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Activity patterns of parent Great Tits *Parus major* feeding their young during rainfall

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The influence of rainfall on the foraging patterns of Great Tit Parus major *parents while feeding chicks at the nest was investigated using automated nest monitoring with electronic balances and photography. Great Tit females significantly reduced their visit rate to the nest during all rain intensities, while male feeding frequency did not significantly change. The female response was probably due to increased brooding requirements of young since the reduction in visit rate was most apparent at early nestling stages. At this time the chicks are incapable of thermoregulation and females significantly increased their nestbox occupancy time during rain. There was no indication that parents were compensating for periods of female inactivity during rainfall: there was no significant increase in visit rate following rainfall and no significant increase in prey size delivered to the nest during periods of rain. An analysis of data from six consecutive years revealed that the proportion of wet hours within the first week of the nestling period significantly influenced fledging weight in this species.*

Weather conditions can affect birds in many varied and dramatic ways (Elkins 1983). Typically, weather-related studies have focused on those species (e.g. aerial feeders) dependent on prey whose abundance is to some extent determined by weather conditions (Bryant 1978, Alatalo & Lundberg 1989, Martins & Wright 1993). Other such studies have examined species whose foraging is hindered by the prevailing weather, e.g. seabirds that plunge from air to water and are exposed to complex interactions between weather and sea surface conditions (Tuck & Squires 1955, Langham 1968, Dunn 1975, Birkhead 1976). In addition to influencing food availability, weather may also directly affect the energetic expenditure of flight (through reduced manoeuvrability as, for example, feathers become water-logged) and the cost of thermoregulation in birds (Drent 1973, Tinbergen & Dietz 1994).

Little attention has focused on the effects of weather on nestling growth and mortality in Great Tits *Parus major*. The young of this species are protected from the direct effects of adverse weather because nests are in cavities and the chicks are not dependent on the products of aerial foraging (Betts 1955). However, the energetic demands of brood production may far exceed those of other species; Great Tits lay some of the largest clutches reported among altricial birds (mean ± sd for Wytham Wood, Oxfordshire 1965–98: 8.81 ± 1.68). Food supply has been shown to limit directly and indirectly both clutch size and fledgling survival of Great Tits (Drent & Daan 1980, Garnett 1981, Minot 1981, Perrins & McCleery 1989, Perrins 1990). Any conditions which affect the availability of food, the energetic demands of growth in the chicks or adult foraging are

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likely, therefore, to affect reproductive success in these birds.

With rare exceptions, foraging studies of passerines have avoided collecting data during poor weather. Consequently, little is known about the effects of adverse weather conditions on the feeding patterns of breeding and non-breeding birds. Anecdotal evidence suggests that birds reduce feeding during rain, and that feeding declines as rainfall becomes heavier (Kluijver 1950, Perrins 1979, O'Connor 1984). Although some quantitative studies have examined the effects of rainfall on provisioning rates (Keller & van Noordwijk 1994), they have been on a daily scale. In our study, however, visit rate data for Great Tits and weather information were collected on an hourly basis. Automated nest monitoring was performed using electronic balances and cameras. Weather data were provided by an automatic weather station. In addition, sex differences in feeding behaviour during the nestling period and changes in the size of prey brought to the nest during periods of rain were investigated. Environmental influences during ontogeny may have lasting effects on the phenotype, including the fledging weight, of many small passerines. Fledging weights, in turn, play a crucial role in the subsequent survival chances of many species, including Great Tits (Tinbergen & Boerlijst 1990). The impact of wet weather on fledging weights was, therefore, investigated using data from the long-term study by the Edward Grey Institute of Field Ornithology, University of Oxford, UK.

METHODS

Data collection

Data on visit rates, nestbox occupancy times and prey sizes were collected during 1993–95 at Wytham Wood, Oxfordshire. Twenty-nine nestboxes were erected on mature trees in the study area. These nestboxes allowed for the attachment of a 'monitoring' box (Woodburn 1997) (containing a Super-8 mm cine-camera and an electronic balance) once signs of nest occupancy were apparent. Draughts and rain water were excluded from the nestboxes using waterproof tape. Electronic balances (Mettler BB2400, Mettler-Teledo AG, Greifensee, Switzerland) were connected to an IBM-compatible computer via data cabling.[a]

Two modules of developmental stage software ('Nestbug') were provided for data acquisition and preliminary processing (Eotvos University, Budapest, Hungary). The first module (Data Acquisition Module, versions 2.5 and 3.0c) was used to record the weight data from each active balance. A subset of data, based on event recognition (a sudden reduction or increase in nest weight equivalent to the departure or arrival of a parent bird), was recorded. The second module (Visit Analyser Module, version 0.5) condensed raw data into a table, each line of which summarized data from one series. Information included the type and time of event, the number of weighing results and the mean weight of the nest.

