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## **To graze or gorge: consistency and flexibility of individual foraging tactics in tits**

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### **Running headline:**

Consistency & flexibility of individual foraging

### **Summary**

1. An individual's foraging behaviour and time allocated to feeding have direct consequences for its fitness. Despite much research on population-level foraging decisions, few studies have investigated individual differences in fine-scale daily foraging patterns amongst wild animals.

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- Accepted Article
2. Here, we explore the consistency and plasticity of feeding tactics of individual great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*), using a grid of 65 automated feeding stations in a 385-ha woodland, during three winters. We use a principal component analysis to describe individual variation in six feeding parameters and examine how these differences covary with dominance-linked attributes (species, age and sex), the personality trait ‘exploration behaviour’, distance to territory, and local competition intensity.
  3. Analysis of 933,086 feeder visits by 3,134 individuals revealed that the majority of variation in the timing of feeding was explained by two principal components. PC1 (‘binge-eating’), accounting for 38% of variation, captured temporal clustering of feeding, with high repeatability both within and between years ( $r$  range: 0.42 to 0.55). PC2 (‘transience’), accounting for 27% of variance, described how much individuals used feeders and was also repeatable ( $r$ : 0.34 to 0.62). While exhibiting consistent individual differences, birds also showed flexibility in foraging patterns, binge-eating less and using feeders more when they experienced greater local competition.
  4. Individuals in behaviourally dominant states (great tits, males and adults) binged more than subordinate birds (blue tits, females and juveniles) when their territories were distant from feeding stations. Moreover, great tits and males used feeders more than blue tits and females respectively, while birds feeding further from their territory used feeders less than those feeding closer. ‘Exploration behaviour’ was unrelated to both measures of daily foraging behaviour.

5. This study presents some of the first evidence that birds use consistent alternative foraging tactics at a fine temporal scale. Individuals are consistent in their tactics, but also adjust their foraging behaviour with changes in local competition. Hence, studies of foraging behaviour should consider the extent to which such individual-level variability in foraging behaviour is under selection.

**Key-words:** competition, consistent differences, daily routine, diel activity, Paridae, PCA, principal component analysis, repeatability

## Introduction

Traditionally, studies of animal behaviour assumed that all individuals should be fully plastic and dynamically adjust their behaviour to suit each situation (Parker & Stuart 1976; Stephens & Krebs 1986; Piersma & Drent 2003). Individual variation was therefore often considered to reflect stochastic noise around a behavioural optimum (Wilson 1998). However, more recent work on animal personality suggests that individuals may be constrained in terms of behavioural flexibility, behave more consistently and may follow particular behavioural strategies (reviewed in Sih, Bell & Johnson 2004 and Bell, Hankison & Laskowski 2009), in some cases due to morphological or physiological constraints (for example Castellano *et al.* 2002). Consistent individual differences have now been found in a diverse range of behaviours and taxa, including cooperation in meerkats *Suricata suricatta* (English, Nakagawa & Clutton-Brock 2010), search behaviour in northern gannets *Morus bassanus* (Patrick *et al.* 2014), sleep behaviour in blue tits *Cyanistes caeruleus* (Steinmeyer, Mueller & Kempenaers 2013), and foraging ability in scorpionflies *Panorpa vulgaris* (Missoweit, Engels & Sauer 2007). Consistent differences in behaviour can be adaptive across different contexts or when fluctuating environmental conditions lead to the fitness of different

behavioural strategies being equal in the long-term (Wilson 1998; reviewed in Dingemanse & Réale 2005 and Smith & Blumstein 2008).

Foraging behaviour and the time animals allocate to foraging have direct consequences for survival and reproductive success (Stephens, Brown & Ydenberg 2007). Variation in how individuals allocate their time to feeding throughout the day is likely to exist both between and within individuals, due to differences in individual state and the environment over time (Houston & McNamara 1982). These temporal patterns can reflect a trade-off between the risk of starvation (Bednekoff & Krebs 1995) and the risk of predation (MacLeod, Gosler & Cresswell 2005), as predicted by theoretical models (Houston & McNamara 1993; Houston, McNamara & Hutchinson 1993; McNamara, Houston & Lima 1994; McNamara *et al.* 2005; Brodin 2007). In general, optimal foraging models that account for the predation-starvation risk trade-off usually predict a bimodal daily pattern of feeding, under the assumption that foraging increases the risk of predation; this pattern includes a morning peak of feeding which can restore energy reserves that were used overnight, followed by a lull in feeding to minimize predation risk, and then by a second peak of feeding in the evening to increase energy reserve levels to fuel the following night (Houston, McNamara & Hutchinson 1993). However, in winter some small birds, with high energetic demands, have been recorded feeding at a high rate throughout the day (Bonter *et al.* 2013).

Competition for limited resources is also likely to affect how individuals forage. To reduce competition, individuals can partition resources by segregating by habitat, diet, or time (Schoener 1974), often with subordinate classes (e.g. juveniles) being forced to use suboptimal foraging tactics. For example, brown trout *Salmo trutta* of different social rank fed synchronously at night until energetic requirements increased above a certain level, when

subordinate trout then shifted to feed more diurnally (associated with greater risk of predation) causing temporal segregation (Alanärä, Burns & Metcalfe 2001).

Existing theoretical predictions and empirical assessment of temporal patterns of foraging typically focus on average patterns of behaviour in a population, with examples of bimodal (Dall & Witter 1998; Polo & Bautista 2006) and unimodal (Olsson, Wiktander & Nilsson 2000; Bonter *et al.* 2013) daily foraging routines observed. These studies draw conclusions about the general daily pattern of feeding, often based on results described at an hourly timescale, but may therefore overlook patterns at a finer temporal scale. It can be important to quantify these small-scale differences, as factors acting at different timescales can interact with one another, explaining feeding patterns that initially appear maladaptive. For example, eiders (*Somateria mollissima*) have been shown to maximize their daily energetic gain by resting during the times when the short-term rate of energy intake is greatest, due to a combination of digestive and tidal constraints (Heath, Gilchrist & Ydenberg 2010). Few studies have investigated temporal foraging patterns at the individual level, so the extent to which individuals feed at different times remains poorly understood. In addition, most empirical work on the timing of feeding in birds has been conducted in captivity (Dall & Witter 1998; Polo & Bautista 2006), while field studies have generally focused on monitoring temporal patterns in mass gain due to the difficulty in making continuous observations of marked individuals (MacLeod, Gosler & Cresswell 2005; Ratikainen & Wright 2013).

