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Parental foraging strategies and feeding of nestlings in Common Redstart *Phoenicurus phoenicurus*

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Spatial foraging activity and feeding of broods was studied in nine pairs of Common Redstart *(Phoenicurus phoenicurus)* breeding in nest boxes in pine forest. The effect of nestling age on feeding rate was not significant. The number of feedings per chick was similar in small and medium size broods but decreased in the largest broods. Feeding rates in individual pairs did not differ between males and females. Mean nest visit duration were longer for females. Incubation of the youngest chicks was probably the cause of significant decrease of length of feeding visits by females during the chicks' growth. The proportion of foraging techniques was different between males and females, and changed during a nestlings' life. Males foraged predominantly by perching (passive foraging mode) throughout the whole breeding period. Females also foraged mostly by perching, but with younger broods they frequently used an active foraging mode of foliage gleaning. The active foraging mode for younger broods could be either compensation of foraging efficiency for the time spent brooding, or caused by differences in prey selection at different nestling ages, or active foraging does not pay off in the exploited habitat around the nest at the end of breeding.

1. Introduction

In most species of altricial birds both parents on a nest feed the chicks until fledging. As the chicks grow older they differ in parental care needs (Starck & Ricklefs 1998). In the course of the nestling period, parents decrease the incubation of chicks, spend less time on the nest by feeding nestlings and their overall rates of feeding visits to the nest usually increase (e.g. Breitwisch *et al*. 1986, Hendricks 1987, Moreno 1987, Conrad & Robertson 1993, Sanz & Tinbergen 1999). The number of feeding visits alone is, however, an inaccurate measure of parental feeding investment and of the real amount of food brought to individual chicks (Royama 1966, Grundel & Dahlstein 1991, Moreno *et al*. 1995), as the parents could respond to higher demands of food also by change of foraging behaviour and preference to different prey types (Cucco & Malacarne 1997, Bañbura *et al*. 2001, Grieco 2002). Changes in foraging techniques or duration and distance of feeding trips over the

course of the breeding period could be also affected by prey availability on feeding sites, which may be exploited by continual parental predation (Andersson 1981, Kacelnik 1984, Naef-Daenzer *et al*. 2000). Relatively few studies have been concerned with changes in parental space and time activity in feeding during the nestling period and further studies on this topic are needed.

Although both male and female parents take part in feeding the brood, their contribution in the care of chicks and spatial activity around the nest often varies (e.g. Järvinen 1986, Carere & Alleva 1998, Bañbura *et al*. 2001). These differences were assumed as inter-sexual competition for food brought to chicks in a nest (Robins 1971, Hendricks 1987) where parents diversify their foraging behaviour to moderate the competition for food. Another explanation could be found in indirect consequences of sex specific parental roles in reproduction such as nest building, egg and chick incubation, singing, guarding of breeding territory etc. (Porkert & Špinka 2004). The factors affecting the inter-sexual differences may be revealed by continual observations throughout the nestling period.

In the present study, we observed parental foraging behaviour and feeding of nestlings in the Common Redstart (*Phoenicurus phoenicurus)*, a small insectivorous passerine species. Our aim was to assess the effect of number and age of nestlings on parental feeding rates and foraging behaviour in the diverse environment of a pine forest in the period of chicks growing in the nest before fledging. We also compared such behaviour between male and female parents in individual breeding pairs.

2. Material and methods

2.1. Material and study area

This study is based on the observation of nine broods of Common Redstart in nest boxes. Four broods were assumed as the first and five as the second broods of individual parental pairs, according to a study of the same population (Porkert & Zajíc 2005). Every observed brood belonged to a different parental pair.

