferum*, sunflower seed *Helianthus annuus*, buckwheat *Fagopyrum aesculentum*, flax seed *Linum perenne*, wheat *Triticum aestivum*, canary grass *Phalaris canariensis*, hemp seed *Cannabis sativa* and cole seed *Brassica napus*. One segment of a plastic experimental dish contained dried flies *Musca domestica*. Three segments were filled with biscuits, bread and bacon. Birds mainly eat this type of diet on the terraces of mountain restaurants or on mountain peaks in autumn and winter. The seed species were randomly assigned for each day.

2.5. Feeding preferences

Seed species presentation was randomly assigned for each observation. Multiple-offer experiments were used for all birds. Data obtained with one experimental design alone (one different type of diet item per trial) are not "effective" in solving the problem of feeding preferences in birds (Cueto *et al.* 2001). Multiple-offer experiments are recommended because in the course of the trial the consumer has an opportunity to express a dietary choice (Peterson & Renaud 1989). This design assumes that in natural conditions an animal normally faces more than one food item simultaneously, assesses them and then chooses the preferred item. In the field, however, animals could encounter food items sequentially and examine each to determine whether to consume or reject it

(Smallwood & Peters 1986). Moreover, this approach may exacerbate differences in preference (Cipollini & Levey 1997) and hide the use of some less-preferred food items whose use depends on the abundance of preferred items. These less-preferred food items could be crucial for the survival of birds in natural situations when preferred items are scarce. From this point of view, feeding-preference experiments are the most appropriate method for analysing food selection, because food types are presented under controlled conditions and known availability. The approach eliminates the bias caused by differences in availability of the potential food types and allows detection of a group of food items whose use depends on the abundance of the prefered food (Cueto *et al.* 2001).

2.6. Measurement of dominance

Competitive asymmetries may affect foraging when superior competitors (dominants) decide to defend food patches aggressively, leading to the exclusion of subordinate individuals. Thus, the effects of dominance on the use of tactics are expected to be stronger and more detectable when individuals forage on aggregated and abundant food patches (Barta & Giraldeau 1998).

Dominance status was determined by observation and was analysed by video sequences of the individual binomial probabilities of winning with a particular flock member at a localized food source (McKean 1988). An individual was categorized as dominant when it: (1) continued eating while a new arrival (the subordinate) waited at the food source; (2) displaced an individual already at the food source by displaying, pecking or merely by approaching the feeding area; or (3) chased others away. This technique and most of the criteria were discussed by Barkan *et al.* (1986). We also looked for evidence of avoidance behaviours by looking at (1) whether a subordinate waited on the ground adjacent to the feeding area and (2) which individuals used the food source at the same time. When an individual waited for a specific bird to leave the dish, it was considered subordinate (McKean 1988).

2.7. Producer system

We studied some elements of the foraging behaviour that may be related to producer or scrounger tactics. Discovering behavioural cues that indicate whether individuals are searching for or finding new sources of food could help to quantify the use of the two tactics (Giraldeau & Beauchamp 1999). We defined the producer and scrounger roles according to their ability to intake a new food source in a single feeding (Liker & Barta 2002). Because most individuals in a ground-feeding group of birds use both finding and joining tactics to obtain food and the joiners need not be the scroungers (Liker & Barta 2002), we used the concepts of “ecological plasticity” (Greenberg 1990) to define producers. Most observers of wild birds have noted intrinsic differences within and between species in “ecological plasticity”, or the tendency to exploit new resources. Plasticity has most often been related to the lack of specialization, the observed ecological amplitude of a species (specialist versus generalist). Miller (1942) and Klopfer and MacArthur (1960) have associated ecological plasticity with the breadth of resources and habitats used by a species. Variation in plasticity is a direct result of variation in neophobia: the fear of feeding on new foods or approaching new situations. This attribute of ecological plasticity then reflects a bird’s ability to respond to changes in food and the presence of novel resources (Greenberg 1990). Our producer model predicts that an individual using the producer tactic may spend more time in searching for new food sources than scroungers. Scroungers use more time in scanning other individuals in a feeding group to obtain food (e.g. Ranta *et al.* 1996, 1998).