More recently, the development of radio frequency identification (RFID) technology for the automated detection of uniquely identified animals at fixed sites has enabled detailed monitoring of feeding behaviour at a larger scale than was previously possible in the wild (Bonter & Bridge 2011). This automated data collection was used to model hourly patterns of

visits to feeders in four species of passerine bird (Bonter *et al.* 2013). The study demonstrated largely constant feeding rates throughout the day in these species. However, these data were not analysed at the individual level, and therefore it is not known whether all individuals follow the same foraging tactic. Furthermore, it was not possible to test whether individual attributes (such as age or sex) or differences in environmental conditions (such as competition or resource distribution) influenced temporal feeding patterns. A study on great tits (*Parus major*) that also used RFID technology, suggests that individuals may indeed have alternative foraging tactics in terms of how they manage the trade-off between starvation and predation risk throughout the day (Quinn *et al.* 2012). The study showed that ‘exploration behaviour’, a commonly used measure of proactive-reactive personality axis, and social dominance category (age and sex) affected how individuals prioritized productivity or survival at feeders where food quality and perceived predation risk were manipulated. However, only one feeding metric was measured in this study and was averaged over half-day time periods, meaning that additional variation in foraging behaviour occurring over a small temporal scale may have been overlooked.

This study aimed to quantify individual variation in daily foraging routines of a wild population of great tits and blue tits (*Cyanistes caeruleus*) and to characterize patterns in the fine-scale timing of feeding. In the UK, these species are resident throughout the winter, form mixed-species flocks that will readily visit artificial feeders once natural food becomes scarce, and do not cache food (Perrins 1979). In mixed-species tit groups, there are a number of individual attributes and extrinsic factors that are likely to influence feeding routines. Social dominance status (usually higher in great tits, males and adults compared to blue tits, females and yearlings) can constrain access to food (Gosler & Carruthers 1999; De Laet 1984) and therefore the time spent monopolizing food sources (Cole & Quinn 2012).

Furthermore, in great tits, the reactive-proactive personality axis has been shown to relate to how individuals manage the trade-off between survival and productivity, with proactive birds feeding more than reactive individuals when predation risk is high (Quinn *et al.* 2012).

Another factor likely to influence feeding behaviour is the trade-off between time spent traveling to reach a food source and time spent feeding. In the UK, tits have established their territories by January (Kluijver 1951; Perrins 1979) and will roost in these territories throughout the winter (Hinde 1952). Winter food sources such as beechmast are often highly clumped; therefore birds are likely to vary in their daily travel time and subsequently in the time available to consume the food they require.

Here we used automated RFID data loggers at artificial feeders to monitor visits by blue tits and great tits that had been individually tagged with passive integrated transponder (PIT) tags. We used these individual-based feeder visit data to describe daily feeding routines and report findings on the consistency and flexibility of behaviour at a fine temporal scale during midwinter over three consecutive years. Moreover, we explored how foraging patterns varied both between and within individuals. We demonstrated consistent individual differences in how tightly birds clustered their feeder visits within a day and also in how much they used feeders each day. We then tested whether these individual differences could be predicted by the level of local competition experienced by a bird, various individual attributes (age, sex, species and, 'exploration behaviour'), and the distance between its territory and the feeder.

## **Materials and methods**

### **Study population**

The fieldwork for this study was carried out between September 2011 and March 2014 in 385-ha Wytham Woods (51°46'N, 1°20'W), a mixed woodland near Oxford, UK (Savill *et al.* 2010). This study took place in the context of an ongoing long-term population study of tits

(McCleery *et al.* 2004). We identified breeding adults and their offspring at nest boxes during the spring and caught immigrants to the population and birds not trapped while breeding with mist-nets during autumn and winter. We fitted un-ringed individuals with a unique metal British Trust for Ornithology (BTO) ring and a plastic ring containing a unique passive integrated transponder (PIT) tag (IB Technology, Aylesbury, UK). We also recorded biometric data, including age and sex. Age (born in the previous breeding season or before) was determined based on plumage or by year of birth for birds ringed as nestlings; birds in their first year are termed juveniles and older birds adults. The sex of adults was determined by the presence or absence of a brood patch during the breeding season and by plumage during the non-breeding season (Svensson 1992).

The majority of the Wytham population of great tits (GTs) and blue tits (BTs) were PIT-tagged prior to winter feeder data collection. Of birds caught in mist-nets at logger sites between early November and late January over the study period, 71% of GTs and 61% of BTs were already tagged; this method of capture is likely to be biased towards naïve (previously uncaught) individuals since some individuals with prior experience can learn to avoid mist-nets. Of adult birds trapped at nest boxes in the subsequent breeding seasons, 79% of GTs and 69% of BTs were previously tagged. Video data recorded at four of the 65 feeding stations used in this study showed that  $83 \pm 9.4$  % of GT visits and  $70 \pm 9.1$  % of BT visits (mean  $\pm$  1 SD) were by tagged birds.

Exploration behaviour in a novel environment, a proxy for the reactive-proactive personality axis, was assayed in a subset of GTs, using an open-field exploration behaviour test in captivity between 2006 and 2014. GTs were caught using mist-nets during winter and taken, under licence from Natural England, to the John Krebs Field Station, Oxford, UK. Birds were housed individually overnight and then underwent exploration behaviour assays lasting 8



minutes. All birds were released where they were caught within 24 hours of capture. Details of the exploration behaviour assay and how exploration scores were calculated are explained in detail elsewhere (Quinn *et al.* 2009). Exploration behaviour in our population is moderately repeatable both within and across years ( $r$  ranging between 0.30-0.39; Dingemanse *et al.* 2012), and does not change with age (Quinn *et al.* 2009). This personality trait has been shown to predict a range of functional foraging-related behaviours in the wild including the ability to monopolise feeders (Cole & Quinn 2011), how individuals manage the starvation-predation risk trade-off (Quinn *et al.* 2012), social behaviour at feeders (Aplin *et al.* 2013), and the extent to which individuals are attracted towards the centre or periphery of foraging flocks (Aplin *et al.* 2014); as such it can be predicted that exploration behaviour may influence an individual's finer-scale foraging tactics.