The study area is situated at altitude 250 m, east of the town of Hradec Králové, eastern Bohemia, Czech Republic (50°12' N, 15°57' E). The observations were carried out in June and July 1999–2001. The breeding habitat was a managed pine (*Pinus sylvestris*) forest with minor proportions of spruce (*Picea abies*), oak (*Quercus* spp.) and other deciduous trees. A shrub layer was lacking, and the forest ground was bare or covered by bilberries (*Vaccinium myrtillus*). Nest boxes in the observation area were placed at a density of approximately 50 pcs/km^2, in lines with 30–50 m distance between neighbouring nest boxes, and attached to the tree trunk 3 m above the ground. The size of observation area was about 30 km^2.

2.2. Observations

A single observer watched foraging and feeding behaviour of parents from a shelter situated in the vicinity of the nest box. Each nest was observed for altogether 12 hours, at three nestling age intervals (5–6 days, 9–10 days and 13–14 days), two hours in the morning (between 8–12am) and two hours at the afternoon (between 2–6pm) at each interval. Actual observation time (see Table 1) differed, as parents were out of sight for certain parts of the observation. Observations did not occur in rainy or hot weather. A complete continuous record (Altman 1974) of all noticeable activities of parents was made in each observation interval using a tape-recorder for the observer's comments. Both parents were observed at the same time.

Parental behaviour was classified in the following activities:

- presence in a nest box,
- perching (passive foraging mode; sitting on a tree branch or other vantage point),
- foliage gleaning (active searching for prey in the foliage),
- ground foraging (active searching for prey on the ground).

The time parents spent preening, singing or in aggressive display was not counted in the foraging time.

The parental feeding effort was assigned to the following variables: brood feeding rate (number of nest visits by one parent per hour), per chick feeding rate (number of nest visits by one parent per

Table 1. Summary of nest observation data – actual observation time (in hours) of parental foraging behaviour when the focus bird was visible. Each brood was observed for a four hour period at every nestling age category. f = female observation interval, m = male observation interval, x = missing values.

Nest	1		2		3		4		5		6		7		8		9	
Parent sex	f	m	f	m	f	m	f	m	f	m	f	m	f	m	f	m	f	m
Nestling age																		
5–6 days	1.4	1.1	1.4	0.5	0.6	0.6	1.3	1.0	0.8	2.1	1.3	1.2	2.1	1.0	2.9	0.6	2.0	1.1
9–10 days	0.2	0.5	1.1	0.3	1.6	1.3	0.7	0.5	0.9	1.7	0.8	1.4	0.6	2.4	2.5	0.7	1.0	0.5
13–14 days	0.6	0.4	0.5	0.6	1.2	1.3	0.4	0.8	1.3	1.6	1.3	1.8	1.3	1.9	x	x	x	x
Brood size	7		3		6		4		4		6		3		5		4	

hour and chick), and mean nest visit duration (mean time in seconds, spent by male or female in the nest box per one nest visit). Parental foraging techniques (perching, foliage gleaning, and ground foraging) were expressed as the proportion of time spent in each foraging technique to the sum of time of all foraging techniques. Further, we calculated perching efficiency (number of attacks from perch/total number of perchings), mean duration of perching (on one perch), and mean distance from the nest during foraging (mean distance of all observed foraging attempts – all three abovementioned foraging techniques) using sketch-maps of the nest vicinity (5,000 m^2).

2.3. Statistical analysis

Repeated measures ANOVAs were used for the analysis of data (STATISTICA 6.0). The effects

Table 2. Mean values (± standard deviation) of analysed variables for males and females in different nestling age categories.