As chicks mature they become increasingly active, often jumping up to the nestbox hole to remove food items from their parents and exercising their wings. This can cause erroneous weighing results, so data after day 16 (day 1 = hatching, days 18–21 = fledging) were not used in the analysis.

Nestling Great Tits are fed large prey items, which are carried to the nest in the parent's bill. A modified camera system, based on that designed by Royama (1959, 1970), was used to automatically photograph the head and contents of the bill of a bird returning to feed its chicks.[b]

Weather conditions have been monitored on an hourly basis by an Environmental Change Network automatic weather station (Sykes & Lane 1996) at an open site within Wytham Woods since 1992. The weather station is approximately 500 m from the monitored nestboxes and both site and equipment have been fully described elsewhere (Morecroft *et al*. 1998). Rainfall was recorded as hourly totals to the nearest 0.2 mm. Any hour in which 0.2 mm or more rainfall was recorded was classified as a 'wet' hour. Hours when more than 1 mm of rain fell were classified as incidences of 'heavy' rainfall (after Keller & van Noordwijk 1994).

Data analysis

Balance data were collected from seven nests. To calculate the number of visits made to each nest per hour, a program module (Woodburn 1997) was written in FORTRAN. The program calculated the time of the first and the last visit to the nest, the total number of visits and the number of visits per hour.

Photographs from five of the same nests were examined under a binocular microscope in order to determine the time of visit, the sex of the provisioning parent and the number and size of prey items brought to the nest. Data were recorded for each visit, during days 4 to 16 of the nestling period. Each prey item was assigned a 'provisioning score' of 1 (smallest) to 12 (largest) based on length and width determined from the linear scale. The amount of time spent in the nestbox during each visit was also recorded, for hours before and during rainfall.

All statistical analyses were performed using MINITAB version 12 (Minitab Inc. 1998). Only periods of rain following at least four hours with no recorded rainfall were considered in the analyses. Multiple rain events were considered for each of seven nests. A general linear model was performed on each data set to ensure that birds at different nests were responding in a similar way to rainfall events. Chi-squared tests were used to ensure that the data points were evenly sampled across nests and within the nestling period. Matched comparisons of visit rates, for the same individuals in consecutive hours, were made and one-sample *t*-tests used, wherever possible. A general linear model for six years of data tested for the effect of the proportion of wet hours during days 1–7 of the nestling period on the average fledging weight per nest. Only hours in the day when the adults were actively foraging were considered and year and brood size were included as predictors in the model. The proportion of wet hours was arcsine square-root transformed before inclusion in the model.

RESULTS

Visit rate during rainfall

Separate rain events involving the same nest were treated as independent (see sample sizes in Table 1), since analyses correcting for nest produced similar results to those shown in Table 1. As the effect of nest was not significant in any of the data sets (*F*-range: 0.20–1.23, *P*-values all > 0.10) it was removed from all models. All adult birds responded in consistently the same way (Table 2).

Great Tits significantly decreased their visit rate to the nest during wet hours (Table 1). During heavy rainfall the reduction in visit rate was more significant than when all wet hours were considered (Table 1). For subsequent analyses, data collected during all wet hours (mean rainfall: 0.44 ± 0.05 mm, n = 57) are presented.

Photographs revealed that the reduction in visit rate shown by Great Tit parents during rain is explained by the female (Table 1). This result is not a consequence of an uneven sampling method (χ^2 = 3.647, df = 4, P = 0.465). Females significantly increased their nestbox occupancy time during rainfall, compared with the preceding dry period (one-sample *t*-test, t_{30} = 4.67, P < 0.001; Fig. 1). Males did not significantly alter either their visit rate to the nest (Table 1) or their nestbox occupancy time

Table 1. Mean number (±se) of visits by seven pairs of Great Tits to the nestbox in an hour before and in an hour during rainfall in the nestling period.