### **Automated data logging**

We set up 65 feeding stations across Wytham Woods, in a square grid formation with sides of approximately 250m. To exclude squirrels and large birds, each feeding station was housed in a 1m<sup>3</sup> heavy duty mesh cage on 1m legs. Mesh spacing was 5cm. Each feeding station contained a two-hole feeder to dispense whole black sunflower seeds *ad libitum*, with an RFID antenna in front of each feeder hole that was connected to an automated data logger (Dorset ID, Aalten, The Netherlands). The feeders had an automated opening mechanism so that they could be scheduled to open at specific times. When the feeder was open, the two antennae independently scanned for PIT-tags three times per second for the duration of the recording session. When a PIT-tagged bird perched on an antenna to retrieve a seed, the data logger recorded the unique PIT-tag code, antenna number, date, time, and feeder location. This study was part of a larger project where the feeding stations were scheduled to open pre-

dawn and close post-dusk each Saturday and Sunday between September and February inclusive (except those dates prior to December in the first winter when feeding stations opened one day per week for logistical reasons). To reduce the effect of changes in day length, for this study we only used the data collected over five consecutive weekends in December and January, centred around the winter solstice (i.e. 21<sup>st</sup> or 22<sup>nd</sup> December).

### **Defining visits and bouts**

We collected 3,980,339 raw data records from the feeding stations across the study period. These records excluded a subset of date  $\times$  site combinations (indicated in Table S1 as N/A) that were involved in other experimental studies in which the data collection protocol varied from that described above, or that were incomplete due to technical issues. Records of both species were logged at all sites, but not necessarily on all dates (see supplementary table S1). Bird densities varied across feeding sites and some sites were consistently busier than others (see supplementary table S1), which was also apparent from catching rates during mist-netting and the amount of seed taken from feeding stations (data not shown).

Since the data loggers recorded up to three records per second and individuals would often perch on a feeder's antenna for more than 1/3 second, we used the distribution of inter-record intervals to set the criteria by which we allocated records to separate feeder visits. We calculated inter-record intervals per individual GT and BT, which in combination formed a bimodal distribution (Fig. S1a). The large peak of intervals occurring below two seconds was attributed to multiple consecutive records when a bird remained perched on an antenna; the broader peak of intervals, around 60 seconds, was ascribed to the time necessary for a bird to take a seed from the feeder to a nearby perch, open and consume the seed, and return for another seed. We calculated the minimum point of the bimodal distribution between the two

peaks (17 seconds) to use as a threshold value in allocating raw data records to feeder visits.

Thus we defined all records of an individual bird within 17 seconds of another record of that same individual to be part of the same visit. The visit time was then calculated as the midpoint between the first and last record of that visit. The resulting inter-visit intervals also followed a bimodal distribution (Fig. S1b), with a large peak around 1 minute and a much flatter peak around 15 minutes. Observations of birds at feeders suggest that birds cluster feeder visits into feeding bouts. We therefore attribute the first peak to within-bout intervals and the second peak to inter-bout intervals. The minimum point between these peaks occurred at 514 seconds and this threshold value was used to allocate feeder visits to feeding bouts.

Individuals used on average 2.4 different feeding stations within a winter season. 20.8% of individuals visited more than one feeder within a single day, and the tendency to move between feeders within days was significantly repeatable within individuals ( $r=0.31$ ). Furthermore, juveniles and individuals with subsequent breeding territories further from feeders were more likely to visit multiple feeders on the same day. Since we used site as a random effect in analysis and because the principal component scores of foraging behaviour were based on daily measures, we excluded visits for individuals for the dates on which they moved between feeding stations within the same day from our analyses. This affected 21% of recorded visits and resulted in 3% of individuals being entirely excluded from analyses. We tested whether excluding these individuals biased the results by assigning within-day movers to the site where they spent the majority of their time and then rerunning analyses on all individuals; but this has no impact on the reported effect sizes (data not shown). Visits made by within-day movers were included in the measure of daily feeder traffic (local competition). Since inter-bout interval was used as a parameter in the principal component

analysis (PCA) described below, we excluded visits for the dates on which individuals only visited a feeding station in one bout. This resulted in 0.5% of visits being excluded and dropping 6% of individuals from further analyses; these visits also contributed to the daily measure of feeder traffic.

### Statistical analysis

We conducted all statistical analyses using R 3.1.1 (R Development Core Team 2014). To describe the daily patterning of feeder visits in a PCA, we extracted six parameters for each individual for each recording date: time (GMT) of first visit, time (GMT) of last visit, number of feeding bouts, mean length of bouts, mean inter-bout interval, and mean number of visits per bout. Bout lengths were calculated as the sum of the inter-visit intervals of the constituent visits plus 513s; the addition of 513s prevented one-visit bouts from having zero length, without causing consecutive bouts to overlap in time. High values of PC1 were characterized by highly clustered visits: more visits per feeding bout, fewer bouts, longer bouts, and longer inter-bout intervals; low values of PC1 indicate more spread out feeding patterns: more feeding bouts that are shorter, with smaller intervals and fewer visits per bout (Fig. 1). This axis therefore captures the extent to which individuals ‘binge-eat’ (high PC1) or ‘graze’ (low PC1). The timing of visits by an example binge-eater and an example grazer are illustrated in Fig. 2. In contrast, birds with high PC2 values arrived at feeders later in the day, stopped feeding at them earlier in the day, had fewer feeding bouts, shorter bouts, and fewer visits per bout. Low values of PC2 indicate that birds had many feeding bouts and visits spread over a longer day of feeder visits. PC2 therefore measures an individual’s ‘transience’ at a feeding site, which was negatively correlated with the daily number of feeder visits by individuals (GTs: Pearson’s  $r=-0.80$ ,  $df=11349$ ,  $p<0.001$  and BTs: Pearson’s  $r=-0.88$ ,  $df=12992$ ,  $p<0.001$ ; Figs S2c & S2d).