Response variables	Parent sex	Nestling age (days) 5–6	9–10	13–14
Brood feeding rate [parent^{-1}.hour^{-1}]	f	6.39 ± 3.05	6.83 ± 3.89	7.03 ± 3.35
	m	6.78 ± 1.84	7.81 ± 2.38	9.22 ± 4.72
Per chick feeding rate [parent^{-1}.hour^{-1}.chick^{-1}]	f	1.40 ± 0.67	1.51 ± 0.98	1.51 ± 0.74
	m	1.54 ± 0.46	1.81 ± 0.75	2.11 ± 1.27
Mean nest visit duration [s]	f	143.67 ± 159.21	41.11 ± 75.36	22.78 ± 28.29
	m	13.56 ± 4.50	8.67 ± 2.06	8.00 ± 2.69
Proportion of perching	f	0.77 ± 0.17	0.88 ± 0.08	0.90 ± 0.09
	m	0.91 ± 0.04	0.89 ± 0.09	0.92 ± 0.06
Proportion of foliage gleaning	f	0.18 ± 0.19	0.07 ± 0.06	0.06 ± 0.07
	m	0.05 ± 0.03	0.06 ± 0.06	0.04 ± 0.03
Proportion of ground foraging	f	0.05 ± 0.04	0.05 ± 0.04	0.04 ± 0.03
	m	0.04 ± 0.02	0.05 ± 0.06	0.04 ± 0.04
Mean duration of perching [s]	f	20.49 ± 7.40	21.36 ± 10.18	21.81 ± 7.51
	m	20.75 ± 8.80	20.03 ± 14.15	20.20 ± 8.61
Perching efficiency [attacks from perching/number of perchings]	f	0.34 ± 0.15	0.32 ± 0.09	0.32 ± 0.12
	m	0.35 ± 0.12	0.34 ± 0.12	0.33 ± 0.11
Mean distance from nest during foraging [m]	f	10.97 ± 4.38	11.48 ± 4.28	10.08 ± 4.97
	m	8.67 ± 2.90	9.00 ± 2.70	8.98 ± 3.25

Table 3. Results of repeated measures ANOVA on the relation between chicks' feeding and mean nest visit duration as response variables, and the effects of brood size, parent sex and nestling age.

	Brood feeding rate			Per chick feeding rate		Mean nest visit duration	
	df	F	p	F	p	F	p
Between-subject effect							
Brood size	2	4.55	0.063	2.43	0.169	2.36	0.175
Within-subject effects							
Parent sex	1	0.88	0.384	1.35	0.289	24.03	0.003
Nestling age	2	1.96	0.183	1.68	2.227	11.10	0.002
Parent sex * nestling age interaction	2	0.40	0.679	0.42	0.667	4.57	0.033

tested were brood size (random factor, categories: 3, 4–5, 6–7) and two repeated measures factors parent sex and nestling age (5–6, 9–10, 13–14 days) categories. All response variables (see previous section) were tested for normality before entered into the model. If deviating from normality, the variables were log-transformed (mean nest visit duration) or arc sin-transformed (foliage gleaning) to fit a normal distribution. Differences among categories of statistically significant factors with more than two levels (nestling age, brood size) were tested by Fisher's Least Square Difference test (STATISTICA 6.0).

In two nests, the data were missing for the last nestling age interval due to predation (Table 1). The data from these intervals were substituted by the average values from two previous nestling age intervals of the same nest.

3. Results

3.1. Feeding of nestlings

The brood feeding rate was affected by the number of chicks in the brood at a marginally significant level ($P < 0.1$) (Tables 2 and 3; Fig. 1). There was a significant difference between broods of 3 chicks

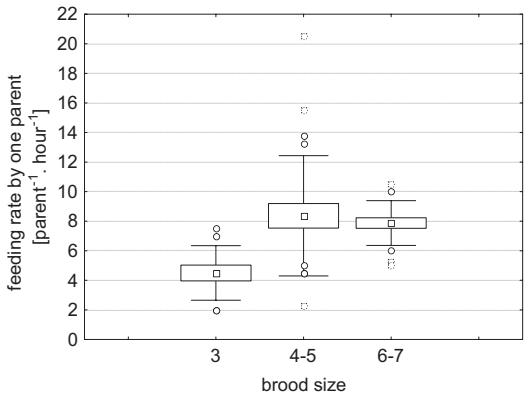

Fig. 1. Brood feeding rate by one parent [parent^{-1}. hour^{-1}] in broods with different number of chicks (squares = means; boxes ±SE; whiskers ±SD; circles = outliers; asterisks = extremes).

