Alternative foraging strategies in a wild population of tits (Paridae)

Nicole Milligan

New College

A thesis submitted for the degree of
Doctor of Philosophy
University of Oxford
Michaelmas Term 2015

ABSTRACT

Alternative foraging strategies in a wild population of tits (Paridae)

DPhil thesis by Nicole Milligan, New College, submitted Michaelmas Term 2015

How individual animals divide their time between activities such as feeding, predator vigilance, resting, and interacting with conspecifics reflects trade-offs between different fitness related traits (e.g. starvation avoidance, predator avoidance or reproductive performance). Time allocated for foraging to meet energy requirements forms an essential component of animals' daily time budgets. Furthermore, individuals vary in state and the environment they experience, which will influence how they prioritize and organize different behaviours – the dynamics of which may be affected by processes acting at different timescales. Small animals with high metabolic rates must feed frequently each day, enabling fine control of the precise timing of feeding. However, little is known about how fine temporal-scale variation in individual behaviour scales up to shape daily routines, or what the consequences of inter- and intra-individual differences in this process may be. The main objective of this thesis was to investigate the causes and consequences of individual variation in the foraging behaviour of wild great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*) visiting artificial feeders during winter, ranging in temporal scale from single feeder visits to seasonal shifts in behaviour.

First, I described a novel axis of individual variation in how individuals distribute their feeder visits across the day. This captured the extent to which single feeding events were clustered into foraging bouts, with 'binge-eaters' and 'grazers' at either end of a continuous spectrum. This axis (level of binge-eating) described 38% of individual variation in observed feeder behaviour and was repeatable within individuals both within and across seasons. Dominance-related factors (species, age and sex) and territorial location predicted inter-individual differences. Individuals exhibited some flexibility in their foraging strategy in relation to local competition, binge-eating more when feeders were quieter than their average experience. The abiotic environment also influenced feeding patterns; birds clustered their feeding behaviour more tightly within a day as day length decreased in midwinter, while visiting feeders more frequently overall on colder days. I then demonstrated that individuals can vary both in overall foraging behaviour, and in their susceptibility to interference, with subordinate individuals responding more negatively to an increase in competition. An experimental manipulation revealed that interference competition at feeders can reduce foraging efficiency. Next, by incorporating a social network approach, I showed that great tit foraging strategies were related to patterns of social interaction and were non-randomly distributed across the social network. This positive assortment indicated a link between foraging behaviour and social structure, likely due to positive feedback. Finally I found evidence that social bonds influence foraging behaviour: pairs of great tits that subsequently bred together exhibited similar foraging strategies, but only after pair formation, suggesting convergence of foraging behaviour.

This thesis represents the first investigation of individual differences in high temporal-resolution patterns in foraging behaviour in a wild population, carried out across multiple years. The work emphasizes the importance of monitoring individual behaviours at appropriate timescales and relating these measures to relevant processes, e.g. pair formation. The results presented here demonstrate how fine-scale behavioural differences can influence how: individuals cope with a changing environment, interact with other individuals in a group context, and shape social structure which can then feed back to impact on individual behaviour. The interaction of these behavioural processes may have consequences for fitness, population dynamics and community composition.

ACKNOWLEDGEMENTS

First and foremost, I am very grateful to my supervisors Ben Sheldon, Reinder Radersma, and Ella Cole – thank you for steering my DPhil in the right direction; I would have been lost without your guidance, support and intellectual input. Second, I am indebted to Lucy Aplin for incredibly helpful discussions and to Josh Firth, Damien Farine, and Lucy (again) for your prowess in permutations and social network analysis: a certain chapter would have been impossible without your input. I am also grateful to my examiners, Tommaso Pizzari and John Quinn, for an enjoyable and thought-provoking discussion of my thesis during the viva.

Thanks to my officemates, past and present, for putting up with me and keeping the tea flowing. Thank you to everyone at the EGI, both in the field and at the department, for making it such a lively environment to work in, including: Lindall Kidd, Ross Crates, Ada Grabowska-Zhang, Colin Garroway, Bernhard Voelkl, Cam Allen, Antica Čulina, Irem Sepil Oz, Stu Wigby, Jen Perry, Tobias Uller, Grant McDonald, Emily Simmonds, Keith McMahon, Stephen Lang, Nico Alioravainen, Adèle Mennerat, Brecht Verhelst, Camilla Hinde, Uri Roll, Matilda, and Georgina (RIP); Sozos Michaelides aka comrade-in-writing-up, thanks for also burning the midnight oil. I would like to thank Andy Gosler for all the ringing training and my appreciation also goes to those at the field station who helped to keep the fieldwork going so smoothly, especially Julian Howe. I'm grateful to Lynne Bradley and Heather Green for guiding me through the administrative system so patiently. I'd also like to thank Deborah Brown for meticulous proofreading.

Thanks to all my housemates over the course of this project – you've kept me well fed, sociable and, most importantly, sane when life was hectic. The Casa Hart St crews, Western Rd posse, Warham House New Collegians, and Allam Streetites.

Finally, an immense thank you to my family and friends for all the support over the years. Natasha, Matthew, Abi, Amy, Bex, Charles, Chris, Dite, Ewan, Freya, Grif, Hanaan, Kat, Madjdy, Melanie, Nathi, Rach, Ros, Sepideh, Shelly, and Simon. And to my parents – this thesis is dedicated to you and I hope I have made you all proud.

AUTHOR CONTRIBUTIONS

Main contributors

Nicole D. Milligan had independent intellectual input into all aspects of the thesis and contributed to four years of spring field data, three years of winter field data, and collected one winter of experimental feeder manipulation data. Also conceived, analysed data, wrote drafts, and incorporated comments from co-authors for each data chapter.

Ben C. Sheldon (supervisor and co-author of all data chapters) secured funding and provided intellectual input. Also gave guidance on research techniques, experimental design, and analytical methods. Gave detailed comments on all chapter drafts.

Reinder Radersma (supervisor and co-author of all data chapters) provided intellectual input and gave guidance on research techniques, experimental design, analytical methods, and graphical methods using R. Gave comments on all chapter drafts.

Ella F. Cole (supervisor and co-author of all data chapters) provided intellectual input, gave guidance on writing and detailed comments on all chapter drafts.

Additional contributors

Lucy M. Aplin (co-author chapter 5) calculated network metrics, created a social network figure for each winter using the R package iGraph, advised on social network analyses, and gave comments on the drafts of chapters 2, 4 and 5.

Damien R. Farine (co-author chapter 5) ran the Gaussian mixture models, built the social network (association matrix) for each winter, and advised on social network analyses.

Josh A. Firth (co-author chapter 5) advised on social network analyses and running permutations and gave comments on the drafts of chapters 2 and 5.

CONTENTS

CHAPTER 1

Introduction

Introduction

Individuals must choose how to allocate their time between the many tasks required for survival and reproduction. All animals have daily nutritional and energy requirements; the time allocated for foraging to meet these requirements will be a fundamental component of an individual's time budget.

