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Sex differences in feeding visit rates in Northern Wheatears *Oenanthe oenanthe*

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Abstract

The Northern Wheatear (*Oenanthe oenanthe*) is a small insectivorous passerine bird living in open landscapes. Both parents feed the brood of approximately five chicks, but little is known about how each sex allocates their feeding effort.

In this study I investigate feeding nest visit differences between male and female Northern Wheatears relative to the age of the chicks, the number of chicks and the quality of the territory for 17 pairs from 2008-2010. Data were collected using automated data loggers to record nest visitation rates during chick feeding, and the sex of the parent was determined from nest video cameras. I also examine if the parents' rate of feeding visits changes over the nestling period.

The predictions were that: (1) the male would visit relatively more when the chicks were young compared to the female, and that these roles would reverse (i.e. the female would become the parent with most feeding visits) when the chicks grew older; (2) any differences between the feeding rates of parents would be smaller for larger broods; (3) any differences between the feeding rates of parents would be relatively small when the quality of the territory was low; and (4) parents would increase their rate of feeding visits as the chicks grew. The predictions are based on the theory of resource limitation.

I found some support for differences in feeding nest visits between the sexes. The male had a greater share of feeding visits when the chicks were young, but there was no difference when the chicks were older. There was no difference between the male and the female in their feeding visit rates with varying numbers of young. The quality of the territory had a small effect on the sexes' feeding visits, but only when the age of the chicks was added to the analysis. The rate of feeding visits was higher when the chicks were older.

This study is the first to provide information on wheatear behaviour in the nest relative to its sex and should outline the basis of future research on sex differences in the Northern Wheatear.

Sammanfattning

Stenskvättan (*Oenanthe oenanthe*) är en liten insektsätande tätting som lever i öppna landskap. Båda föräldrar matar kullen på ca fem ungar, men kunskapen om hur könen fördelar sina ansträngningar är liten.

I den här studien undersöker jag skillnader i matningsfrekvens mellan hane och hona av stenskvätta i förhållande till ungarnas ålder, deras antal och kvaliteten på reviret hos 17 par under 2008 till 2010. Data samlades in med en automatiserad datalogger för att registrera bobesöksfrekvens medan ungarna matas, och den matande förälderns kön bestämdes från filmer av boet. Jag undersökte också om föräldrarnas matningsfrekvens ändras under tiden ungarna är i boet.

Jag antog att: (1) hanen skulle mata oftare relativt honan när ungarna är små, och att rollerna skulle bli ombytta (d.v.s. honan skulle bli föräldern med högst matningsfrekvens) när ungarna blivit äldre; (2) skillnader i matningsfrekvens mellan föräldrarna skulle vara mindre ju fler ungar det är i boet; (3) skillnader i matningsfrekvens mellan föräldrarna skulle vara relativt liten när kvaliteten på reviret var låg; och (4) föräldrarna skulle öka matningsfrekvensen allteftersom ungarna växte. Antagandena är baserade på teorin om begränsade resurser.

Jag fann visst stöd för skillnader i matningsfrekvens mellan könen. Hanen hade en större del av matningen när ungarna var små men det var ingen skillnad när ungarna var större. Det var ingen skillnad mellan hane och hona med varierande antal ungar. Kvaliteten på reviret hade en liten effekt på könens matningsfrekvens, men bara när ungarnas ålder togs med i analysen. Matningsfrekvensen var högre för äldre ungar än för yngre.

Den här studien är den första att förse information om hur stenskvättor beter sig i boet i förhållande till dess kön och bör utgöra grunden för framtida forskning på könsskillnader hos stenskvätta.