In order to test for consistent individual differences in the timing of feeding, we estimated the repeatability of binge-eating and transience per individual. We used a generalized linear mixed-effect model (GLMM)-based method to calculate repeatability (Dingemanse & Dochtermann 2013) per species-year combination: individual ID was fitted as a random effect with PC1 as the dependent variable; the variance attributed to individuals was taken as a proportion of the total recorded variance. After calculating the individual-level repeatability of PC1 for each species within each winter, we then fitted an additional GLMM for each species, to estimate the individual repeatability of PC1 between years. These models had the individual intercept values (individual yearly averages of PC1) from the within-winter models as the dependent variable and individual ID as a random effect. We estimated repeatabilities for PC2 in the same way as for PC1.

To determine the effect of species, age, sex, distance to territory, personality and competition on PC1, we fitted GLMMs, with individual identity, feeder location, and recording date as random effects. We used the Kenward-Roger approximation to calculate the approximate degrees of freedom, and along with the t-distribution, calculated p-values for each fixed effect (Kenward & Roger 1997). We define distance to territory (DTT) as the distance between the feeding station and the location of the nestbox used in the subsequent spring breeding season. Birds that did not breed within our population in the following spring were excluded from the analysis (N=1468, 38% of recorded individuals of known age and sex). To normalize the distribution, we took the logarithm of distance to territory. We used feeder traffic, defined as the total number of visits by other tagged birds (GTs and BTs) at a feeding station in one day, as a daily measure of competition experienced by each individual. We added two fixed effects of competition to the GLMMs: the mean competition (MC) level experienced by each individual within a winter season, and the deviation from the mean

competition (DC) experienced by each individual for each date that it was recorded. This partitioned competition into between- and within-individual components, allowing us to test the plasticity of individuals' PC1 with changes in local competition DC. We also modelled a random effect on the slope of DC per individual, so that different responses to changing competition could be accounted for. Otherwise the model would assume that all individuals respond with the same pattern of behavioural change relative to the change in competition level experienced. To test how age and sex affected PC1 at different distances to territory, we added interaction terms for age  $\times$  DTT and sex  $\times$  DTT. Since significant covariate interaction terms do not immediately imply that factors have an effect over the whole range of the continuous variable (Engqvist 2005), we used the Johnson-Neyman procedure (Johnson & Neyman 1936; Huitema 1980) to determine regions of significance to estimate the threshold distance to territory above or below which age or sex had a significant effect on PC1. We fitted a second set of GLMMs in the same way to determine how species, age, sex, distance to territory, personality and competition relate to the transience of individuals at feeders.

## **Results**

### **Characterizing foraging behaviour**

We analysed a total of 933,086 feeder visits in 270,978 bouts by 1,406 individual great tits and 1,728 blue tits across 65 feeding stations during five consecutive weekends in the winters of 2011-2012, 2012-2013, and 2013-2014 (Table S2). The mean daily number  $\pm$  1 SD of visits per individual was  $34 \pm 15$  and of bouts per individual was  $10 \pm 4$ . Assuming that each feeder visit results in one seed being consumed, and using the caloric intake of tits reported by Gibb (1954), the individuals in this study were gaining approximately 75% of their daily energy expenditure from feeders (Milligan 2015).

The PCA on 6 daily feeding pattern parameters revealed that variation loaded heavily on two components: PC1 (hereafter binge-eating) and PC2 (hereafter transience), both reaching the Kaiser-Guttman criterion (Kaiser 1991) with eigenvalues of 2.28 and 1.63, accounted for 38.0% and 27.1% of the total variation respectively. Binge-eating quantified the clustering of feeder visits within a day while transience quantified the extent of feeder use in a day.

### **Individual consistency and state-dependent differences in foraging patterns**

Individuals showed repeatability in the level of binge-eating ( $r$  ranging from 0.42 to 0.55 within winters and from 0.47 to 0.55 between winters; Fig. 3a) and transience at feeders ( $r$  ranging from 0.39 to 0.62 within winters and from 0.34 to 0.48 between winters; Fig. 3b).

Great tits binged to a greater extent (Figs 4a & 4b; estimated mean GT PC1: 0.44, BT PC1: -0.24, SE=0.04,  $t=18.45$ ,  $P<0.001$ ,  $n=24,271$ ) and were less transient than blue tits (Figs 4c & 4d; estimated mean GT PC2: -0.23, BT PC2: 0.66, SE=0.03,  $t=-29.37$ ,  $p<0.001$ ,  $n=24,271$ ). Males of both species used feeders more than females while juvenile great tits used feeders more than adult great tits (Figs 4c & 4d; see Table 2 for model estimates).

Overall, individuals of both species with subsequent breeding territories further from feeding stations binged more (Figs 4a & 4b) and were more transient at feeders (Figs 4c & 4d) than those with closer territories (see Tables 1 & 2 for model estimates). The distance to territory also interacted with age and sex in predicting the level of binge-eating, in both species. With  $DTT > 1069\text{m}$  (GTs) or  $DTT > 1124\text{m}$  (BTs), males binged more than females, while with  $DTT > 696\text{m}$  (GTs) or  $DTT > 1184\text{m}$  (BTs), adults binged more than juveniles (Figs 4a & 4b; see Table 1 for model estimates).

We had assayed exploration behaviour for 251 (18%) individual great tits that were detected over the course of this study. This measure of behavioural variation did not predict either the level of binge-eating ( $\beta=0.04$ ,  $SE=0.03$ ,  $t=1.48$ ,  $P=0.14$ ,  $df=409$ ) or transience ( $\beta=-0.01$ ,  $SE=0.02$ ,  $t=-0.32$ ,  $p=0.75$ ,  $df=254$ ) when added to the respective models.

### **Effects of change in local competition on foraging tactics**

The extent of binge-eating by an individual was predicted both by the mean level of competition experienced and by the daily deviation from its mean level of competition (Table 1): individuals binged less at busy sites and on days when feeders were busier than they normally experienced (Fig. 5a). Both the average competition and deviation from average competition experienced predicted individual transience at feeders (Table 2), with individuals using feeders more when feeders were busy (Fig. 5b).

### **Discussion**

In this study, we quantified individual variation in the foraging routines of a population of great tits and blue tits and characterized the daily patterns of timing of feeding. When investigated at a fine time-scale, pronounced variation in the temporal clustering of feeder visits within a day was apparent along a binge-eating–grazing axis (illustrated in Fig. 2), with consistent differences between individuals both between and within years. Repeatability estimates in studies of animal behaviour above 0.25 are generally considered moderately repeatable and values above 0.5 highly repeatable (Dingemanse & Réale 2005; Bell, Hankison & Laskowski 2009). We found individuals were repeatable in both the level of binge-eating and transience at feeders with  $r$  above 0.3 for all within-year and between-year estimates. Moreover, individuals shifted their foraging patterns with a change in local competition, binge-eating less and using feeders more when daily feeder traffic was greater.