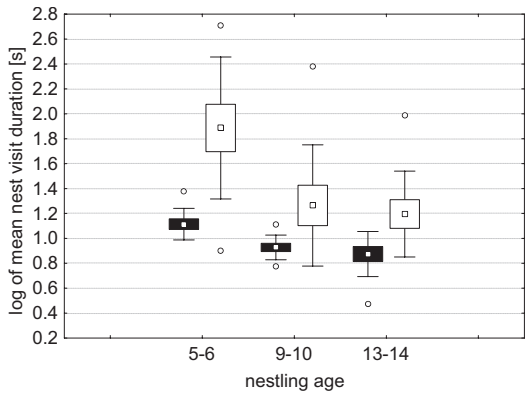

Fig. 2. Mean nest visit duration [s] (log transformed) of the broods of different age categories in male and female parents (open boxes: females, full boxes: males; squares = means; boxes ±SE; whiskers ±SD; circles = outliers).

Table 4. Results of repeated measures ANOVA on the relation between proportions of various foraging techniques as response variables, and the effects of brood size, parent sex and nestling age.

		Perching		Foliage gleaning		Ground foraging	
	df	F	p	F	p	F	p
Between-subject effect							
Brood size	2	0.71	0.528	1.93	0.225	3.44	0.101
Within-subject effects							
Parent sex	1	6.21	0.047	23.66	0.003	0.00	0.991
Nestling age	2	5.57	0.019	4.87	0.028	0.21	0.812
Parent sex * nestling age interaction	2	3.89	0.050	3.78	0.053	0.05	0.954

and broods of 4–5 chicks, which were fed more often (Fisher's LSD test, P = 0.027), but the difference between broods of 4–5 chicks and 6–7 chicks was not significant. The effects of parent sex and nestling age category on feeding rates were not significant. Per chick feeding rate was not significantly affected by any of the tested effects.

3.2. Duration of nest visit

Mean nest visit duration was not affected by the brood size. Females spent significantly longer times on the nest than males and the mean nest visit duration of both parents decreased throughout the nestling period (Table 2, 3; Fig. 2). Both males and females spent significantly longer times on nests with 5–6 day old chicks than with 9–10 day old chicks (Fisher's LSD test, P = 0.021, P = 0.01, respectively). The mean nest visit duration between the 9–10 and 13–14 day old categories did not differ significantly for either sex.

3.3. Foraging techniques

The predominating technique of both parents was perching (Table 2). The proportion of time spent perching was significantly higher in males than in females and it increased throughout the nestling

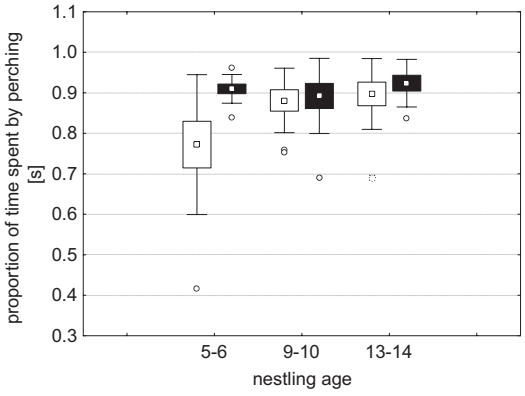

Fig. 3. Proportion of time spent by perching of the broods of different age categories in male and female parents (open boxes: females, full boxes: males; squares = means; boxes ±SE; whiskers ±SD; circles = outliers; asterisks = extremes).