Visit rate (h^{-1})	*n*	Before rain	During rain	Difference	*t*	*P*
Parents in all wet hours	57	18.09 ± 1.22	16.33 ± 1.34	1.75 ± 0.85	2.08	0.04
Parents in all hours of heavy rainfall	26	17.62 ± 1.69	13.27 ± 1.31	4.35 ± 1.26	3.45	0.002
Males in all wet hours	30	11.83 ± 0.88	12.03 ± 1.00	–0.20 ± 0.94	–0.21	ns
Females in all wet hours	30	8.80 ± 0.88	7.33 ± 0.90	1.47 ± 0.57	3.09	0.016
Parents during days 1–7 of nestling period	29	13.79 ± 1.60	11.00 ± 1.25	2.83 ± 0.92	3.09	0.005
Parents during days 10–16 of nestling period	25	23.12 ± 1.57	22.44 ± 2.12	0.68 ± 1.62	0.42	ns

One-sample matched pair *t*-tests were carried out on the difference in visit rate for the same individuals before and during rainfall.

Table 2. Difference in visit rate (mean ± se) between hour before rain and hour during rain for each nest (A–G) separately.

Nest	Parents in all wet hours	Parents in heavy rainfall hours	Females in all wet hours	Parents during days 1–7 of nestling period
A	0.80 ± 1.40	2.00 ± 4.08	–	1.40 ± 2.69
B	0.50 ± 1.99	5.17 ± 3.34	1.88 ± 1.19	2.33 ± 1.09
C	1.83 ± 1.94	0.25 ± 1.44	–	0.60 ± 1.83
D	1.83 ± 1.56	4.80 ± 2.13	2.00 ± 0.89	0.00 ± 1.29
E	3.56 ± 2.54	8.00 ± 3.22	1.20 ± 1.24	5.20 ± 2.42
F	1.83 ± 3.74	7.00 ± 2.56	0.50 ± 1.93	3.00 ± 1.62
G	5.50 ± 2.33	2.00 ± 3.11	1.67 ± 1.12	9.67 ± 3.18
P	0.022	0.022	0.059	0.036

–, Missing value. *P*-values are from Wilcoxon signed rank tests.

(one-sample t-test, t_{30} = 0.11, P = 0.914; Fig. 1) during rainfall.

A significant decrease in the number of visits made to the nest by Great Tits was found during periods of rain in the first seven days of the nestling period (Table 1), but not during days 10–16 (Table 1). Again, these results are not the result of an unmatched sampling of nests (χ^2 = 5.959, df = 6, P = 0.428).

Compensatory behaviour

No significant change in size of prey delivered to the nest during rainfall was found for either sex (one-sample t-test, female: t_{21} = –0.75, P = 0.44; male: t_{21} = 0.45, P = 0.66).

No significant increase was found in visit rate following a period of rain; the final hour of rain was compared with the first dry hour following rainfall (hour during rain: mean 16.83 ± 1.40; hour after rain: mean 16.11 ± 1.46; one-sample t-test, t_{56} = 0.61, P = 0.54). There was also no significant increase found when rain events from only the first seven days of the nestling period were considered (during rain: mean 13.31 ± 1.82; after rain: mean 14.07 ± 1.65; one-sample t-test, t_{27} = –0.18, P = 0.86).

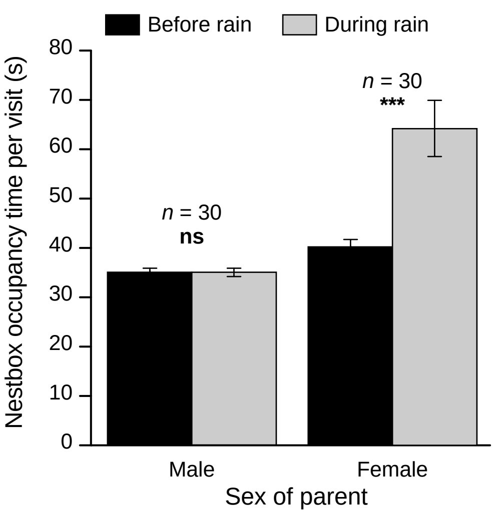

Figure 1. Mean nestbox occupancy time per visit (± 1 se) of five male and female Great Tits before and during rainfall in the nestling period (one-sample t-test: ns, non-significant; ***P < 0.001).

Consequence of rain

After correcting for both year and brood size effects, there was a significant negative influence of the proportion of wet hours during days 1–7 of the nestling period on average fledging weight (Table 3). In other words, differences in rainfall within a season have a significant effect on fledging weight.

There was a highly significant negative correlation between air temperature and rainfall during the hours of provisioning (r_{1549} = –0.170, P < 0.001). However, there was no significant change in ambient temperature when rain started (hour before rain: mean 12.02 ± 0.42; hour during rain: mean 11.82 ± 0.38; one-sample t-test, t_{56} = 1.66, P = 0.10).

DISCUSSION

The significant reduction in visit rate to the nest shown by Great Tit adults at all rainfall

Table 3. Results of ANOVA testing for an effect of the proportion of wet hours in the first week of the nestling period on fledging weight.