The number of different segments used by a bird in the two successive trials enabled us to define the producer or scrounger ability of an individual. Producer was defined as an individual which used a relatively high number of new segments for feeding during each successive trial. We calculated the percentage of the same segments used in the second trial in comparison to the first one, then in the third compared to the second and so on. Consequently, we calculated the mean percentage of all successive trials for an individual. A low number indicated that an individual had a relatively high ability to be a producer, because in ev-

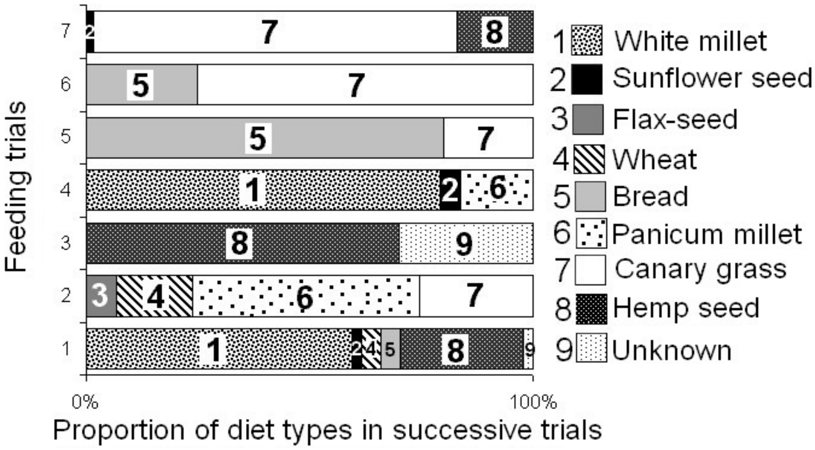

Fig. 1. An example of a more plastic bird (No. 3), a "producer" of new types of diet for other individuals. 252 pecks were video-taped in seven trials of feeding in one day (white millet – 62; sunflower seed – 4; flax-seed – 5; wheat – 12; bread – 16; panicum millet – 37; canary grass – 72; hemp seed – 37; unknown – 7). This bird often changed the type of diet in successive trials. Trial number 1 (along the y-axis) means the first trial, and number 7 the last one.

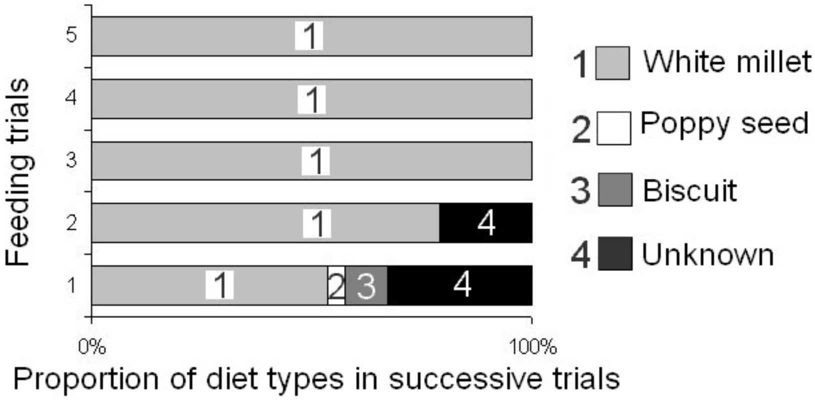

Fig. 2. An example of a less plastic bird (No. 24) in finding new types of diet. 436 pecks were video-taped in five trials of feeding in one day (white millet – 356 pecks; poppy seed – 41; biscuit – 5; unknown – 34). This bird always used the same food types when successive and previous trials were compared. Trial number 1 (along y-axis) means the first trial, and number 5 the last one.

ery new trial it used a relatively high number of new food types. Examples of producers and of less plastic food finders are shown in Figures 1 and 2, respectively. A less plastic food finder may be also a producer but its ability to find (produce) new food sources for potential scroungers is lower than in individuals which use relatively high numbers of different types of food. More plastic food finders are important in taxa in which substantial individual preferences in the diet exist.