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Introduction

In modern human society there is increasing cultural pressure for both male and female parents to invest equally in raising children. This originally stems from the high demand of bringing up a human child and the mother needing an assistant in the process. However, in most mammalian species it is the mother who, often, singularly invests in offspring after conception (Gross 2005). In birds, on the other hand, approximately 90% of all species have biparental care (Gross 2005), although male and female parents seldom share this care equally. This immense difference is due to a number of reasons. One is caused by the difference in reproductive systems. Both groups have internal fertilization, but while mammal young develop in the womb of the mother, bird chicks develop in an egg outside the mother, making it possible for the male to help with chick rearing as soon as the eggs have been laid. Another reason is the way they provide food for their young. In mammals it is primarily the female who lactates and can feed the offspring; in birds there is no such physical difference between the sexes, and they rely on an outer source of food, thus both parents have the potential of providing for the chicks. Since both mammals and birds have internal fertilization it is possible for males of both groups to desert directly after mating, which mammal males often do. Nevertheless, the high proportion of biparental care in birds indicates that the reproductive success of the male increases greatly if he cooperates with the female in the rearing of young. Among songbirds the female is generally the only parent incubating and often provides more food for the chicks (e.g. MacGregor & Cockburn 2002, Ardia 2007). One reason for this is that the female is prepared to invest more in offspring she knows to be her own, while the male is unwilling to spend energy on chicks that are not his because of extra pair copulations (EPCs; Møller & Cuervo 2000). In the well-known polyandrous case of Dunnocks (*Prunella modularis*), males care for the young according to their perceived paternity of a brood (Davies 1992 p. 205). However, Dunnocks show all kinds of mating systems - monogamy, polyandry, polygyny and polygynandry - and individuals adapt to the system they are currently in.

EPCs in socially monogamous species do not exclude the possibility that the parents can have an equal share of the care, which behaviour is often caused by a shortage of food, such that both parents are needed to successfully raise a brood (Mizuta 2005, Quillfeldt *et al.* 2007), or that the male is the main provider (Grundel 1987). A male will invest more than a female in a brood if it benefits him in terms of his life-time fitness. The share of chick feeding may also change as over time (e.g. as the chicks grow and their energy needs change), which Mitrus *et al* (2010) showed in the Red-breasted Flycatcher (*Ficedula parva*). As the chicks grew older the male's share of chick feeding decreased from more than 60% to less than 50%. Mitrus *et al* argue that the male's greater share earlier in the nestling period is due to the disadvantage of the female leaving the naked chicks early in the period, thus leaving the male to find food. Many studies on parental care in birds have focused on how brood size, and manipulations of it, affects parental provisioning. In some species there is no difference between the sexes in their response to manipulation (Magrath *et al.* 2007, García-Navas & Sanz 2010), however, in other studies males had large changes in effort (Ardia 2007). Habitat quality may interact differently with costs associated with chick rearing for males and females. Ardia (2007) found that in Alaska male Tree Swallows (*Trachycineta bicolor*) increased their feeding

effort less than the females when the brood was enlarged and decreased their effort more than the female when the brood was reduced. In New York, where food availability was lower, both parents had similar increases and decreases in feeding effort. Because of this it is important to consider these three factors: parental sex, chick needs and habitat quality to best understand parental feeding decisions.

In this study I have concentrated on sex differences in feeding nest visit rates in the Northern Wheatear *Oenanthe oenanthe*, relative to the needs of the chicks (brood age and number) and habitat quality. Some previous work has focused on sex differences in this species: e.g. sex differences in migration dates (Currie *et al.* 2000; Dierschke *et al.* 2005) where males were shown to migrate earlier and establish good territories on the breeding grounds; also, Arlt & Pärt (2008) have found that experienced breeders may shift territories post-breeding and that most who did had a low quality territory. This is important as the availability of food is positively correlated with the quality of the territory.

Very few studies have investigated detailed parental differences between the sexes in the Northern Wheatear. Brooke (1981) found that the female was more prone to use supplementary sources of food while feeding chicks. Based on these data and additional detailed data collected from video recorders from wheatear nests, my aim is to answer whether there is a difference between male and female parents in their feeding visits of offspring depending on (1) the age of the chicks, (2) the number of chicks in the nest, (3) the quality of the territory and if the total hourly variation in nest visits is the same throughout the nestling period. I expect the male to have a greater share in the number of feeding visits when the chicks are young, since the female needs to stay on the naked chicks to warm them; as the chicks grow older the female will visit the nest more often than the male. The difference in feeding visit rates between the sexes will be smaller when there are more chicks in the nest, because more chicks will have a greater huddling effect, enabling the female to be out longer in search for food, thus reducing the difference between the sexes early in the nestling period, and more chicks need more food so the male will have to increase his effort more than he otherwise would. In a low quality territory the availability of food is reduced and I expect the difference between the sexes to be smaller than in a high quality territory, since the parents have to cooperate at a higher level to secure the offspring. For the last point of investigation I think the total rate of visitation will be higher when the chicks are older.