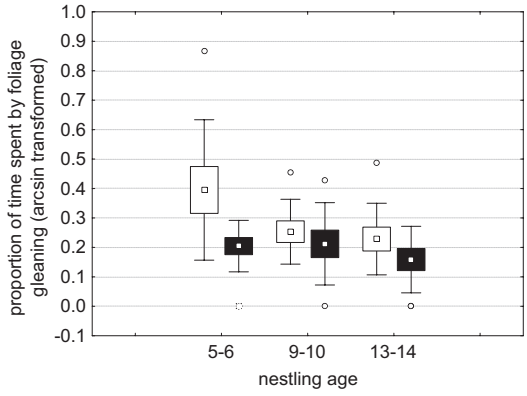

Fig. 4. Proportion of time spent by foliage gleaning (arc sin transformed) of the broods of different age categories in male and female parents (open boxes: females, full boxes: males; squares = means; boxes ±SE; whiskers ±SD; circles = outliers; asterisks = extremes).

period for both parents (Table 4; Fig. 3). On the contrary, females spent relatively more time foliage gleaning than males and the proportion of this foraging mode decreased as the chicks became older (Fig. 4). Brood size affected neither proportions of perching nor foliage gleaning. Ground foraging was a minority foraging technique and was not affected by any of the tested effects.

Perching efficiency, mean duration of perching and the mean distance from the nest during foraging were affected neither by nestling age nor by brood size and did not differ between males and females (all P-values > 0.05).

4. Discussion

4.1. Feeding of nestlings

Although the feeding rate provides only indirect information about the care the chicks have received without direct information on the type and amount of food brought to the nestlings during individual nest visits (Royama 1966, Grundel & Dahlstein 1991, Moreno *et al*. 1995) it is, nonetheless, a good measure of parental investment as the flight energetic requirements are high (Nur 1984, Cucco & Malacarne 1997). According to the trade-off model of parental behaviour (Charnov & Krebs 1974) the feeding rate is predicted to increase with nestling age and brood size.

In our study, we found increasing feeding rates with increasing numbers of chicks from small to medium broods and about the same provisioning level between medium and large broods. This result corresponded with similar per chick feeding rates across the broods with different chick numbers unless they were at the upper end of the brood size range. Although we do not have information about the amount of food brought by parents, the non-significant brood size effect on the per chick feeding rate may indicate that individual chicks are given similar amounts of parental feeding effort, particularly in small and medium broods. Thus, the number of offspring adjusted the parental feeding. The constant per chick feeding rate probably could not be sustained in the largest broods due to increased cost or limits of parental feeding capacity. In some studies of different passerine species constant per chick feeding rates were observed (Nur 1984, Haggerty 1992, Conrad & Robertson 1993, Laiolo *et al*. 1998), but in others, the per chick feeding rate decreased with the brood size (Gibb 1955, Knapton 1984, Breitwisch *et al*. 1986, Moreno 1987, Schad & Ritchinson 1998). The different results may be attributed to methodological reasons or to species (or even population) specific traits, such as different parental feeding abilities and chick thermoregulation where larger broods may need lower food supplies due to lower heat losses and better energetic balance. In the Common Redstart, the ability of parents to increase the feeding rate dramatically was reported from nests cared for by a single parent (Doerbeck 1966, Porkert & Špinka 2004). However, the cost of high provisioning effort may reduce the future reproductive success or parental survival until the next reproductive season as documented in many species and studies (e.g. Nur 1988, Nilsson & Svensson 1996, Cichon *et al*. 1998, Dhondt 2001).

In contrast to many studies of passerine species (e.g. Pinkowski 1978, Breitwisch *et al*. 1986, Hendricks 1987, Conrad & Robertson 1993, Karlsson 1994, Sanz & Tinbergen 1999, Porkert & Špinka 2004), we did not find a significant increase of parental feeding rate with increasing age of nestlings. The most probable explanations are that our observations do not include nests in a period before chick ages of 5–6 days when the feeding rate is very low (Bedard & Meunier 1983, Haggerty 1992). Differences between the latter age categories are not so sharp and the feeding rate usually reaches the plateau phase when the nestlings are about 10 days old (Moreno 1987, Conrad & Robertson 1993). Moreover, parents slightly decreased their feeding of the broods at the time before fledging in 14 day-old chicks. If the feeding rate is similar as the chicks grow, their higher food demands can also be supplied by different prey type or prey size (Knapton 1984, Hellmich 1987, Moreno 1987), which can also lead to the use of different foraging techniques.