The large scale use of automated RFID loggers and PIT-tags allowed the production of an extensive data set on the timing of feeding in a wild population, as has been done in a previous study on small passerines in winter (Bonter *et al.* 2013), showing similar overall hourly feeding patterns (Fig. S3). However, analysis of the clustering of individuals' visits over a day gave the potential for the identification of more structure in feeding behaviour than previously documented. An experiment that manipulated intraspecific competition in trout demonstrated coarse temporal partitioning of feeding, when subordinate fish shifted from nocturnal to more diurnal feeding with increasing intensity of competition (Alanärä, Burns & Metcalfe 2001). The results presented here also suggest individual differences in temporal feeding patterns, but at a much finer time-scale. Principal component analysis revealed that 65% of variation in the timing of feeding was explained by two principal components, which we considered to represent binge-eating and transience. The binge-eating axis quantified how clustered an individual's feeding was while transience quantified how much individuals used the feeders.

Social dominance is likely to play a role in determining the timing of feeding in this study system, since dominant individuals have been shown to have priority access to feeders over subordinates (De Laet 1985; Hegner 1985). This ability to monopolize the use of feeders could allow a greater level of binge-eating in dominants by reducing the time spent waiting between visits within the same feeding bout. We showed that great tits, adults and males, which are the dominant classes of bird in this system (Perrins 1979), binged more than blue tits, juveniles and females, but only when their territory was not in close proximity to the feeder. In the UK, both great tits and blue tits are resident and tend to hold territories throughout the winter (Kluyver 1951; Perrins 1979). There is some evidence that holding a territory near to a feeding station increases social dominance (De Laet 1984; Oberski &

Wilson 1991) and thus could allow more binge-eating. However, if the distance to territory is great, then binge-eating may be the optimal tactic as it is likely to reduce travel time and any other associated travel costs. Our results support the latter explanation: birds with territories further from feeders binge-eat more than birds with territories closer to feeding stations. We also found that an interaction between age/sex class and distance to territory explained some of the variation in foraging tactic: with greater distance to territory, males and adults increased binge-eating to a greater extent than females and juveniles (Figs 4a & 4b). Since adult great tits tend to become territorial before juveniles in the non-breeding season (Kluijver 1951), and are often returning to an existing territory rather than establishing a new one, adults are likely to have stronger ties to their territories during winter than juveniles. In addition, males are more territorial than females (Hinde 1952; Perrins 1979; Gosler 1993) and so will tend to have stronger ties to their territories. Birds with a strong link to their territory should spend more time near their territory and we found that birds visiting feeders that are further from their territories are more transient at feeders than those with closer territories (Figs 4c & 4d).

Males of both species used feeders more than the females of their own species. Assuming a similar proportion of daily food intake from feeders and natural sources for both sexes (Brittingham & Temple 1992), this is likely related to the larger body size and energetic requirements of males (Broggi *et al.* 2007; Bouwhuis, Sheldon & Verhulst 2011). However in great tits, males have beak structures which are better adapted to opening beechmast seeds quickly and have a higher proportion of seeds to invertebrates in their diet (Gosler 1987), so this might also contribute to males visiting seed feeders more than females. Since search and handling times of supplemental food tend to be relatively short and predictability high, males might not necessarily prefer natural food sources. Juvenile great tits visited feeders more than

adults. Since older birds tend to be more skilled at foraging, with more experience in finding natural food sources (Enoksson 1988; Desrochers 1992), this could indicate a greater reliance on artificial feeders by juveniles than by adults. In addition, it has been shown in herring gulls (*Larus argentatus*) that young birds are less efficient foragers, spending more energy per unit of food gained (Greig, Coulson & Monaghan 1983). This could lead to young birds needing to consume more food than adults. Another potential reason for juveniles requiring more food could also be the decrease in basal metabolic rate (BMR) with age (Broggi *et al.* 2007, Moe *et al.* 2009); however, there is some evidence that this only affects great tit populations with the highest BMRs, at very high latitudes (Broggi *et al.* 2010), so may not be a factor in this study. No age difference was apparent in blue tit transience at seed feeders, but this could be linked to the higher proportion of invertebrates in the blue tit diet during winter (Perrins 1979) and potentially a lesser reliance on seed feeders.

Given the reported links between personality and foraging in great tits (Quinn *et al.* 2012, Cole & Quinn 2012), we predicted that fast-exploring individuals would prioritize productivity and growth over survival by binge-eating more than slow-exploring individuals that would prioritize survival. However, we did not find a relationship between either the clustering of feeder visits or transience and exploration score. While the traits typically measured as components of the proactive-reactive axis are correlated in most species, there are some exceptions. For example, in the case of blue tits, exploration score and neophobia are independent (Herborn *et al.* 2010). Therefore it is possible that a different measure of personality could be linked to the foraging patterns described in this study.

Individuals showed repeatability in both binge-eating and transience across the study period – i.e. both within and between years (Fig. 3). With values between 0.3 and 0.6, the repeatabilities of these feeding patterns are high for behavioural measures. This was due both to differences between individuals in mean feeding pattern and consistency within individuals across time. However, we also demonstrated individual flexibility in foraging tactic with change in local competition: individuals binged less when feeders were busier than they usually experienced (Fig. 5a). This suggests that a binge-eating tactic may be the preferred tactic over grazing. In this study system, birds face the risk of predation by sparrowhawks when exposed at feeders (Newton 1986) and fly back and forth to nearby cover to process and consume individual seeds. This might make binge-eating a safer tactic than grazing by reducing the total daily time spent near feeders (Fig. S4). Over the course of this study, we have seen both attempted and successful predation events on tits by sparrowhawks at feeding stations. Since feeding stations are at conspicuous fixed locations, this is likely to increase the risk of predation at feeders relative to territory sites; this may also be the case at sites where tits feed on natural food resources such as beechmast. Reducing the number of feeding bouts by binge-eating to a greater extent could also make it a more efficient tactic by reducing longer-distance travel, or ‘commuting’, costs and increasing the amount of time available for rest and other behaviours. Furthermore, a theoretical model has shown that increasing the commuting distance to food can limit the reduction in feeding rates due to interference competition and site-related dominance (Ydenberg *et al.* 1986).