2.8. Statistical analysis

To compare food preferences in individual birds we estimated the percentage of seeds consumed by each experimental bird. To measure the significance of preferences between seasons we used an interaction G_h test (Sokal & Rohlf 1981) on food type pecks (Giraldeau & Lefebvre 1985). The frequencies of nutritive components were compared by Chi-square goodness of fit tests (Sokal & Rohlf 1981). T-tests were used to compare the effects of diet diversity, feeding rate and producer role between dominant and subordinate birds. To compare diet diversity, we used the Shannon index of diversity

$$H' = -\sum_{1}^{d} \frac{N_i}{N} \ln \frac{N_i}{N},$$

where there are *d* different types of diets, where N_i is the number of pecks of the i-type of diet, and N the total number of pecks by an individual. The Shannon index measures the evenness of diet

Table 1. Seasonal heterogenity in feeding preferences of Alpine Accentors. Thirty-three birds were video-taped. The numbers denote the proportional amount of pecks (% in concrete diet) from the video monitored total number of pecks (n).

Season	Type of seeds and food (%)														
	W. mill.	P. mill.	Pop. seed	Flax seed	Can. gras.	Hem. seed	Wh.	Sun. seed	Buc.	Col. seed	Bisc.	Bre.	Bac.	Fli.	Un	n.
Aut.	11.7	17.7	0.5	11.2	21.3	5.7	2.5	1.3	2.3	0.7	7.8	15.2	–	0.2	2.1	2,596
Win.	27.1	0.4	39.7	1.0	1.2	1.3	0.4	0.1	0.3	–	20.1	2.6	–	2.8	2.0	2,255
Spr.	6.7	–	21.8	7.7	10.0	0.5	1.6	0.8	1.0	–	32.5	12.3	0.6	4.4	–	2,795

Aut. – autumn, Win. – winter, Spr. – spring, W. mill. – white millet, P. mill. – Panic millet, Pop. seed – Poppy seed, Can. gras. – Canary grass, Hem. seed – Hemp seed, Wh. – wheat, Sun. seed – sunflower seed, Buc. – buckwheat, Col. seed – cole seed Bisc. – biscuit, Bre. – bread, Bac. – bacon, Fli. – flies, Un. – unknown

choice. Complete evenness [H' = ln(d)] is obtained in cases where all diets are chosen equally.

3. Results

3.1. Feeding preferences

The Alpine Accentors showed a strong degree of heterogenity in their food specializations in different seasons (autumn–winter: $G_h = 2729$, df = 10, $P < 0.001$; autumn–spring: $G_h = 1531$, df = 10, $P < 0.001$; winter–spring: $G_h = 1000$, df = 10, $P < 0.001$). Table 1 illustrates some of the preferences. In autumn, millet and canary grass were the preferred seed species; in winter, millet and poppy seeds were consumed more than other offered food items. The proportion of biscuits increased in winter (birds wintering in ski areas) and mainly in early spring. Diet diversity was lowest in winter and highest in autumn, while feeding rate was lower in spring than in autumn (t = 3.57, P = 0.0005, df = 121) or winter (t = 2.1, P = 0.04, df = 89). Feeding rate did not differ between autumn and winter (t = 1.1, P = 0.28, df = 118, Table 2). Consumption of flies (animal proteins) tended to increase from autumn to spring (Table 1). Calculations of diet nutritive values showed that birds received relatively more carbohydrates in the autumn than in spring or winter (Fig. 3). In the "snowy" seasons, the diet contained a relatively high number of lipids (autumn–winter: $\chi^2 = 14.9$, P = 0.002; autumn–spring: $\chi^2 = 10.3$, P = 0.02; winter–spring: $\chi^2 = 1.7$, P = 0.6).