Materials and Methods

The species and study area

The species in this study is the Northern Wheatear *Oenanthe oenanthe*. It is a small passerine bird (~20g), in the flycatcher family, which breeds in the northern hemisphere and winters in Africa south of Sahara (Conder 1989, p. 35). In the study area it can nest in rock piles, stone walls and under roof tiles. The wheatear is a socially monogamous bird with biparental care where the female incubates and both parents feed the chicks (Conder 1989 p. 183 and p. 208). 10-20 % of all chicks are the result of EPCs (Pärt & Arlt, unpublished data). The wheatears in the prevailing population lay ~6 eggs per nesting attempt, of which more than 5 hatch on average and approximately 4 fledge (Pärt, unpublished data), and they may have two broods in a season. The bird is an insectivore and chicks are fed various flies, moths, beetles and larvae.

The study area is located southeast of Uppsala (59°50'N, 17°50'E), Sweden, and covers approximately 60 km^2. It consists of a mosaic of crop fields, pastures, farms and woods. The Swedish University of Agricultural Sciences, with Tomas Pärt at the head of the project, has studied the Northern Wheatears in this area since 1993. Between 120 and 190 pairs are observed from their arrival in April till they have finished breeding each year. The birds are observed every third day on average, to accurately determine the stage of breeding, and four times during the breeding season the local vegetation is mapped, determining vegetation height and land use, to assess the quality of each habitat. Wheatears prefer short vegetation, where food availability is higher (ground vegetation is closely linked to habitat quality and in turn reproductive succsess; e.g. Pärt 2001). Where possible, all birds are colour ringed for easy identification. The chicks are ringed when they are 5-7 days old and if the parents are not already ringed they are caught and ringed during the nestling period.

Data collection and analysis

The parental nest visitation data were collected in the field with electronic data loggers and video recorders during the years 2008-2010. The logger is a tube-like instrument, with diodes registering passing objects, put in the entrance of the nest (Appendix 1a). It then recorded each time a bird entered or left the nest. The logger also started the video recorder, which filmed the birds in the nest for approximately 10 seconds at each visit. For more information on the logger see Low *et al* (2008), the video recorder was an Archos504 external hard-drive linked to an infrared camera (Appendix 1b). I decided to use parental feeding visits as a measure for parental effort, since it is a major part of parental care in birds. I did not estimate load size or try to determine the type of food given to the chicks, seeing that few nests had videos in which it was possible to observe those things, especially for the older chicks.

The data for this study were extracted from manual studying of the video recordings from the nests and I noted the sex of the feeding parent on each feeding (see Appendix 1c-1h). Video data were collected from two periods in nestling development: early (chicks 0-3 days old) and in the middle of the nestling period (7-9 days old), when the chicks are at their maximum growth (Conder 1989 p. 221). In total 17 nests were used, 12 with good recordings early and 13 with good recordings later. By cross-referencing information from the data-loggers to the video recordings, I only recorded the sex of parents feeding between 08:00 and 18:00 and only ca 100 feedings from each time period for each nest. However, in a small proportion of the nests the recordings were of poor quality, but at least 50 feedings were registered from those nests. The time-periods were chosen to maximise the possibility of detecting differences in nestling feeding visits, and to avoid the problem of chicks being fed outside the nest late in the nestling period. 100 feedings were estimated to be a good sample of the feeding visits over the day, though four nests had videos with too poor quality to achieve that number. From the feedings noted the proportion of feeding visits for each parent was calculated and with data over the total number of feedings per day the total feeding nest visits per parent was estimated.

The analysis of the data was done with Microsoft Office Excel 2003 and Minitab Statistical Software (version 15.1.1.0). The tests used were 2-sample t-test, logistic and general regression analyses, also accounting for interactions, and Wald-test including a χ^2.