In order to determine whether the reported change in foraging patterns is in response to competition, future studies should manipulate the level of competition. This could be achieved by altering the number of competitors, access to food, or both. It would then be possible to test whether individuals that vary in dominance rank respond differently to the

effects of competition during foraging or perhaps whether they differ in the extent of their foraging plasticity.

To investigate the consequences of foraging patterns, it would be useful to test whether foraging tactic has an effect on survival, recruitment to the breeding population, or reproductive success. A recent study on our population showed that the number of visits to feeders over the whole winter has no effect on these measures of fitness (Crates *et al.* 2016), but the fitness consequences of alternative foraging tactics were not explored. Variation in the timing of feeding is also likely to be caused by differences in physiological state and the environment so it will be important to investigate the effects of condition, perceived predation risk, temperature and flock structure in future studies. Individuals used feeders more on days when sites were busy and local competition was high. This is likely due to environmental conditions affecting the population; for example, low temperatures increasing energetic requirements and low availability of natural food could both lead to increased use of artificial feeders.

When animals forage in groups, as the birds in this study system often do, feeding behaviour will have links with social behaviour. Thus, individual variation in feeding patterns will have consequences for group structure and the processes that are driven by social structure. For example, grazers are likely to have higher encounter rates with other individuals than binge-eaters, suggesting that feeding behaviour is important for the spread of information or disease. Different probabilities of encounter will also have consequences for social processes such as mate choice.

To conclude, this study identified, for the first time, consistent individual differences in alternative foraging tactics that differ at a fine temporal scale. The analyses presented here revealed considerable variation in the timing of foraging behaviour, with over half of this variation explained by two principal components. There were consistent differences between individuals in both the temporal clustering of feeder visits and how much they used feeders. In addition, individuals reduced the temporal clustering of their visits as local competition increased. Adaptive variation in foraging tactics may have important implications for survival and reproductive success; therefore future studies should also explore their fitness consequences.

### **Data Accessibility**

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.jr48p> (Milligan *et al.* 2017).

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## Figures

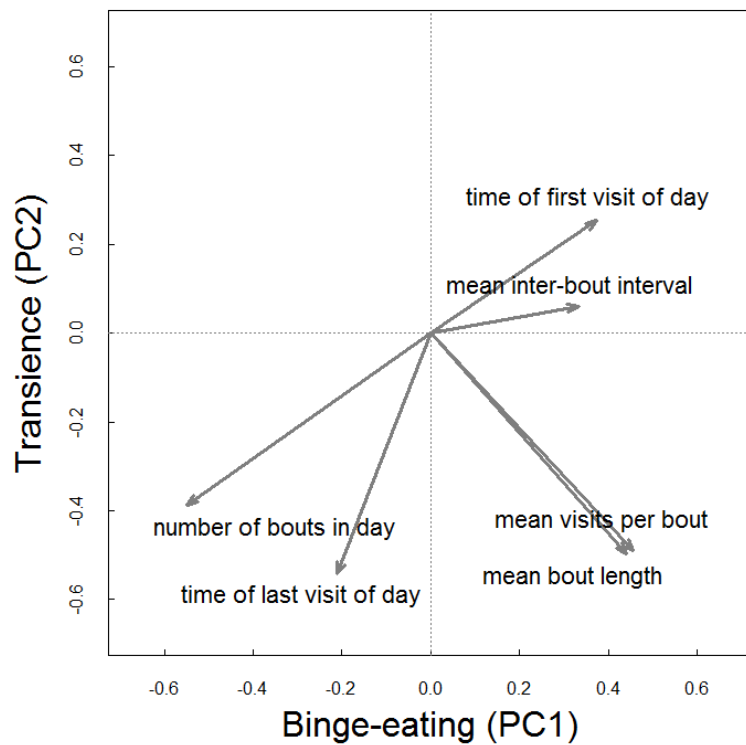


Fig. 1. Graphical representation of the degree to which different measures of the timing of feeding of individual great tits and blue tits load onto the first two axes of a principal component analysis. The length and direction of the arrows indicate the loading on the principal component axes.

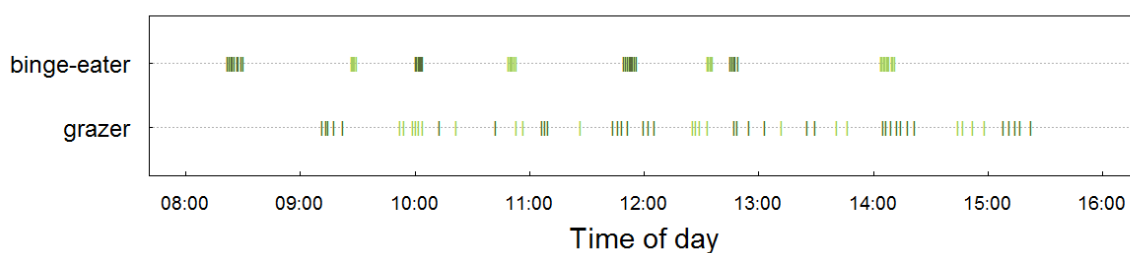


Fig. 2. Illustration of variation in timing of visits by two individual great tits at the same feeder on the same day; each bird made an identical number of visits.  $PC1_{\text{binge-eater}} = 1.54$ ;  $PC1_{\text{grazer}} = -0.39$ . Alternate feeding bouts are shown in different shades.