Foraging theory

Foraging research has its roots in behavioural ecology, with the original motivation stemming from understanding behaviour using optimality models (Stephens & Krebs 1986). These models generally assumed that animals should follow one 'best' strategy when making foraging decisions, an example of which is rate-maximization, when the currency that individuals prioritize is a high intake rate, e.g. over high efficiency (Pyke *et al.* 1977). Subsequent conceptual advances include (i) state-dependence which allows models to dynamically update an individual's strategy based on its current state (Caraco 1980), (ii) risk sensitivity which allows models to incorporate stochasticity into the rate of gain (Kacelnik & Bateson 1996), (iii) trade-offs between conflicting factors such as starvation and predation risk which can better predict survival (Houston *et al.* 1993), and (iv) foraging in a social context which allows models to take into account the consequences of foraging in a group (Verhulst & Hogstad 1996). There have been two different approaches to modelling behaviour: optimization is used for studying an individual's behavioural decisions in isolation (Pyke *et al.* 1977) and game theory for when an individual's decisions are influenced by the behaviour of others (Maynard Smith 1982). For animals that forage in groups, competition plays an important role in determining when individual group members feed (Giraldeau & Caraco 2000).

Optimal foraging theory (OFT) was introduced in the late 1960s, with two main types of model. *Diet models* concerned optimal choice of when to handle and consume food items as well as choice of food type (MacArthur & Pianka 1966). *Patch models* examined how much time should be spent exploiting one food patch before moving to another patch (Emlen 1966). This seminal idea of diminishing returns is known as the *marginal value theorem* (Charnov 1976). The later concept of state dependence was instrumental in developing *dynamic models* of foraging (Mangel & Clark 1988; Houston & McNamara 1999) which take into account changes in an individual's state. These models predict long-term fitness consequences from sequences of short-term behavioural choices. They also allowed the first analyses of the trade-off between gaining energy and avoiding predation. Risk trade-offs, especially between starvation and predation, have become central concepts in the study of foraging behaviour (Lima & Dill 1990). The *risk-spreading theorem* predicts, in the absence of feeding interruptions or mass-dependent risks or costs, that a constant rate of foraging is optimal (Houston *et al.* 1993). However, stochasticity in food availability and predation risk will lead to variable rates of foraging over a day (McNamara *et al.* 2005), often with a *bimodal* distribution of daily feeding activity predicted as a good strategy to minimize both risks (Aschoff 1966; Morton 1967). Risk-sensitive foraging theory has explained how foraging decisions are dependent on energy budgets: individuals with a negative energy budget are risk prone, increasing the chance of reaching a minimum threshold energy level, while individuals on a positive budget are risk averse in order to reduce the chance of an energy shortfall (Kacelnik & Bateson 1996). A key step in determining the optimality of foraging behaviour is to quantify the extent to which individuals can respond to their environments and how this might vary within and among individuals.

Individual variation

"Individuals always differ; the important question is whether or not the variation has ecological significance." – Giraldeau & Caraco 2000

It was originally assumed in the study of animal behaviour that individuals should be totally plastic and adjust their behaviour dynamically to accommodate each situation (Parker and Stuart 1976; Stephens and Krebs 1986; Piersma and Drent 2003). However, in recent years, work on animal personality has suggested that individuals behave more consistently and may follow particular behavioural strategies (reviewed in Sih *et al.* 2004 and Bell *et al.* 2009), for instance due to morphological or physiological constraints (e.g. Castellano *et al.* 2002). Furthermore, it has now been established that individual differences can be adaptive; particularly in light of multiple contexts or under fluctuating environmental conditions, and natural selection can favour alternative behavioural strategies (Wilson 1998; reviewed in Dingemanse & Réale 2005 and Smith & Blumstein 2008).

Recent studies have demonstrated consistent individual differences in diverse behaviours such as cooperation (English *et al.* 2010), searching (Patrick *et al.* 2014), sleep (Steinmeyer *et al.* 2013), and foraging (Missoweit *et al.* 2007; Quinn *et al.* 2012). In addition, a broad range of factors have been shown to influence individual differences in behaviour. Traits such as age, sex and morphology have been established as important factors explaining variation between different individuals (Bolnick *et al.* 2003) while personality affects suites of behaviours, including foraging decisions (Kurvers *et al.* 2012; Quinn *et al.* 2012). The ecological and social environments also influence how individuals forage (Cowlishaw 1999; Krams *et al.* 2010). Thus, there is growing evidence that many types of factor can interact with consistent individual differences to maintain behavioural variation in a population. Since individuals can differ both in average behaviour and in their behavioural responses to changes in the environment, studies should consider both between- and within-individual differences when investigating the consequences of foraging behaviour such as fitness outcomes. Furthermore, since many factors potentially acting at different timescales can interact to influence foraging behaviour, it is important to monitor foraging behaviour at an appropriate resolution.

Daily foraging routines

Here I define a daily foraging routine as the temporal patterning of foraging across a day. Variation in foraging routine was traditionally thought to be influenced mainly by fluctuations in the environment, such as temperature (Avery and Krebs 1984) and availability of food (Kacelnik 1979). It has since been shown both theoretically (McNamara *et al.* 1994), and empirically (Dall & Witter 1998; Krams 2000; MacLeod *et al.* 2005; Polo & Bautista 2006), that the trade-off between starvation and predation risks is also an important determinant of daily foraging routines; increasing the rate of energy gain decreases the risk of starvation but also increases the risk of predation and individuals must balance these risks in order to survive.

Many existing theoretical predictions and empirical evidence for temporal patterns of foraging explore average patterns of behaviour in a population, often at an hourly timescale (Van der Veen 2000; Polo & Bautista 2006; Bonter *et al.* 2013). These studies make conclusions about the general daily pattern of feeding, but may overlook patterns at a different temporal scale (Heath *et al.* 2010). Moreover, few studies have investigated how temporal foraging patterns vary at the individual level, so the extent to which individuals feed at different times remains poorly understood. Most of the empirical work on the timing of feeding in birds has been conducted in captivity (e.g. Dall & Witter 1998), while field studies have typically monitored temporal patterns in mass gain (Krams 2000; MacLeod *et al.* 2005; Ratikainen & Wright 2013), due to the difficulty in making continuous observations of marked individuals in the wild. Mass gain corresponds with feeding activity (Baldwin & Kendeigh 1938) but the time lag between foraging and digestion will cause some inaccuracy in using mass gain as a measure of feeding rate (Bednekoff & Houston 1994). Therefore it would be better to monitor actual feeding rates rather than mass gain when investigating daily foraging routines.

Competition for limited resources is an important determinant of variation in foraging behaviour. To reduce the impact of competition, individuals can partition resources by segregating in habitat, diet, or time (Schoener 1974). Temporal partitioning of foraging behaviour at the daily scale has been demonstrated in trout (*Salmo trutta*) by manipulating energetic demands to increase the competition level. This resulted in subordinate individuals shifting their feeding activity to forage more nocturnally, with greater risk of predation but less temporal foraging overlap with dominant individuals (Alanärä *et al.* 2001).

Large scale monitoring of wild animals at fixed feeding stations has been made possible by the development of radio-frequency identification (RFID) technology (Bonter & Bridge 2011); data loggers automatically detect and record when uniquely tagged individuals approach antennae at feeding stations. A recent study by Bonter *et al.* (2013) showed support for the risk-spreading theorem over the bimodal hypothesis – four species of passerine visiting bird feeders in mid-winter exhibited constant or gradually increasing feeding rates over the day. The authors suggested that the birds were prioritizing the reduction of starvation risk over the reduction of predation risk. However, the data were not analysed at the individual level so it is unclear whether this conclusion applies to all individuals. For instance, it could be that certain individuals forage more in the morning while others forage more later in the day, which would imply two alternative foraging strategies. Previous work on another passerine species has identified alternative foraging strategies in how birds manage the trade-off between starvation risk and predation risk over a day, with proactive (personality axis) birds feeding more than reactive individuals when predation risk was high (Quinn *et al.* 2012). Furthermore, the pattern of feeder visits by an individual could contain more heterogeneity at a finer temporal scale than described in Bonter *et al.* (2013). For example, an individual's visits to a feeder may cluster into feeding bouts with short intra-bout visit intervals and longer inter-bout intervals. While larger species or species with lower metabolic rates, such as the trout mentioned above, are able to shift their foraging behaviour from one half of a day to the other, small birds must feed regularly throughout the day in order to maintain their high metabolic rates. Therefore, if small birds are to divide limited resources between potentially unequal competitors across a short winter day, this would only be possible with variation in the pattern (e.g. clustering) of feeding at a finer temporal scale than a single diurnal-nocturnal shift. On the other hand, there could also be trends over a longer time scale, leading to seasonal patterns in foraging routine with changes in day length, temperature, precipitation or food availability (Cope 2006; Pita *et al.* 2011). Differences between individuals in their ability to shift behaviour with environmental conditions implies variation in their capacity to cope with seasonal change, with consequences for patterns of survival and population dynamics.