Source	df	Adjusted SS	Adjusted MS	*F*	*P*
Brood size	12	5328.9	444.1	2.23	0.009
Wet hours	1	804.4	809.4	4.06	0.044
Year	5	12206.9	2441.4	12.26	0.000
Error	1531	304923.6	199.2		
Total	1549				

intensities is caused by females alone, rather than by a behavioural response of both sexes. This implies that the decrease is due neither to a direct energetic effect on the parent birds nor to an indirect influence on food availability or ease of prey capture. It is important to note that, although the total number of nests studied was small, the consistent behaviour patterns found indicate a real effect. The reduction in visit rate by females during rain may be a consequence of an increased brooding requirement of the young, to compensate for increased thermoregulatory demands. By nesting in holes, Great Tit broods are largely freed from the direct influences of weather, since by their location they are thermally buffered from changes in ambient temperature and they are sheltered from wind and rain. Any moisture unintentionally brought into the nest by parents during times of rain will, however, increase evaporative heat loss by the young. Although there is a strong negative correlation between air temperature and rainfall, there is no significant drop in ambient temperature when rainfall starts. It is not unreasonable to assume, therefore, that rainfall has a significant influence on the feeding rate of young in this species. Chicks require more brooding during wet periods than during dry periods, resulting in females sacrificing foraging time (Drent 1973).

Female Great Tits spend longer in the nestbox during rainfall, compared to the preceding dry period. A decrease in visit rate during rain is only found early in the nestling period. At hatching, chicks of altricial species do not respond metabolically to cold ambient temperatures and are unable to maintain their body temperature above that of their surroundings (King & Farner 1961). In all species, the level of thermoregulation increases during the development period, and Great Tit chicks are believed to self-thermoregulate from day 8 (Perrins 1979). Consequently, young chicks are more dependent than older offspring on parental brooding.

Both duration and quantity of rainfall are likely to affect growth of nestlings. However, our study does not allow us to ascertain when the rain stopped in any given hour; the recorded amount could have been the result of a short, heavy shower or prolonged, light rain. Hourly rainfall data tell us nothing about rainfall intensity at any given time and we do not know if adults can fine-tune their foraging behaviour to changes in rainfall intensity. The significant reduction in visit rate found may, therefore, be a conservative estimate of the actual effect. If a period of rainfall could be matched to a period of equivalent duration of dry weather, a much stronger comparison could be made. In this way, we may be able to understand how foraging patterns are affected by rain and how parents trade off self-maintenance requirements with those of thermoregulating their chicks.

Kluijver (1950) reported that adult Great Tits in Holland, which had taken shelter during a rain shower, accelerated their feeding rate in the period immediately following rain. However, no such compensatory increase was found in our study. It is possible that compensation might be delayed until the vegetation has dried out; foliage would still be wet immediately following rain, causing birds similar problems to those experienced during actual rainfall. Any resulting compensation spread over a period of time would be difficult to detect. There was also no significant increase in prey size delivered to the nest during wet hours, so the reduction in visit rate found in this study does appear to represent a decrease in provisioning quantity to the chicks.

Any decrease in food delivery rate by parents to chicks might be expected to have some long-term consequences on fledging weight (Naef-Daenzer & Keller 1999) and ultimately survival of offspring. Indeed, we found that the proportion of wet hours during the first week of the nestling period had a significant negative influence on fledging weight. Our study demonstrates, therefore, that weather conditions as well as food availability are crucial to breeding success in the Great Tit.

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ENDNOTES

a. Electronic balances received instructions from the computer and transferred weighing results at a rate of one reading per second in 1993 and six to eight readings per second in 1994–95. Even with cables of 200 m in length, this system resulted in the collection of no artefactual data and no data were lost. The computer monitored up to four electronic balances at any one time with a serial interface (RS-232C) expansion card. Balances were switched on from the time of placement in the nestbox.

b. Photographs within the nest were obtained from super-8 mm cine-cameras set to single frame advance with electronic flash synchronization. The cameras were not switched on until three days after hatching. This minimized disturbance in the first few days of the nestling period, when chicks are most vulnerable to chilling if they are not brooded by the female. A metal plate at the back of the nestbox was replaced with the camera, which took unobstructed photographs of the entrance hole. The circuit was closed by a micro-switch at the entrance hole. The wire of the switch was positioned to ensure that the camera was triggered as soon as a bird entered or left the nestbox. An analogue watch and linear scale were placed next to the entrance hole, on the inside of the nestbox, to record the time and to enable an estimation of prey size from each photograph.

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