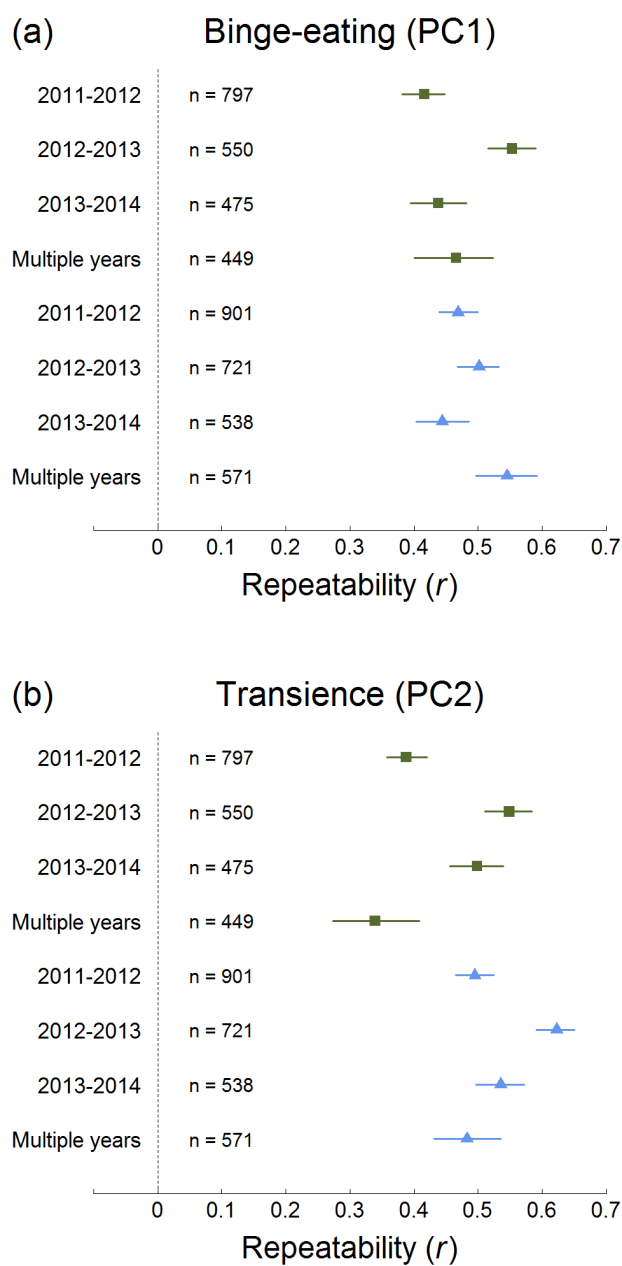


Fig. 3. Repeatability  $r \pm 95\%$  CI of (a) binge-eating and (b) transience by winter; great tits: green squares, blue tits: blue triangles. Estimates with confidence intervals that do not cross the dotted line at  $r=0$  are significantly repeatable at the  $\alpha=0.05$  level;  $n$ =number of individuals with at least two daily measures per winter.

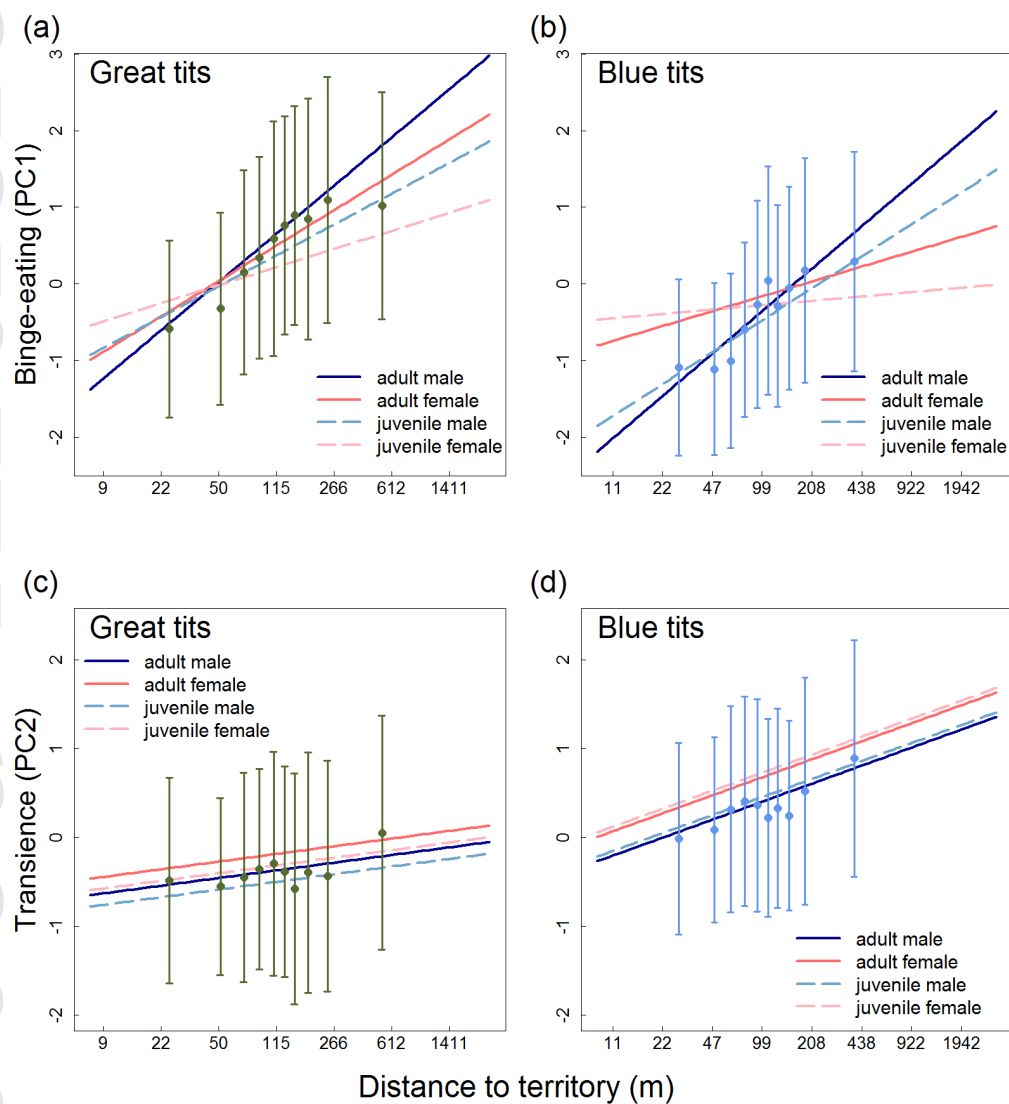


Fig. 4. Mean level of binge-eating (PC1)  $\pm$  1 SD for (a) great tits and (b) blue tits and mean transience  $\pm$  1 SD for (c) great tits and (d) blue tits with increasing distance to subsequent breeding territory; data were binned into tenths by distance to territory. Lines show fitted model effects for age and sex class.