STUDY SYSTEM AND GENERAL METHODS

My focal study system is a wild population of great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*). In the UK, these tit species are resident throughout the winter and readily visit birdfeeders; their typical preference for breeding in nest boxes over natural cavities also allows a large proportion of the population to be captured and identified (Fig. 1) during spring. These two passerine species do not cache food (store food for later retrieval) and are therefore a good system for studying individual variation in daily feeding patterns. Great tits are close to twice the size (by mass) of blue tits and are typically dominant over blue tits (Perrins 1979). Of the individuals captured during winter mist-netting over the course of this study, mean±SD mass of great tits was 18.4±1.1g and of blue tits was 10.7±0.6g.

Fig. 1. Blue tit (left) and great tit (right) fitted with a metal British Trust for Ornitholody ring and plastic ring containing a PIT-tag.

Both species defend small breeding territories in pairs during spring and early summer and form mixed-species flocks at other times of year (Hinde 1952). In Wytham, these winter flocks can also comprise a number of other birds including three caching species: marsh tit, coal tit and nuthatch, which are also monitored in Wytham as part of a study on the social ecology of small passerines (Farine *et al.* 2012). Great tits and blue tits are mainly insectivorous during the breeding season and summer, incorporating an increasing amount of plant-based food, mainly seeds, into their diet as winter approaches (Gibb 1954). Beechmast is an important autumn and winter food source for both species, especially great tits (Perrins 1966); however, beech crops are irregular and large numbers of seeds are typically only produced every second or third winter. The two tit species are ecologically very similar, although in winter great tits forage more at ground level and blue tits higher up in twigs and branches (Betts 1955). Both species readily visit artificial feeders, particularly when natural food sources are scarce or during harsh weather conditions (Perrins 1979). Woodland residents will leave the woods to visit bird feeders during the day but return by the end of the day to roost (Kluijver 1951). Outside the breeding season, individuals of both species will join mixed-species flocks during the day but roost solitarily at night in natural cavities or nest boxes. Adults and a few first year birds tend to establish their territories in autumn while most first year birds do so in late winter. While territories are only strongly defended during the nesting period, individuals typically roost within their territory (or domicile if no territory) during autumn and winter, re-joining the flock each morning (Kluijver 1951; Hinde 1952).

Sparrowhawks, especially the smaller males, are the main predators of tits during winter (Newton 1986). This threat of predation is traded-off against the risk of starvation (MacLeod *et al.* 2005). When sparrowhawks were absent in the UK in the 1960s, great tits increased their body mass, suggesting that they could minimize the risk of starvation in response to low predation risk (Gosler *et al.* 1995).

My study site is Wytham Woods (Savill *et al.* 2010), a 385-ha mixed deciduous woodland in Oxfordshire, UK (51˚46′N, 1˚20′W). Wytham contains 1203 nest boxes which are monitored as part of a long term study which was started by David Lack in 1947 with 200 nest boxes (Gibb 1950). The study was expanded to cover Wytham Woods, increasing the number of boxes (suitable for both great tits and blue tits) to 1020 by 1965. In recent years, 180 nest boxes with smaller entrance holes, excluding great tits, have been added for use by blue tits. Early work focussed on the population biology of the great tit, with later studies incorporating aspects of, for instance, territoriality, foraging, and communication

(Perrins 1979). There is now a wealth of information on the life history and behavioural ecology of both great tits and blue tits in Wytham. More recent studies of this population have branched out to include epidemiology (Knowles *et al.* 2010), climate change (Garant *et al.* 2008; Charmantier *et al.* 2008), and phenology (Cole *et al.* 2015).

For this study, I used automated RFID data loggers at artificial feeders to monitor visits by individual great tits and blue tits which were individually tagged with unique passive integrated transponder (PIT) tags. 65 feeding stations (Fig. 2) were set up across Wytham Woods, in a grid with 250m spacing, in the winter of 2010-2011 (see map in Fig. 3). 5634 individuals (2076 great tits, 3063 blue tits and 495 individuals of caching species) have been recorded over seven months of each of the subsequent three winters which is a substantial increase in scale over the 94 individuals recorded by Bonter *et al.* (2013) over two months of two winters.

Fig. 2. Feeding station containing an automated data logger and feeder with grey sleeve and two black RFID antennas (one visible) in front of seed access holes. A motor moves the sleeve up two inches to open the feeder and down to close the feeder. All equipment is housed in a squirrel-proof metal cage which allows access to small birds through the mesh.

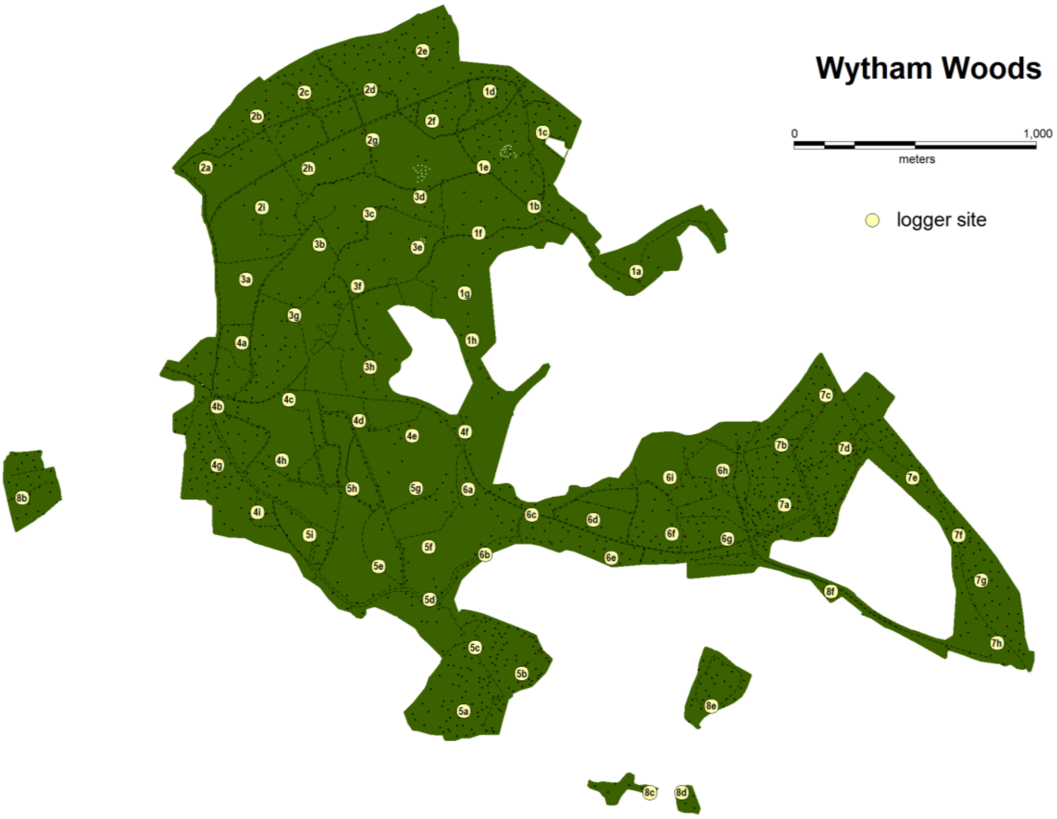


Fig. 3. Map of Wytham Woods showing the location of 65 feeding stations. Nest boxes are shown as black dots and tracks as dotted lines.