Results

1. Sex differences in feeding visit rate relative to chick age.

There was no consistent effect of sex on feeding visits for the two periods (Figure 1), although feeding rates for both sexes did increase with chick age (Logistic regression: χ^2 = 38.3, df = 1, P < 0.001). However there was an interaction between chick age and the proportion of visits by each sex (Logistic regression: χ^2 = 22.4, df = 1, P < 0.001; Figure 1); males were providing proportionally more when the chicks were young. It is important to note that the female was present in the nest 46.9 % of male feedings when the chicks were young. When the chicks grew older the female fed proportionally more as compared to the early chick stage. When the chicks were young, the male did 58.23 % (95 % CI=57.3-59.2) of the feedings, but when the chicks had grown older he only visited 46.44 % (95 % CI=44.2-48.4) of the times. This can be seen in Figure 1, where the male increased feeding between the young and old periods by less than 50%, while the female increased her total daily visits by more than 100%.

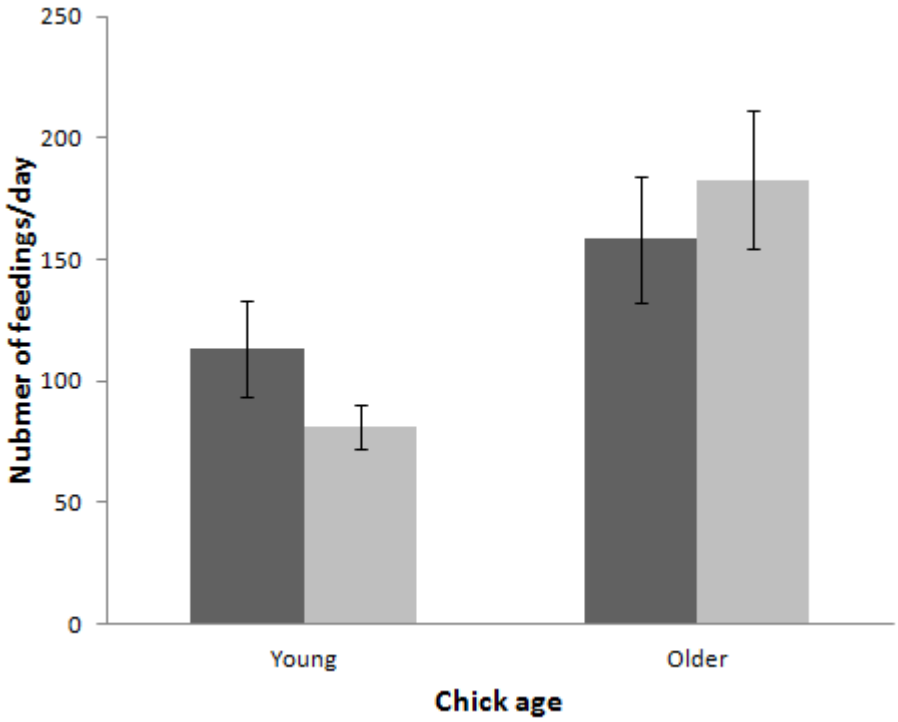

Figure 1: Graph showing total daily male (dark grey) and female (light grey) feeding rate when the chicks are young and when they are older (with SE-bars). Sample size for young chicks is 12 and for older chicks it is 13.

2. Sex differences in feeding visit rate relative to the number of chicks in the nest.

The number of chicks did not affect either parent's feeding visit rate when the chicks were young or when they were older (table 1). When the chicks were young the male seemed to be feeding less the more chicks there were and when they had become a little older both parents seemed to increase their efforts, though the male does not increase as much (Figure 2).

Table 1: Regression coefficients and associated statistics for predicting number of nest visits depending on the age of the chicks, the sex of the parent and the number of chicks. The constant is where the line intercepts the y-axis, * signifies interactions between the variables.

Predictor	Coef	SE Coef	T	P
Constant	242.3	125.1	1.94	0.059
Age	-16.6	167.1	-0.10	0.921
Sex	-148.8	176.9	-0.84	0.405
No Chicks	-24.95	23.78	-1.05	0.300
Age*Sex	1.3	236.4	0.01	0.996
Age*No Chicks	11.51	32.20	0.36	0.723
Sex*No Chicks	22.57	33.63	0.67	0.506
Age*Sex*No Chicks	11.80	45.54	0.26	0.797