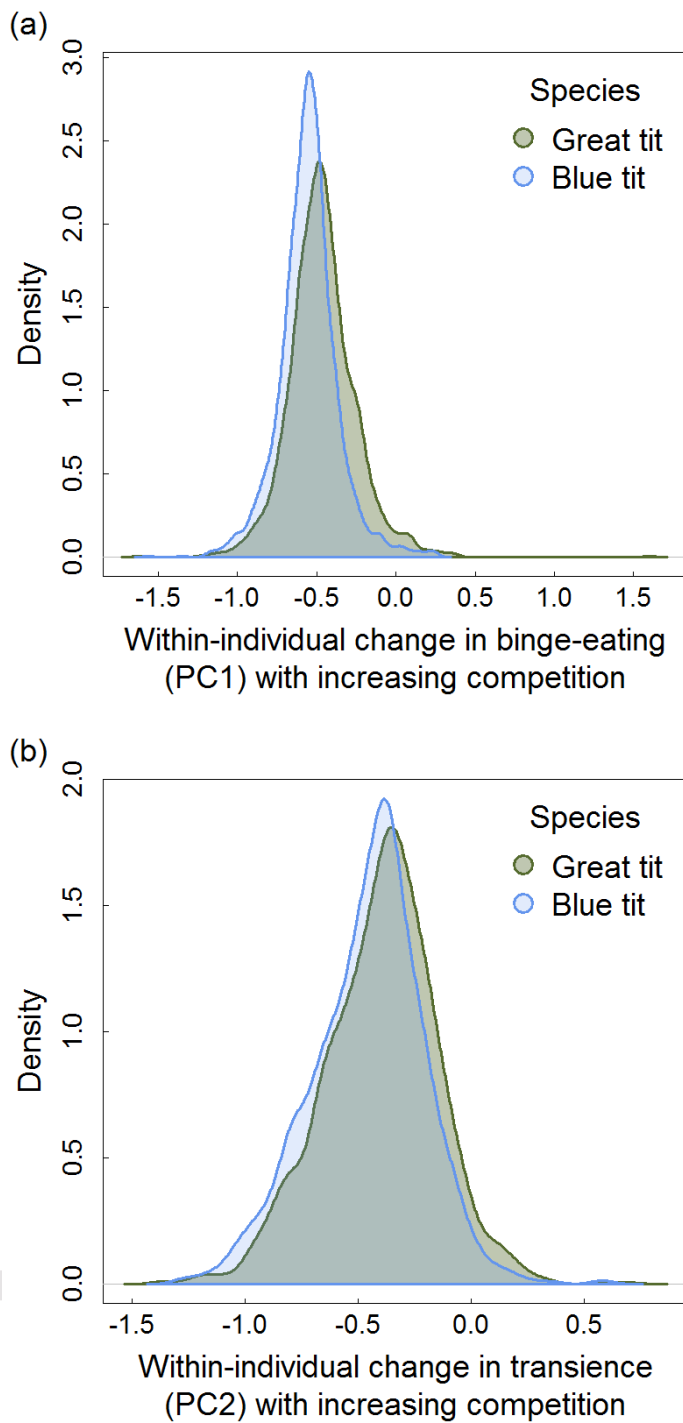


Fig. 5. Density plot of predicted change in (a) binge-eating and (b) transience with an increase of 1 SD of competition for all individuals with observations on multiple days. Competition is defined as the total visits by all other tagged individuals at feeder over a day.

## Tables

Table 1. Linear mixed model on factors affecting the level of binge-eating (PC1). Number of observations: great tit n=4895; blue tit n=3405.

Fixed effect	great tits					blue tits				
	Coefficient	SE	t	d.f.	P	Coefficient	SE	t	d.f.	P
age	-0.28	0.06	-4.70	430	<0.001	-0.12	0.07	-1.65	795	0.100
sex	0.15	0.08	2.01	430	0.045	-0.19	0.09	-2.21	795	0.027
distance to territory	0.46	0.05	10.00	430	<0.001	0.19	0.05	3.61	795	<0.001
average competition	-0.13	0.05	-2.81	430	0.005	-0.16	0.05	-3.02	795	0.003
deviation from average competition	-0.50	0.04	-12.64	430	<0.001	-0.57	0.05	-11.62	795	<0.001
age * distance to territory	-0.23	0.05	-4.48	430	<0.001	-0.14	0.06	-2.40	795	0.017
sex * distance to territory	0.17	0.06	3.03	430	0.003	0.36	0.06	5.73	795	<0.001

Random term	great tits			blue tits		
	Variance	SD	n	Variance	SD	n
individual ID	0.68	0.83	623	0.61	0.78	504
individual ID with random slope for competition deviation	0.13	0.36	623	0.19	0.44	504
site	0.20	0.45	64	0.17	0.42	63
date	0.07	0.27	30	0.06	0.24	30
residual	1.11	1.05		0.87	0.93	

Table 2. Linear mixed model on factors affecting transience (PC2) at feeders. Number of observations: great tit n=4895; blue tit n=3405.

Fixed effect	great tits					blue tits				
	Coefficient	SE	t	d.f.	P	Coefficient	SE	t	d.f.	P
age	-0.13	0.05	-2.79	565	0.006	0.05	0.06	0.82	402	0.413
sex	-0.18	0.06	-3.34	565	0.001	-0.27	0.08	-3.40	402	0.001
distance to territory	0.09	0.02	3.63	565	<0.001	0.20	0.03	6.97	402	<0.001
average competition	-0.38	0.04	-9.21	565	<0.001	-0.32	0.05	-6.52	402	<0.001
deviation from average competition	-0.40	0.04	-11.00	565	<0.001	-0.38	0.05	-8.34	402	<0.001

Random term	great tits			blue tits		
	Variance	SD	n	Variance	SD	n
individual ID	0.37	0.61	623	0.56	0.75	504
individual ID with random slope for competition deviation	0.17	0.41	623	0.23	0.48	504
site	0.28	0.52	64	0.23	0.48	63
date	0.09	0.31	30	0.03	0.17	30
residual	0.76	0.87		0.63	0.79	