When feeders were open, the attached data loggers wrote up to three records per second whenever a PIT-tagged bird perched on an antenna to access food at the feeder. To analyse patterns in feeder visits by individuals, I filtered the raw data by collapsing each run of consecutive records of an individual down to one feeder visit. I then used the distribution of inter-visit intervals to assign clusters of visits to ‘feeding bouts’ for each individual (see Chapter 2 for more details). Table 1 and Fig. 4 show an example of all visits by tagged birds at a relatively busy feeding station on one recording date in December 2012, with a summary of the number of individuals, visits and bouts by species given in Table 1. On that date, this example site was the 11th most busy, by visit number, out of the 65 sites (example site indicated by arrows in Fig. 5). This includes data for all five species that were fitted with PIT-tags at the study site, including marsh tits, coal tits and nuthatches. These caching species were tagged as part of a larger study on the social ecology of small passerines in Wytham, but were excluded from analyses for my thesis due to their different use of supplemental feeders and the relatively small number of individuals visiting feeders.

Table 1. Summary by species of the number of individuals, visits and bouts recorded at site “1G” on 9th December 2012.

Species	Individuals	Visits	Bouts	Visits per individual	Bouts per individual	Visits per bout
great tit	15	858	207	57	14	4
blue tit	22	883	304	40	14	3
coal tit	1	166	13	166	13	13
marsh tit	3	303	37	101	12	8
nuthatch	2	182	20	91	10	9

The larger study encompassing the work presented here aimed to investigate the social and ecological factors that shape population processes and structure (Farine *et al.* 2015). The grid of 65 feeding stations described above was used to monitor feeder visits by all tagged individuals each weekend[*] from early September through to late February or early March in the non-breeding season of 2011-2012, 2012-2013, and 2013-2014. Co-occurrences of individuals at feeders were used to infer social associations. Gaussian mixture models identified bursts of activity in the temporal data stream of each feeder and then assigned each individual visit to one of these bursts, or ‘gathering events’ (Psorakis *et al.* 2012). A gambit of the group approach was then used to construct an individual-by-individual association matrix for each winter, summing the number of gathering event co-occurrences for each dyad (Whitehead 2008; Franks *et al.* 2010). Social network analyses could then be conducted to ask a range of questions about the causes and consequences of association patterns, group dynamics, and social structure.

---

[*] Except prior to December 2011, when feeding stations were programmed to open on Thursdays only.

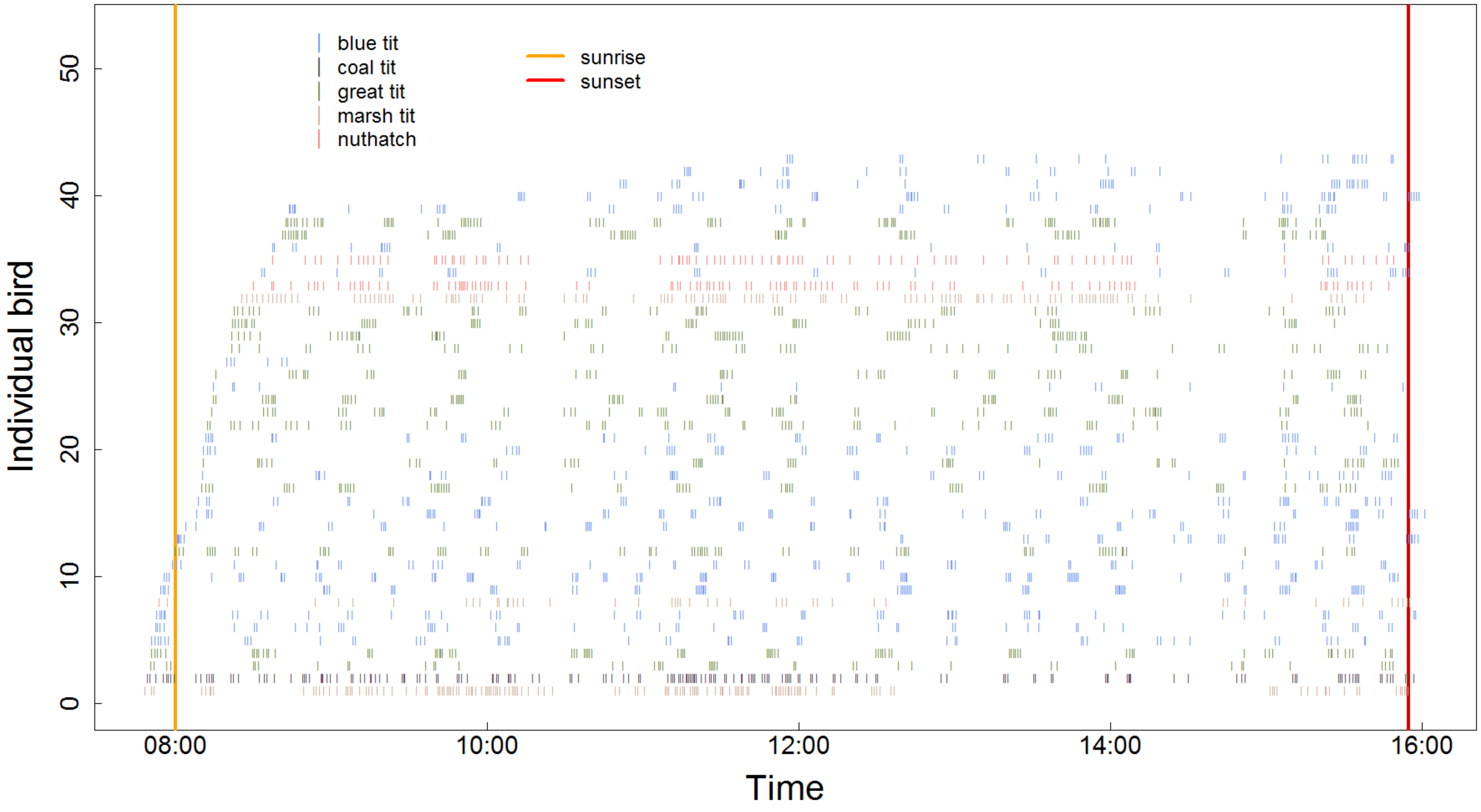


Fig. 4. Visits by all birds recorded at feeding station “1G” on 9th December 2012.