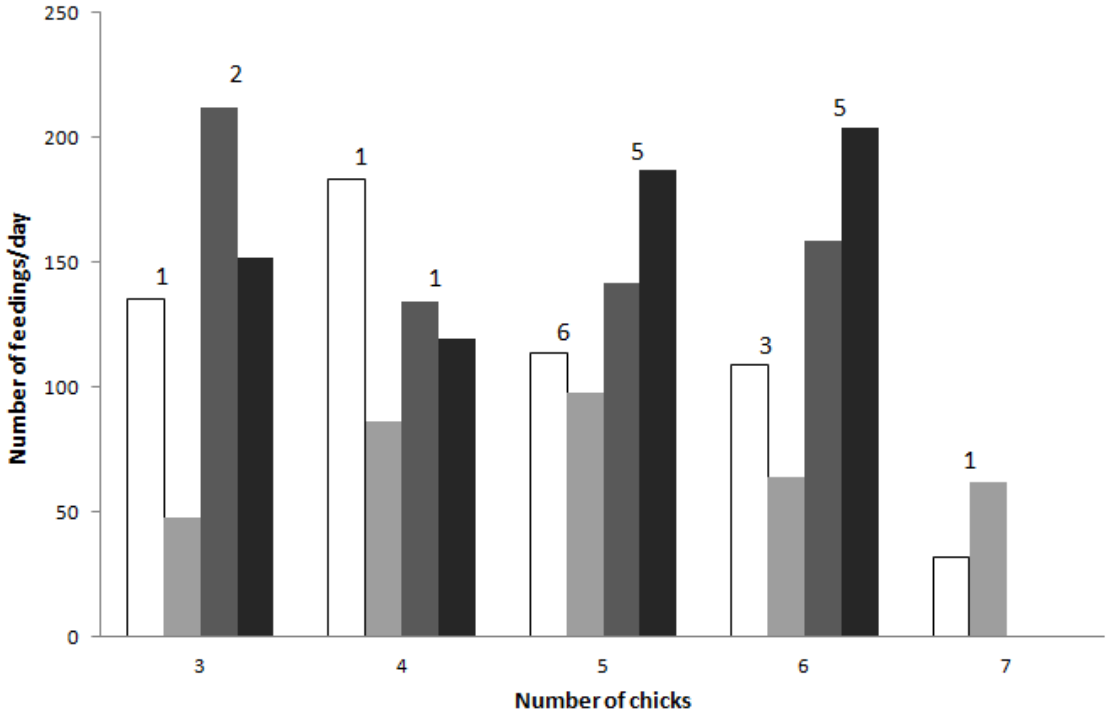

Figure 2: Average number of feedings per day when the chicks are young and older. White=male feeding young chicks, light grey=female feeding young chicks, medium grey=male feeding older chicks and dark grey=female feeding older chicks. Numbers above columns show sample size: young chicks to the left and older chicks to the right.

3. Sex differences in feeding visit rate relative to territory quality.

There was no difference between the sexes in feeding visit rate relative to territory quality (table 2). The results in table 3, however, indicate that the rate is affected by the quality of the territory and there is an interaction between the age of the chicks and the territory quality. In the high quality territory there is a great difference in feeding visit rates relative to chick age (Figure 3). Both parents approximately double their effort between when the chicks are young and when they are older. In the low quality territories this change in

effort is only visible for the female; the male does not show any alteration in feeding visit rate.

Table 2: Regression coefficients and associated statistics for predicting number of nest visits depending on the age of the chicks, the sex of the parent and the quality of the territory. The constant is where the line intercepts the y-axis.

Predictor	Coef	SE Coef	T	P
Constant	132.91	23.14	5.74	0.000
Sex	2.48	32.73	0.08	0.940
Territory quality	9.90	36.59	0.27	0.788

Table 3: Regression coefficients and associated statistics for predicting number of nest visits depending on the age of the chicks, the sex of the parent and the quality of the territory. The constant is where the line intercepts the y-axis, * signifies interactions between the variables.