Table 2. Seasonal values of the feeding rate and diet diversity (H') in Alpine Accentors (H' – Shannon index of diversity of diet calculated from the sums of pecks over all feeding trials, but separately for each season, n – number of video monitored feeding trials, t – total time of video observations of bird pecking). Number of trials include all trials of all measured individuals of Accentors in a season. Feeding rate = number of pecks per second

Season	Feeding rate	n	t(s)	H'
Autumn	0.79	76	3,300	2.18
Winter	0.78	44	2,394	1.53
Spring	0.60	47	4,685	1.91

3.2. Dominance

No significant differences in foraging tactics, feeding rate or diet diversity were detected between dominant and subordinate birds (Table 3). The producer role (finder of a new type of food in

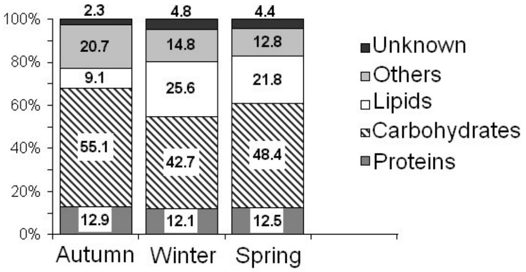

Fig. 3. Relative occurrence of nutritive components in the diet of Alpine Accentors in different seasons. Unknown – unidentified diet, others – other components (e.g. vitamins, minerals, etc.) in identified diet.

Table 3. Behavioural characteristics of 24 individuals of Alpine Accentors. Presented for each individual are a quantity to indicate its role as a producer or a scrounger, where low numbers indicate individuals that are producers to other birds, because of a tendency to change between variable food types from trial to trial. H' is the Shannon index of food diversity. Feeding rate was measured in number of pecks per second. Birds are characterised as either dominant (D) or subordinate (S). The individual's main diet type and the proportion the individual feeds on that diet type is given. Summary statistics are provided for dominant (D) and subdominant birds (S) with sample size between brackets. There were no differences in foraging role(t = 0.34, P = 0.73), feeding rate (t = 0.54, P = 0.59), and diet diversity (t = 1.37, P = 0.18) between dominant and subordinate birds.

Individual	Role	H'	Feeding	Dominance	Main diet	
1	0.00	1.158	0.95	S	Flax-seed	45.2%
2	26.52	1.408	0.67	S	Canary grass seed	37.9%
3	32.83	1.831	0.64	D	Canary grass seed	28.6%
4	36.74	1.472	0.86	S	Panicum millet	38.8%
5	37.30	1.456	0.78	D	Poppy seed	52.5%
6	40.59	1.753	0.95	D	White millet	27.3%
7	44.12	1.646	0.76	S	Biscuit	47.2%
8	44.29	1.300	1.10	S	White millet	33.6%
9	44.68	1.515	0.81	D	Biscuid	33.9%
10	46.04	1.396	0.66	S	Canary grass seed	58.9%
11	47.41	1.273	0.64	D	Biscuit	44.2%
12	50.00	1.678	0.72	S	Biscuit	25.0%
13	55.28	1.807	0.54	D	Poppy seed	34.9%
14	56.74	1.191	0.96	S	Panicum millet	57.7%
15	57.14	1.130	0.60	S	Poppy seed	43.5%
16	61.93	1.347	0.32	D	Flies (Musca dom.)	44.6%
17	63.89	1.146	0.40	D	Biscuit	44.7%
18	72.92	1.124	0.64	S	Canary grass seed	48.2%
19	80.00	1.068	0.64	S	Biscuit	45.0%
20	91.67	1.188	0.61	S	Poppy seed	41.5%
21	100.00	0.778	0.44	S	Bread	72.4%
22	100.00	1.242	0.94	unknown	Panicum millet	48.7%
23	100.00	0.603	0.81	S	Bread	70.9%
24	100.00	0.638	1.17	D	White millet	81.7%

Dominance	Role	H'	Feeding
D (9)	53.8(20.4)	1.42(0.38)	0.69(0.27)
S (14)	57.6(28.8)	1.22(0.30)	0.74(0.17)

each trial) does not depend on social hierarchy. Diet diversity was high in those birds which changed their diet in every successive trial (Fig. 4). Such birds are able to respond to novel stimuli and may really be considered as producers.