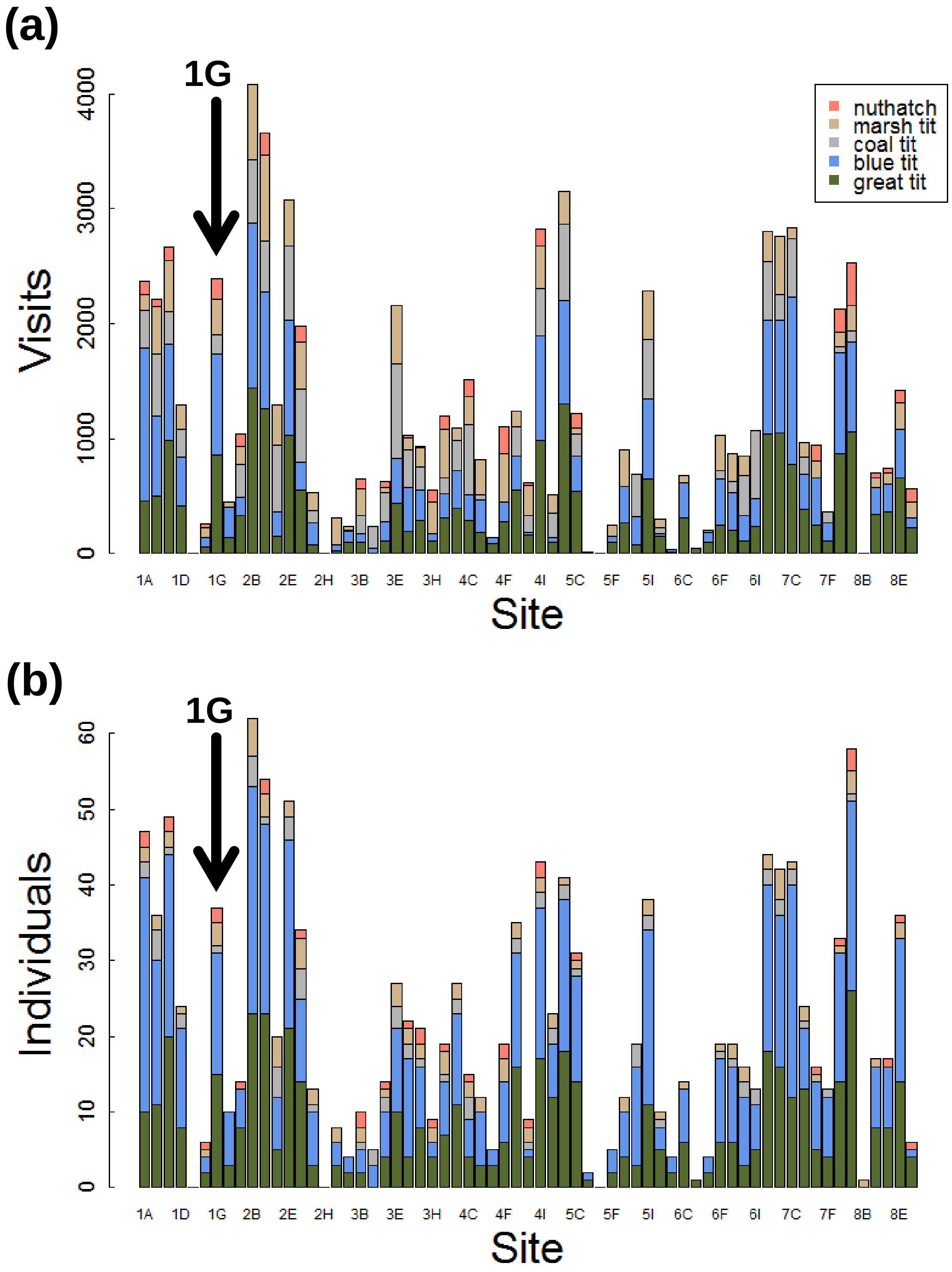


Fig. 5. Number of (a) visits and (b) individuals of all birds recorded across 65 sites on 9th December 2012; species shown by colour. Example site (“1G”) indicated by arrow.

After multiple years of network sampling, it was established that social phenotypes, based on social network metrics such as gregariousness or betweenness, were repeatable over both short (week to week) and long (year to year) timescales (Aplin *et al.* 2015). Inter-individual differences in these stable social phenotypes may have diverse fitness consequences. For example, socially central individuals were more likely to locate novel food patches (Aplin *et al.* 2012) which may be advantageous when feeding on ephemeral food sources. Social phenotypes have also been linked to consistent individual behaviour, with proactive (personality axis) individuals having weaker social connections with more conspecifics than reactive individuals that maintained fewer but stronger and more stable relationships. Furthermore, experimental manipulations have shown that social relationships (e.g. pair bonds) can affect both social structure (Firth & Sheldon 2015) and choice of foraging location (Firth *et al.* 2015). This suggests that social interactions may mediate the relationship between foraging behaviour at the individual level and social structure at the population level.

While social dynamics and social structure have been investigated, the link between temporal patterns in individual foraging and social associations at feeders has yet to be explored in detail. A recent experimental study has shown that interactions at feeders can carry over to other (non-foraging) contexts, such as patterns of association at nest boxes during spring nesting site prospecting (Firth & Sheldon 2015). Thus, despite social interactions and foraging behaviour being measured in the same context (at feeders), feeding patterns may still have implications for social organisation more broadly.

THESIS AIMS & OVERVIEW

My main objective for this thesis is to understand the causes and consequences of individual variation in the daily foraging behaviour of two related species in a wild population, with three main goals. First, I quantify a novel measure of fine temporal scale patterns in individual foraging behaviour. The second aim is to identify the intrinsic and environmental determinants of daily foraging patterns. Thirdly, since great tits and blue tits feed in groups, I investigate how individuals' foraging patterns affect each other, both through competition and social interactions. This thesis comprises a series of four papers followed by a general discussion which places the work within the broader context of behavioural ecology.

Chapter 2

Here I quantify the within- and between-individual variation in the daily patterning of visits to feeders to explore how consistent individual foraging routines are, and whether different individuals use alternative strategies. I use a principal component analysis approach to establish a key axis of variation in daily foraging patterns and test whether dominance-related attributes, territory location, or a personality trait influence this measure of foraging behaviour. Furthermore, I show how individual foraging patterns shift with day-to-day changes in local competition.

Chapter 3

In this paper I go on to investigate seasonal shifts in foraging patterns in relation to time of year, day length and temperature, predicting that shorter days will increase the need for efficient foraging while cold days will increase daily energy requirements. I find evidence of small dominance-linked differences in seasonal shifts of behaviour in addition to larger general shifts with seasonal factors.

Chapter 4

This paper examines how competition level influences individual foraging patterns and efficiency; the proportion of daytime spent at feeders, controlling for daily visit rate, is used as a proxy for foraging efficiency. I experimentally altered access to feeders in order to manipulate the effect of interference competition on individual feeding patterns, predicting that a reduction of interference will allow more efficient foraging. I also explore the relationship between feeder ‘traffic’ (the daily total number of visits recorded at a given feeder) and the timing of feeding. Once again, I test for an effect of dominance status on foraging patterns, predicting that subordinates will be more susceptible to an increase in competition.

Chapter 5

In this final paper I explore how foraging behaviour in a social context is related to social structure. Non-random associations with other individuals will have implications for the resultant group structure which is important in the spread of information and disease. Furthermore, if similarity of feeding patterns influences who an individual encounters, there may also be consequences for mate-choice.

REFERENCES

Alanärä, A., M. D. Burns and N. B. Metcalfe (2001). Intraspecific resource partitioning in brown trout: the temporal distribution of foraging is determined by social rank. *Journal of Animal Ecology* **70**(6): 980-986.

Aplin, L. M., D. R. Farine, J. Morand-Ferron and B. C. Sheldon (2012). Social networks predict patch discovery in a wild population of songbirds. *Proceedings of the Royal Society B: Biological Sciences* **279**(1745): 4199-4205.