Predictor	Coef	SE Coef	T	P
Constant	86.49	27.70	3.12	0.003
Sex	-9.93	39.17	-0.25	0.801
Age	99.47	40.54	2.45	0.018
Territory quality	80.83	47.97	1.68	0.099
Sex*Age	26.60	57.34	0.46	0.645
Sex*Territory quality	-66.84	67.84	-0.99	0.330
Age*Territory quality	-140.31	64.82	-2.16	0.036
Sex*Age*Territory quality	83.38	91.66	0.91	0.368

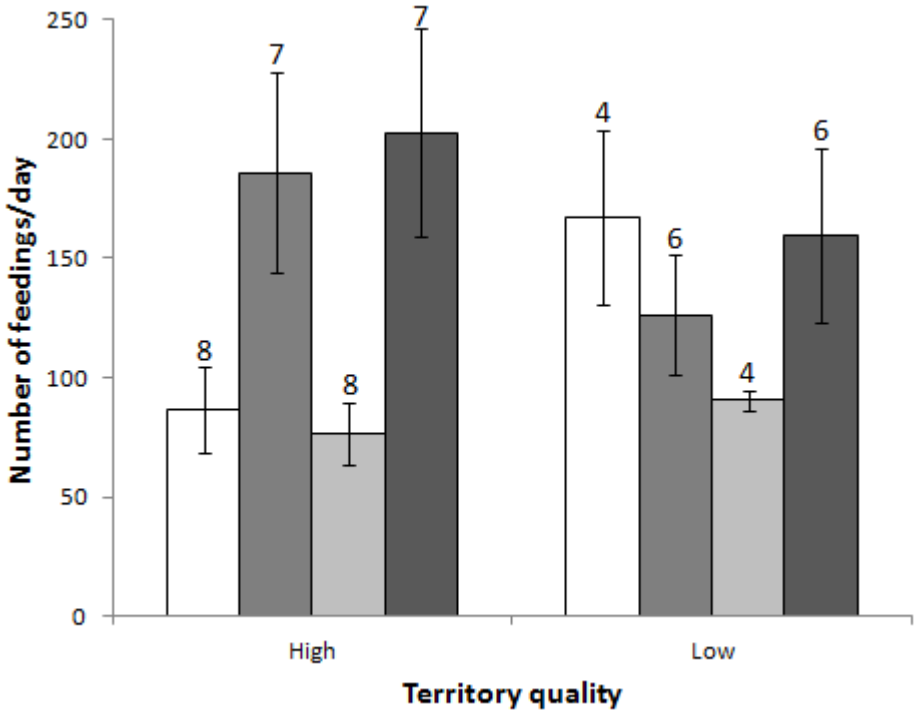

Figure 3: Average number of daily feedings depending on chick age and sex of the parent (with SE-bars). White=male feeding young chicks, light grey=female feeding young chicks, medium grey=male feeding older chicks and dark grey=female feeding older chicks. Numbers above bars show sample size.

4. Hourly variation in nest visiting rate relative to chick age.

There was a strong time effect on nest visitation, with feeding visits increasing during the morning and declining in the afternoon. For older chicks the midday feeding peak was significantly higher than for young chicks (Table 4; Figure 4).

Table 4: Regression coefficients and associated statistics for predicting number of nest visits depending on the age of the chicks, the hour of the day and the hour of the day squared. The constant is where the line intercepts the y-axis, * signifies interactions between the variables.

	Results with interactions				Results without interactions			
Predictor	Coef	SE Coef	T	P	Coef	SE Coef	T	P
Constant	5.346	2.376	2.25	0.030	3.184	1.741	1.83	0.075
Age	0.130	3.360	0.04	0.969	4.4548	0.8616	5.17	0.000
Hour	1.3541	0.4334	3.12	0.003	1.8126	0.3077	5.89	0.000
Hour sq	-0.05361	0.01691	-3.17	0.003	-0.07178	0.01200	-5.98	0.000
Age*Hour	0.9171	0.6130	1.50	0.143				
Age*Hour sq	-0.03633	0.02391	-1.52	0.137				