We found no significant difference between males and females in the feeding rate, similarly to many previous studies of monogamous passerine species (Pinkowski 1978, Knapton 1984, Hendricks 1987, Dittami *et al*. 1991, Schad & Ritchinson 1998). Differences between males and females in the feeding rate are mostly limited to the period of attending very young nestlings when females

are engaged in brood incubation (Moreno 1987, Sanz & Tinbergen 1999). This is also the case in Common Redstarts, where incubation of chicks is exclusively performed by females (Buxton 1950, Menzel 1984). A lower feeding effort in Redstart males may occur in rare cases of male polygyny (Levin & Gubin 1985).

4.2. Duration of nest visits

Durations of nest visits correspond mainly with brooding the chicks. In most passerine species, including the Common Redstart, only females incubate the brood (Moreno 1989) and their time spent on the nest is greater than in males. The nest attendance time was also predicted to correlate with age and number of nestlings in a brood (Mertens 1969, Clark 1984, Moreno 1987).

The chicks capacity of thermoregulation increases as they grow on the nest and the brooding behaviour of the female parent is adjusted accordingly (Royama 1966, Clark 1984). Many studies of different species documented the decrease of nest visit duration by females during the nestling period (Moreno 1987, Sanz & Moreno 1995, Schad & Ritchinson 1998, Sanz & Tinbergen 1999, Chastel & Kersten 2002). In our study, the duration of parental nest visits shortened and the difference between male and female decreased as the chicks grew older. The significant difference in nest attendance between males and females even when brooding visits were omitted was observed in another study of Common Redstarts (Porkert & Špinka 2004). Such differences might be caused by different patterns of food allocation among the chicks in the nest (Stamps *et al*. 1989) or other nest care duties such as nest sanitation (Porkert & Špinka 2004). The overall decline in the duration of nest visits during the nestling period may be also attributed to the time shortage caused by higher feeding rates with increased feeding demands of older chicks. Decreased frequency of brooding but stable time length of individual nest visits during the nestling interval was observed in the Northern Wheatear *Oenanthe oenanthe* (Moreno 1987).

The nest visit duration was negatively correlated with the number of chicks in a nest in many passerine species (Dunn 1976, Moreno 1987, Sanz & Tinbergen 1999, Chastel & Kersten 2002). The overall time of incubation in larger broods was lower because of the lower heat loss of these nests (Mertens 1969). Our data did not correspond with these results. This could be caused by small size variation of the natural broods, or, due the fact that our data do not include observation of nests with very young chicks where the correlation should be pronounced.

4.3. Foraging techniques

Inter-sexual differences in various properties of parent foraging behaviour have been predicted as a result of the potential competition for food between the members of a pair in the area around the nest (Selander 1966, Robins 1971). Several field studies have confirmed some of the predictions in various species by observed diversification of height of foraging perches (Santos & Suárez 1985, Petit *et al*. 1990), use of different foraging modes (Power 1980), different foraging habitat (Hendricks 1987) or day hours of the main foraging activity (Knapton 1984) between males and females. Several studies reported females foraging closer to the nest than males (Pinkowski 1978, Knapton 1984, Wasserman 1986). The differences may, however, not always be the results of inter-sexual competition for food but could also be an indirect consequence of sex specific roles in reproduction. While males are engaged in singing and territory defence they tend to use more of a sit-and-wait foraging mode and stay on higher perches than females. Similar sex specific foraging modes to our observations were documented in other studies of Common Redstarts (Buxton 1950, Ward 1956, Hogstad 1977, Järvinen 1986).