Aplin, L. M., J. A. Firth, D. R. Farine, B. Voelkl, R. A. Crates, A. Culina, C. J. Garroway, C. A. Hinde, L. R. Kidd, I. Psorakis, N. D. Milligan, R. Radersma, B. L. Verhelst and B. C. Sheldon (2015). Consistent individual differences in the social phenotypes of wild great tits, *Parus major*. *Animal Behaviour* **108**: 117-127.

Aschoff, J. (1966). Circadian activity pattern with two peaks. *Ecology* **47**(4): 657-662.

Avery, M. I. and J. R. Krebs (1984). Temperature and foraging success of great tits *Parus major* hunting for spiders. *Ibis* **126**(1): 33-38.

Baldwin, S. P. and S. C. Kendeigh (1938). Variations in the weight of birds. *Auk* **55**: 416-467.

Bednekoff, P. A. and A. I. Houston (1994). Avian daily foraging patterns: effects of digestive constraints and variability. *Evolutionary Ecology* **8**(1): 36-52.

Bell, A. M., S. J. Hankison and K. L. Laskowski (2009). The repeatability of behaviour: a meta-analysis. *Animal Behaviour* **77**(4): 771-783.

Betts, M. M. (1955). The food of titmice in oak woodland. *Journal of Animal Ecology* **24**(2): 282-323.

Bolnick, D. I., R. Svanback, J. A. Fordyce, L. H. Yang, J. M. Davis, C. D. Hulsey and M. L. Forister (2003). The ecology of individuals: incidence and implications of individual specialization. *American Naturalist* **161**(1): 1-28.

Bonter, D. N. and E. S. Bridge (2011). Applications of radio frequency identification (RFID) in ornithological research: a review. *Journal of Field Ornithology* **82**(1): 1-10.

Bonter, D. N., B. Zuckerberg, C. W. Sedgwick and W. M. Hochachka (2013). Daily foraging patterns in free-living birds: exploring the predation-starvation trade-off. *Proceedings of the Royal Society B: Biological Sciences* **280**(1760): 20123087.

Caraco, T. (1980). On foraging time allocation in a stochastic environment. *Ecology* **61**(1): 119-128.

Castellano, S., B. Cuatto, R. Rinella, A. Rosso and C. Giacoma (2002). The advertisement call of the European treefrogs (*Hyla arborea*): A multilevel study of variation. *Ethology* **108**(1): 75-89.

Charmantier, A., R. H. McCleery, L. R. Cole, C. Perrins, L. E. B. Kruuk and B. C. Sheldon (2008). Adaptive phenotypic plasticity in response to climate change in a wild bird population. *Science* **320**(5877): 800-803.

Charnov, E. L. (1976). Optimal foraging, the marginal value theorem. *Theoretical Population Biology* **9**(2): 129-136.

Cole, E. F., P. R. Long, P. Zelazowski, M. Szulkin and B. C. Sheldon (2015). Predicting bird phenology from space: satellite-derived vegetation green-up signal uncovers spatial variation in phenological synchrony between birds and their environment. *Ecology and Evolution* **5**(21): 5057-5074.

Cope, D. R. (2006). Variation in daily and seasonal foraging routines of non-breeding barnacle geese (*Branta leucopsis*): working harder does not overcome environmental constraints. *Journal of Zoology* **260**(1): 65-71.

Cowlishaw, G. (1999). Ecological and social determinants of spacing behaviour in desert baboon groups. *Behavioral Ecology and Sociobiology* **45**(1): 67-77.

Dall, S. R. X. and M. S. Witter (1998). Feeding interruptions, diurnal mass changes and daily routines of behaviour in the zebra finch. *Animal Behaviour* **55**(3): 715-725.

Dingemanse, N. J. and D. Réale (2005). Natural selection and animal personality. *Behaviour* **142**(9-10): 1159-1184.

Emlen, J. M. (1966). Role of time and energy in food preference. *American Naturalist* **100**(916): 611-617.

English, S., S. Nakagawa and T. H. Clutton-Brock (2010). Consistent individual differences in cooperative behaviour in meerkats (*Suricata suricatta*). *Journal of Evolutionary Biology* **23**(8): 1597-1604.

Farine, D. R., C. J. Garroway and B. C. Sheldon (2012). Social network analysis of mixed-species flocks: exploring the structure and evolution of interspecific social behaviour. *Animal Behaviour* **84**(5): 1271-1277.

Firth, J. A. and B. C. Sheldon (2015). Experimental manipulation of avian social structure reveals segregation is carried over across contexts. *Proceedings of the Royal Society B: Biological Sciences* **282**(1802): 20142350.

Firth, J. A., B. Voelkl, D. R. Farine and B. C. Sheldon (2015). Experimental evidence that social relationships determine individual foraging behavior. *Current Biology* **In press**.

Franks, D. W., G. D. Ruxton and R. James (2010). Sampling animal association networks with the *gambit of the group*. *Behavioral Ecology and Sociobiology* **64**(3): 493-503.

Garant, D., J. D. Hadfield, L. E. B. Kruuk and B. C. Sheldon (2008). Stability of genetic variance and covariance for reproductive characters in the face of climate change in a wild bird population. *Molecular Ecology* **17**(1): 179-188.

Gibb, J. A. (1950). The breeding biology of the great and blue titmice. *Ibis* **92**(4): 501-539.

Gibb, J. A. (1954). Feeding ecology of tits, with notes on treecreeper and goldcrest. *Ibis* **96**(4): 513-543.

Giraldeau, L.-A. and T. Caraco (2000). Social foraging theory. Princeton, Princeton University Press.

Gosler, A. (1993). The great tit. London, Hamlyn.

Gosler, A. G., J. J. D. Greenwood and C. Perrins (1995). Predation risk and the cost of being fat. *Nature* **377**(6550): 621-623.

Heath, J. P., H. G. Gilchrist and R. C. Ydenberg (2010). Interactions between rate processes with different timescales explain counterintuitive foraging patterns of arctic wintering eiders. *Proceedings of the Royal Society B: Biological Sciences* **277**(1697): 3179-3186.

Hinde, R. A. (1952). The behaviour of the great tit (*Parus major*) and some other related species. *Behaviour (Supplement)* **2**: 1-201.

Houston, A. I. and J. M. McNamara (1999). Models of adaptive behaviour. Cambridge, Cambridge University Press.

Houston, A. I., J. M. McNamara and J. M. C. Hutchinson (1993). General results concerning the trade-off between gaining energy and avoiding predation. *Philosophical Transactions of the Royal Society B: Biological Sciences* **341**(1298): 375-397.

Kacelnik, A. (1979). Foraging efficiency of great tits (*Parus major* L.) in relation to light intensity. *Animal Behaviour* **27**(1): 237-241.

Kacelnik, A. and M. Bateson (1996). Risky theories - the effects of variance on foraging decisions. *American Zoologist* **36**(4): 402-434.

Kluijver, H. N. (1951). The population ecology of the great tit, *Parus m. major* L. *Ardea* **39**(1): 1-135.

Knowles, S. C. L., V. Palinauskas and B. C. Sheldon (2010). Chronic malaria infections increase family inequalities and reduce parental fitness: experimental evidence from a wild bird population. *Journal of Evolutionary Biology* **23**(3): 557-569.

Krams, I. (2000). Length of feeding day and body weight of great tits in a single- and a two-predator environment. *Behavioral Ecology and Sociobiology* **48**(2): 147-153.