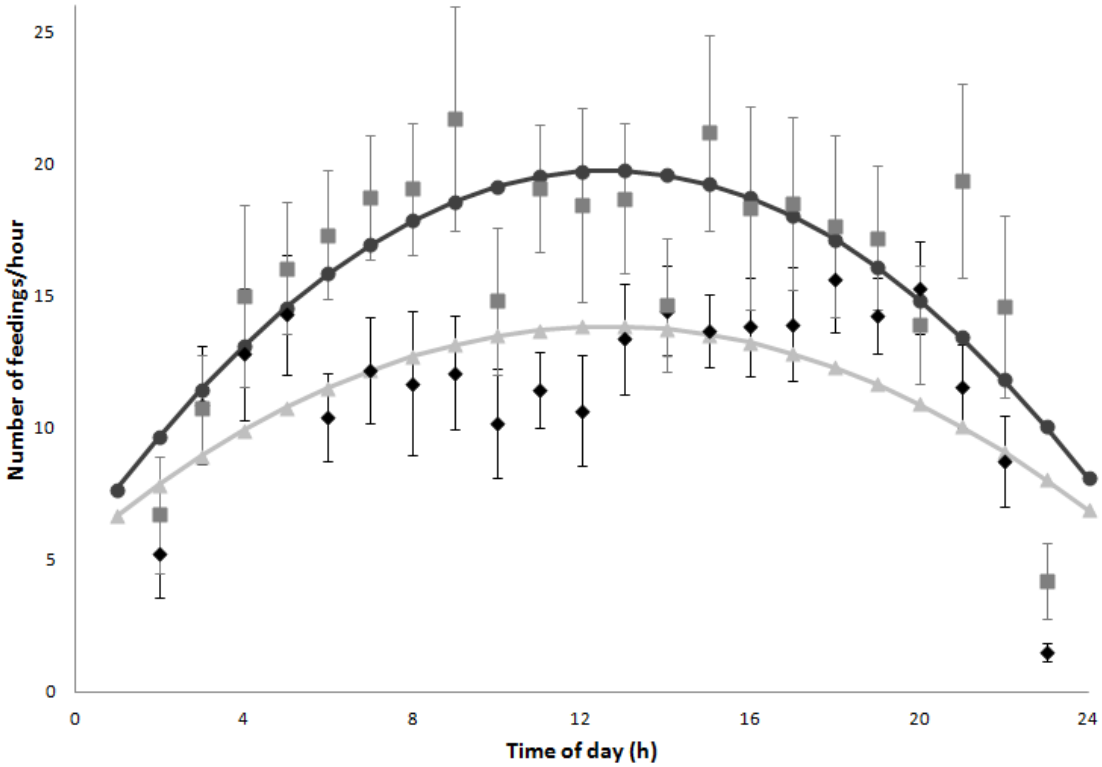

Figure 4: Graph showing parent feeding visits per hour when the chicks are young (black, SE-bars) and when they are older (medium grey, SE-bars). The regression lines show the estimated feeding visit effort throughout the day (young=light grey, older=dark grey). Sample size for young chicks is 12 and for older chicks it is 13.

Discussion

Males contributed to a higher proportion of the feedings when the chicks were young as compared to when the chicks were at their maximal growth stage. This is possibly because the chicks are almost naked when they are young and cannot retain the heat created within them or which is given to them, by the female, during the night (Mitrus *et al* 2010). Thus the female stays on the chicks to warm them in the first few days and this limits the time she can go out to find food for the chicks or herself. Both she and the chicks are then dependent on the male for survival. As the chicks grow bigger and feathers begin to cover their bodies the female can leave the nest more often and help with feeding the chicks. The male increases his feeding visits as the chicks grow older and though the male and the female have an equal share of feeding visits it seems that the female is doing more to feed the chicks. This slight reluctance in the male to increase the feeding visits may result from extra-pair young in the nest, or him trying to engage in EPCs at other locations. Another explanation is that the male engages in other forms of parental care. Instead of searching for food he may stand guard watching for predators or defending the territory from intruders. The differences in this study between males and females at different ages of the brood are not consistent with those by Tye (personal communication in Conder 1989 p. 213) who found that females spend more time foraging early in the nestling period than the males. In this case it is important to remember that time spent foraging is not necessarily the same as time spent feeding chicks. Brooke (1981) implies that the female is generally the parent feeding the chicks most, but does not state it clearly. The fact that my results differ from theirs is probably because I only noted feeding visits in the early and middle part of the nestling period and not later. It is quite possible that the male is the main provider only early in the nestling period and that the female provides more during a longer time, which would then result in the female providing more overall.