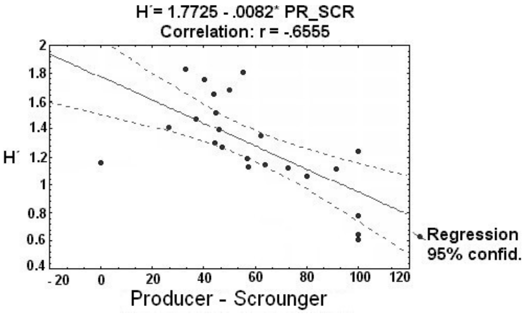

Fig. 4. Birds which play the role of producers for other birds have more diverse diets. The ability of a bird to find new food sources in every feeding trial is denoted by low numbers on the x-axis. H' – index diversity of different food types, high numbers on the y-axis denote more variable diets.

4. Discussion

Our results suggest that a preference for several seeds will allow a bird to cope with seasonal variations in its food supply, so that it not only finds food but maintains a balanced diet throughout the year (Brown 1969). There are obvious disadvantages to specialising in a single seasonal seed. But apart from nutritional effects (Fig.3), it may be better for birds to prefer a seasonal seed to a non-seasonal one, given a direct choice, since they could deal more efficiently with the former during the short period that it was available. This might be one of the reasons why accentors preferred biscuits in the early spring to the millet and canary grass which were their staple diet in autumn. This was also the reason why poppy seed prevailed in winter. The design assumes that in natural conditions animals may encounter food items sequentially and examine each to determine whether to consume or reject it (Smallwood & Peters 1986). Moreover, the approach may exacerbate differences in preference (Cipollini & Levey 1997) and hide the use of some less-preferred food items whose use depends on the abundance of preferred items. These less-preferred food items could be crucial for the survival of birds in natural situations when preferred items are scarce (Cueto *et al.* 2001). As we have shown in the results, a mixed diet may be nutritionally essential. The winter diet contained more lipids and less carbohydrates than the autumn diet. Organisms need energy stores because energy need is continuous while food intake is intermittent, and food availability varies with short- and long-term fluctuations (Lundborg & Brodin 2003). This especially applies to accentors living in very variable weather conditions.

The analyses of the behaviour of accentors showed that the features of individuals (individual feeding preferences, individual feeding rate, dominance) were not related to their foraging tactic use. Finding no differences reflects a high degree of behavioural plasticity and the fact that both dominants and subordinates move a lot during feeding. Although Alpine Accentors live in family groups, the species is not a typical social one in which all members move around together within their group territory (Nakamura 1995a). We assume that this is the reason why our results contrast with those reported by Liker and Barta (2002), who suggested an opposite positive relationship between dominance and some forms of joining in sparrows. When competitive asymmetries are high (i.e. when dominants compete for food much more successfully than subordinates), tactic use changes as a step function of dominance rank. For a moderate degree of competitive asymmetries all birds in a group may use both tactics (Barta & Giraldeau 1998, Liker & Barta 2002). This is probably the case in many species of alpine passerines including Alpine Accentors. Similar to some other species, accentors may use both producing and scrounging to find food (e.g. Giraldeau & Livoreil 1998) and some individuals seem to alternate between both feeding tactics. We video-taped some individuals which played different roles at different times.