Krams, I., D. Cirule, V. Suraka, T. Krama, M. J. Rantala and G. Ramey (2010). Fattening strategies of wintering great tits support the optimal body mass hypothesis under conditions of extremely low ambient temperature. *Functional Ecology* **24**(1): 172-177.

Kurvers, R. H. J. M., B. A. Nolet, H. H. T. Prins, R. C. Ydenberg and K. van Oers (2012). Boldness affects foraging decisions in barnacle geese: an experimental approach. *Behavioral Ecology* **23**(6): 1155-1161.

Lima, S. L. and L. M. Dill (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* **68**(4): 619-640.

MacArthur, R. H. and E. R. Pianka (1966). On optimal use of a patchy environment. *American Naturalist* **100**(916): 603-609.

MacLeod, R., A. G. Gosler and W. Cresswell (2005). Diurnal mass gain strategies and perceived predation risk in the great tit *Parus major*. *Journal of Animal Ecology* **74**(5): 956-964.

Mangel, M. and C. W. Clark (1988). Dynamic modeling in behavioral ecology. Princeton, Princeton University Press.

Maynard Smith, J. (1982). Evolution and the theory of games. Cambridge, Cambridge University Press.

McNamara, J. M., Z. Barta, A. I. Houston and P. Race (2005). A theoretical investigation of the effect of predators on foraging behaviour and energy reserves. *Proceedings of the Royal Society B: Biological Sciences* **272**(1566): 929-934.

McNamara, J. M., A. I. Houston and S. L. Lima (1994). Foraging routines of small birds in winter: a theoretical investigation. *Journal of Avian Biology* **25**(4): 287-302.

Missoweit, M., S. Engels and K. P. Sauer (2007). Foraging ability in the scorpionfly *Panorpa vulgaris*: individual differences and heritability. *Behavioral Ecology and Sociobiology* **61**(3): 487-492.

Morton, M. L. (1967). Diurnal feeding patterns in white-crowned sparrows, *Zonotrichia leucophrys gambeli*. *Condor* **69**(5): 491-512.

Newton, I. (1986). The Sparrowhawk. Calton, Poyser.

Parker, G. A. and R. A. Stuart (1976). Animal behavior as a strategy optimizer: evolution of resource assessment strategies and optimal emigration thresholds. *American Naturalist* **110**(976): 1055-1076.

Patrick, S. C., S. Bearhop, D. Grémillet, A. Lescroël, W. J. Grecian, T. W. Bodey, K. C. Hamer, E. Wakefield, M. Le Nuz and S. C. Votier (2014). Individual differences in searching behaviour and spatial foraging consistency in a central place marine predator. *Oikos* **123**(1): 33-40.

Perrins, C. M. (1966). The effect of beech crops on great tit populations and movements. *British Birds* **59**(10): 419-432.

Perrins, C. M. (1979). British Tits. London, Collins.

Piersma, T. and J. Drent (2003). Phenotypic flexibility and the evolution of organismal design. *Trends in Ecology & Evolution* **18**(5): 228-233.

Pita, R., A. Mira and P. Beja (2011). Circadian activity rhythms in relation to season, sex and interspecific interactions in two Mediterranean voles. *Animal Behaviour* **81**(5): 1023-1030.

Polo, V. and L. M. Bautista (2006). Daily routines of body mass gain in birds: 2. An experiment with reduced food availability. *Animal Behaviour* **72**(3): 517-522.

Psorakis, I., S. J. Roberts, I. Rezek and B. C. Sheldon (2012). Inferring social network structure in ecological systems from spatio-temporal data streams. *Journal of the Royal Society Interface* **9**(76): 3055-3066.

Pyke, G. H., H. R. Pulliam and E. L. Charnov (1977). Optimal foraging: a selective review of theory and tests. *Quarterly Review of Biology* **52**(2): 137-154.

Quinn, J. L., E. F. Cole, J. Bates, R. W. Payne and W. Cresswell (2012). Personality predicts individual responsiveness to the risks of starvation and predation. *Proceedings of the Royal Society B: Biological Sciences* **279**(1735): 1919-1926.

Ratikainen, I. I. and J. Wright (2013). Adaptive management of body mass by Siberian jays. *Animal Behaviour* **85**(2): 427-434.

Savill, P. S., C. M. Perrins, K. J. Kirby and N. Fisher (2010). Wytham Woods: Oxford's ecological laboratory. Oxford, Oxford University Press.

Schoener, T. W. (1974). Resource partitioning in ecological communities. *Science* **185**(4145): 27-39.

Sih, A., A. Bell and J. C. Johnson (2004). Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution* **19**(7): 372-378.

Smith, B. R. and D. T. Blumstein (2008). Fitness consequences of personality: a meta-analysis. *Behavioral Ecology* **19**(2): 448-455.

Steinmeyer, C., J. C. Mueller and B. Kempenaers (2013). Individual variation in sleep behaviour in blue tits *Cyanistes caeruleus*: assortative mating and associations with fitness-related traits. *Journal of Avian Biology* **44**(2): 159-168.

Stephens, D. W. and J. R. Krebs (1986). Foraging theory. Princeton, Princeton University Press.

Van der Veen, I. T. (2000). Daily routines and predator encounters in yellowhammers *Emberiza citrinella* in the field during winter. *Ibis* **142**(3): 413-420.

Verhulst, S. and O. Hogstad (1996). Social dominance and energy reserves in flocks of willow tits. *Journal of Avian Biology* **27**(3): 203-208.

Whitehead, H. (2008). Analyzing animal societies: quantitative methods for vertebrate social analysis. Chicago, University of Chicago Press.

Wilson, D. S. (1998). Adaptive individual differences within single populations. *Philosophical Transactions of the Royal Society B: Biological Sciences* **353**(1366): 199-205.

CHAPTER 2

To graze or gorge: consistency and flexibility of individual foraging strategies in tits

To graze or gorge: consistency and flexibility of individual foraging strategies in tits

Nicole D. Milligan, Reinder Radersma, Ella F. Cole and Ben C. Sheldon

1. An individual's foraging behaviour and the time it allocates to feeding have direct consequences for its fitness. While there has been much research on the determinants of population-level foraging decisions, to date few studies have investigated individual differences in fine-scale daily foraging patterns amongst wild animals.

2. Here, we explore the consistency and plasticity in feeding strategies of individual great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*), using data collected from a grid of 65 automated feeding stations distributed across a 385-ha deciduous woodland, during three winter seasons. We use a principal component analysis to describe individual variation in six different 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 of the two species 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* ranging from 0.42 to 0.55). PC2 ('Transience'), accounting for 27% of variance, described how much individuals used the feeders and related very strongly to the number of visits a bird made to a feeder in a day, which was also repeatable within and between years (*r*: 0.45 to 0.60).

4. Birds in behaviourally dominant categories (great tits, males and adults) binged more than birds of the respective subordinate categories (blue tits, females and juveniles) when their territories were distant from feeding stations. Moreover, great tits and males visited feeders more times per day than blue tits and females respectively. ‘Exploration behaviour’ was unrelated to both measures of daily foraging behaviour. We found that birds feeding further from their territory visited fewer times than birds feeding closer.

5. While exhibiting consistent individual differences, birds also showed flexibility in foraging patterns, binge-eating less and making more daily visits to feeders when they experienced greater local competition.

6. This study presents some of the first evidence that birds use consistent alternative foraging strategies at a fine temporal scale. Birds are relatively consistent in their strategies, but also adjust their foraging behaviour in response to 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.