There was no difference in feeding visit rates between the male and the female depending on the size of the clutch. This result is surprising since more chicks need more food and more chicks also have a greater huddling-effect, thus the mother can and may have to leave the nest more often, even early in the nestling period (Walsh 1978, Grundel 1987). On the other hand, instead of increasing the number of feeding nest visits with increasing chick numbers the parents may increase the size of the loads they bring to the chicks. This increase in provisioning would not show in the analysis, as load size or type was not recorded from the videos. The lack of significance may result from the small sample size, high variation in feeding rates and the unbalanced design of the study. Most nests had five or six chicks, very few had three or four and only one had seven chicks. Sadly, the nest with seven chicks only had one left when the recordings ended. The other six were probably lost due to insufficient feeding; the male had the by far lowest rate of feeding visits when the chicks were young and the female was below average at that point.

The quality of the territory had little effect on the feeding visits of the parents, and I was not able show any difference between the sexes. Considering that the result of the study taken as a whole is that there is no difference between the sexes in their feeding visits this result is not strange. On the other hand, figure 3 indicates that there is a difference in how the parents respond to the aging of the chicks. When the quality of the

territory is high both parents increase their feeding visits greatly as the chicks grow older, but when the quality of the territory is low the male seems to decrease his efforts as the chicks age. Nests in a low quality territory have a greater chance of being predated and it is possible that the male devotes most of his time to vigilance and defending the nest. The relatively high number of male feeding visits when the chicks are young could be an artefact due to the difference in vegetation height between the hatching of eggs and when the chicks have grown to the age of 8 days. A territory classified as overall low quality may have the short preferred vegetation at the beginning of the breeding season making it possible for the male to feed the chicks at a high rate. It is important to note again that sample sizes are very small making it unadvisable to draw any actual conclusions.

The feeding visit rates varied over the day and increased with age. This is a very reasonable result since larger chicks need more food for maintenance and growth, which also explains the fact that the slope of the curve for the older chicks is steeper. The parents then have to increase feeding visits more in the morning and can decrease feeding visits more in the afternoon. Regardless of the age of the chicks the parents have some inactive hours during the night.

When I was watching the video recordings from the nests I noticed on several occasions that the female took food from the male and then ate it herself instead of giving it to the chicks. This is a reasonable behaviour as the female stays on the chicks much of the first days and is unable to feed herself sufficiently. However, this is contrary to the lack of courtship feeding observed by Conder (1989 p.114) who never saw courtship feeding on Skokholm. On the other hand, he rarely had the opportunity to see what happens in the nest and I did not see the female taking food from the male in all the nests. It should also be considered that it may not be a case of court-ship feeding when the female takes the food in the nest, because it is necessary for her and the chicks' survival and it is possible that the male had meant the food only for the chicks.

This was a small study and there are several factors possibly affecting parental care that were not taken into account. Studies have shown that the size of the food given to chicks varies negatively with visiting rate (García-Navas & Sanz 2010). If this is true for Northern Wheatears, the difference in provisioning between individuals is much smaller than the difference in feeding nest visit rates. Since the quality (prey identity, prey quality) and quantity (number, size) of the provided food was not considered it is impossible to fully evaluate the care given by each parent and if it varies with chick age, number and territory quality. Future studies on this species should try to look into the quality and quantity of the food provided by the male and the female. Also, for a more complete comparison between the sexes the whole period between hatching and chick independence should be included. Another factor that could have an effect on the parental effort is whether it is a first or second clutch or a retry after predation. Individuals that have already successfully fledged one brood or who have had their first nest predated have less resources to use for a new clutch; not only because of the energy already spent on the previous attempt, but also because it is later in the season when vegetation has grown higher and the availability of food is generally lower. Thus, the date of the observations should be considered (García-Navas & Sanz 2010), though this would be more complicated to include in a dataset spanning over several years with varying weather.

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Appendix

Figure 1a: Logger recorder and hard drive. Photo: Matthew Low

Figure 1b: Logger tube positioned in the entrance of a nest. Photo: Matthew Low

Figure 1c: Male feeding young nestlings. (From video)

Figure 1d: Female feeding young nestlings. (From video)

Figure 1e: Image showing six young chicks gaping for food, the male is in the foreground. (From video)

Figure 1f: A common situation early in the nestling period; the male comes into the nest with food while the female is on the nest warming the chicks. (From video)

Figure 1g: Six resting seven-days-old chicks. (from video)

Figure 1h: Seven-days-old chicks gaping for food. (from video)