If the inter-sexual differences would be the results of diversification due to intra-pair competition for food, the differences between males and females should rather increase with time over the breeding period when the demand for food increases but its availability decreases. This was, however, not the case in our study. In our observations males foraged almost entirely by perching throughout the whole nestling period, while females spent a significant amount of time also foliage gleaning when chicks were 5–6 days old. The proportion of foliage gleaning declined as the chicks grew, especially in females, and the differ-

ence in the proportion of this foraging technique between the sexes was negligible before fledging of the chicks at age 13–14 days. At first sight, the significant decrease of foliage gleaning during the nestling period seems to be contra-intuitive. Foliage gleaning, as an active foraging mode, is supposed to be more effective than perching (Huey & Pianka 1981, Zamora 1992, Exnerová *et al*. 2002), and the former is expected to be used more frequently as the food requirements of the chicks increase. We offer four alternative interpretations for such changes in use of foraging techniques, as follows.

1. As the time available for foraging by females is restricted when they have to brood young nestlings (Moreno & Hillström 1992, Chastel & Kersten 2002), they may compensate for time spent brooding by using a more effective yet more energetically demanding foraging technique – foliage gleaning – at the beginning of the nestling period. A similar switch in the foraging technique of females was observed in Northern Wheatears between egg incubation and nestling periods (Moreno & Hillström 1992). In the first period females foraged mainly by ground gleaning and they switched to perching when feeding nestlings.
2. Composition of diet changes as a function of nestling age (Flinks & Pfeifer 1988). Young nestlings are mostly fed small and weakly sclerotised arthropod prey, which may be abundant mainly in the foliage and accessible by gleaning. Catching larger or more sclerotised prey, which is brought to older nestlings, is easier from a perch. Different proportions of soft and hard prey items in the food of Common Redstart nestlings of different age groups were documented in a study of Bösenberg (1960). It is, however, not known whether this difference could be associated with different parental foraging modes.
3. The alternative explanation considers the environmental changes in a breeding territory. As the habitat around the nest may be exploited in older broods before fledging, an active foraging mode – foliage gleaning – might not pay off because of low foraging efficiency. Thus the parents could switch to a less demanding, relatively more efficient, passive foraging mode.
4. An energetically less-demanding foraging method becomes more important at the end of breeding simply as a result of parents' tiredness.

Only the first alternative explains the greater change of foraging behaviour in females. In several other species, the changes in foraging modes or foraging patches during the fledging period were affected rather by environmental changes with the progressing season (Pinkowski 1978, Santos & Suárez 1985, Whittingham & Robertson 1993).

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Leppälintujen ravinnonhankinta ja poikasten ruokkiminen

Tutkimuksessa seurattiin miten yhdeksän pöntössä pesivää leppälintuparia etsi ravintoa poikasilleen ja kuinka usein ne ruokkivat poikuettaan. Poikueen ikä ei vaikuttanut ruokintatiheyteen. Pienissä ja keskisuurissa pesyeissä poikanen sai keskimäärin yhtä usein ravintoa, mutta suurissa pesyeissä poikasta kohti laskettu ruokintakertojen lukumäärä oli pienempi. Vaikka koiras ja naaras ruokkivat poikasiaan yhtä innokkaasti, naaras viipyi pesällä kauemmin. Koska naaras jäi usein lämmittämään pieniä poikasia, naaraan ruokintakäynnit lyhenivät poikasten kasvaessa.

Koiras ja naaras saalistivat eri tavalla, ja niiden saalistuskäyttäytyminen muuttui pesinnän aikana. Koiraat saalistivat koko pesintäajan pääasiassa passiivisesti väijymällä (perching). Naaraatkin saalistivat enimmäkseen väijymällä, mutta pienille poikasille ne etsivät ruokaa aktiivisesti lehvästöstä (foliage gleaning). Tutkijat esittävät kolme vaihtoehtoa selittämään naaraan käyttäytymistä: 1. Saalistamalla aktiivisesti naaraat voivat tehostaa ravinnon löytymistä säästääkseen aikaa poikasten lämmittämiseen. 2. Naaraat voivat valita erilaista saalista eri-ikäisille poikasille. 3. Aktiivinen ravinnonhaku pesän lähiympäristössä ei enää tuota tu-

losta pesinnän loppuvaiheessa, koska ravinto on pesinnän kuluessa vähentynyt.

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