For high competitive asymmetries, strong relationships are predicted between dominance and food intake rate (Barta & Giraldeau 1998), which is again not the case for accentors. There were no significant differences in the feeding rate between dominant and subordinate birds. In this study, as in others (e.g. Baker *et al*. 1981, Ekman & Askenmo 1984), dominance in birds did not influence the feeding rate or foraging tactics of accentors. If the experimental results reflect natural patterns, increased access to food probably provides selective advantages to offspring of dominant individuals of accentors. The Alpine Accentor is a polygynandrous mating species. The breeding unit is a group consisting of about five to seven members. Within one breeding group, the males mainly hold different ranks which do not change during the breeding season. Multiple paternity occurs, with more than one male siring offspring within a clutch. The feeding effort of the dominant males is higher than that of subordinates (Heer 1996).

It is expected that Alpine Accentors would respond more strongly to food addition than passerines of lower altitudes because they breed mainly in the alpine zone where their breeding habitat is unstable, particularly in spring. Supplemental feeding causes an earlier onset of reproduction (Nakamura 1995a) and an increase in group size in Alpine Accentors (Nakamura 1995b). Comparing the results of food supplementation experiments between Dunnocks (*Prunella modularis*, living in lower altitudes than *Prunella collaris*) and Alpine Accentors provides an effective explanation of why an association is not found between dominance and feeding methods in these alpine birds. In dunnocks, the mating system is variable and includes monogamy, polyandry, polygyny and polygynandry (Davies 1983, 1985). When extra food was provided, female ranges became smaller and the mating system shifted towards favourable males, from polyandry to monogamy (Davies

1992). In contrast, the mating system of Alpine Accentors was only polygynandrous, supplemental feeding had no effect on the mating system and on the range size of females (Nakamura 1990, 1995b). Female dunnocks were aggressive to other females and held an exclusive area within which all activities including supplementary feeding occurred, and not all females necessarily had access to a feeder (Birkhead 1981, Davies & Lundberg 1984, Davies 1992). Female Alpine Accentors do not forage exclusively in their territories and they often travel longer distances to exploit a rich source of food within the group territory (Nakamura 1995a). It seems reasonable to suppose that the diet diversity in ground feeding accentors is not related to dominance (this study) because they have large group territories and good foraging grounds are often patchily distributed.

Thus, although theory predicts that dominance may have important effects on tactic use in the foraging behaviour of birds, the Alpine Accentor is a good example of how this operates at high altitudes. It seems crucial to consider that individual species are plastic in their feeding behaviour and, in general, that the phenotypic limitation of foraging tactic use is poorly known in birds (Giraldeau & Beauchamp 1999).

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Alppirautiaisten ravintomieltymyksiä ja ruokailukäyttäytymistä

Seurasimme alppirautiaisparvien ruokailukäyttäytymistä ruudukolla, jolle oli sijoitettu siemenkasoja. Määritimme syödyn ravinnon määrän ja laadun, yksilölliset ja kausittain vaihtelevat mieltymykset tietynlaiseen ravintoon sekä yksilöiden aseman parven hierarkiassa. Toisten yksilöiden hankkiessa ravintoa tarjoutui toisille tilaisuuksia ravinnon rosvoamiseen. Tähän liittyi usein aggressiivista kanssakäymistä. Useimmat yksilöt käyttivät molempia taktiikoita ravinnonhankinnassa. Yksilön asema parven hierarkiassa ei ollut sidoksissa käytettyyn ravinnonhankintataktiikkaan. Asema parven hierarkiassa ei myöskään ollut sidoksissa syödyn ravinnon määrään tai laatuun. Alppirautiaisen ravintomieltymykset vaihtelevat voimakkaasti vuodenaikojen mukaan. Syödyn ruoan ravintoarvojen perusteella selvisi, että alppirautiaisen syysravinto sisälsi enemmän hiilihydraatteja kuin talvi- tai kevätravinto. Talvisin ravinto sisälsi huomattavasti rasvoja. Myös yksilöiden välillä oli eroja ravintomieltymyksissä.

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