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). 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, 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). These differences 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 feeding 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 strategies. 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 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 generally 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); field studies have generally focused on monitored 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 has recently been 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 strategy. Furthermore, it was not possible to test whether intrinsic differences (such as age or sex) or differences in environmental conditions (such as competition or resource distribution) influenced temporal feeding patterns.

In this study we investigate whether individuals exhibit different daily foraging strategies. A recent study on great tits (*Parus major*) that has made use of this RFID technology, suggests that individuals may indeed have alternative foraging strategies in terms of how they manage the trade-off between starvation and predation risk throughout the day (Quinn *et al.* 2012). In this study, 'exploration behaviour', a commonly used measure of proactive-reactive personality axis, and social dominance category (age and sex) together were shown to affect 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 the 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 intrinsic 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 this individual-based 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 the number of times a bird visited a feeder each day. We then tested whether these individual differences could be predicted by the level of local competition experienced by a bird, various intrinsic factors (age, sex, species and, ‘exploration behaviour’), and the distance a bird travelled from its overnight roost site to reach the feeder. We predicted that birds would be able to feed more efficiently (have more highly clustered visits) and visit more often when local competition was low. Furthermore we expected that dominant classes of birds (great tits, males and adults) and ‘proactive’ personality types would be more efficient feeders and visit the feeder more often than subordinate classes (blue tits, females and juveniles) and ‘reactive’ personality types respectively. Finally, we predicted that birds travelling further from their territory to a feeder would feed more efficiently and visit less often than birds roosting close to the feeder due to the associated time constraints.

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 was determined by plumage (born in the previous breeding season or before) or by year of ringing as a chick; 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 reactive-proactive personality axis was assayed in a subset of great tits, using an open-field exploration behaviour test in captivity. Great tits were caught using mist-nets during winter and taken, under licence from Natural England, to the John Krebs Field Station, Oxford, UK. We housed the birds individually overnight before running an 8-minute assay in a novel environment for each great tit. 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).

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^3 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. 21st or 22nd 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 × 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.

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 great tit (GT) and blue tit (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 mid-point 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 in a similar manner as above to allocate feeder visits to feeding bouts.

Individuals used on average 2.4 different feeding stations within a winter season. 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. However, we did include these visits by within-day movers 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; again these visits did contribute to the daily measure of feeder traffic.

Statistical analysis

We conducted all statistical analyses using R 3.1.1 (R 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. 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. Since we have a direct measure of the daily number of feeder visits which is highly correlated with PC2 (Figs S2c & S2d), we consequently analysed the number of visits rather than transience (PC2).

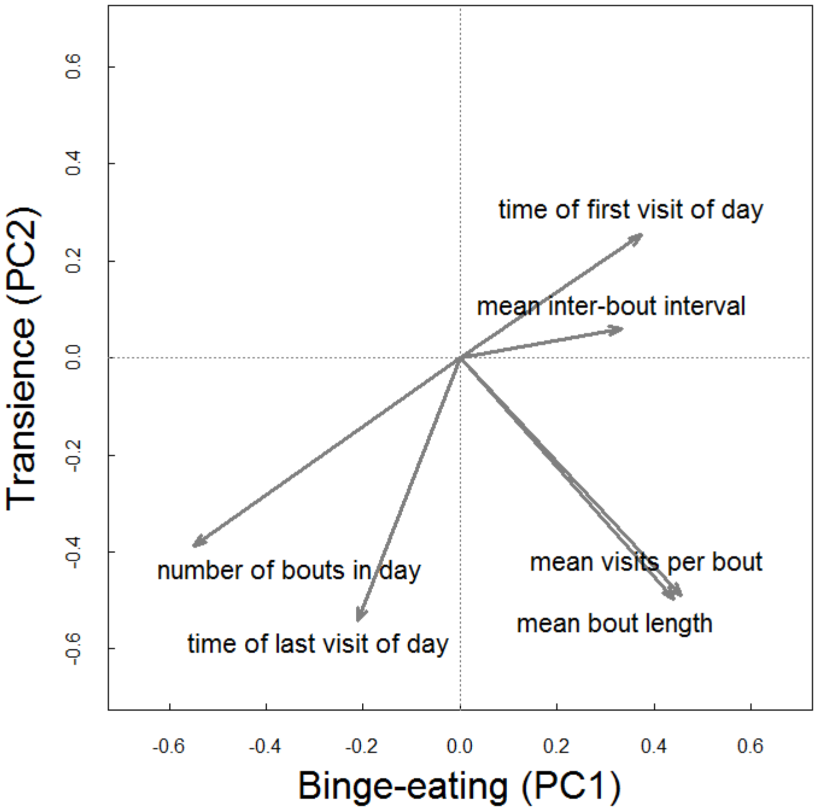


Fig. 1. Graphical representation of the degree to which different measures of the timing of feeding of individual great tits and blue tits load onto the first two axes of a principal component analysis. The length and direction of the arrows indicate the loading on the principal component axes.

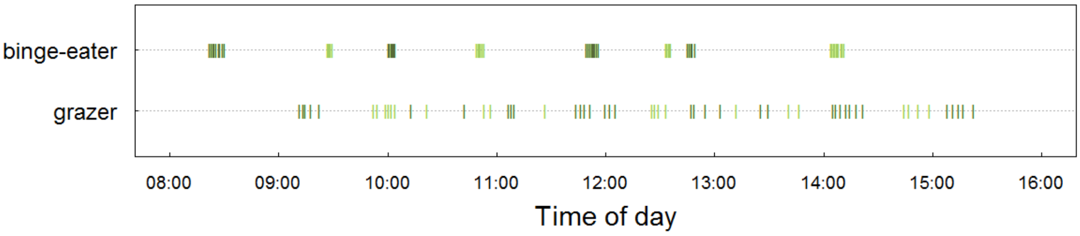


Fig. 2. Illustration of variation in timing of visits by two individual great tits at the same feeder on the same day; each bird made an identical number of visits. Alternate feeding bouts are shown in different shades. $PC1_{binge\text{-}eater} = 1.54$; $PC1_{grazer} = -0.39$.

In order to test for consistent individual differences in the timing of feeding, we estimated the repeatability of PC1 and daily number of visits per individual. We used a generalized linear mixed-effect model (GLMM)-based method to calculate repeatability (Dingemanse & Dochtermann 2013): the variance attributed to individuals was taken as a proportion of the total recorded variance. We calculated individual-level repeatability of PC1 and number of visits for each species within each winter and fitted an additional GLMM for each species, to estimate the individual repeatability of PC1 between years, using individual yearly averages of PC1. We estimated a similar set of repeatabilities for the daily number of visits by individuals.

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. Since the daily number of visits by an individual is negatively correlated with PC1 (GTs: Pearson's r=-0.32, df=11379, p<0.001 and BTs: Pearson's r=-0.43, df=12992, p<0.001; Figs S2a & S2b) we also added the number of visits as a fixed effect to the GLMMs. 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. To test how age and sex affected PC1 at different distances to territory, we added interaction terms for age × DTT and sex × DTT. We fitted similar GLMMs to determine the effect of species, age, sex, distance to territory and competition on the daily number of feeder visits by individuals.

RESULTS

Characterizing foraging behaviour

We analysed a total of 933,086 feeder visits in 270,978 bouts by 1406 individual great tits and 1728 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 ± 1 SD of visits per individual was 34 ± 15 and of bouts per individual was 10 ± 4.

The PCA on 6 daily feeding pattern parameters revealed that variation loaded heavily on two components: PC1 and PC2 accounted for 38.0% and 27.1% of the total variation respectively. Transience was highly 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). Since we have a direct measure of the daily number of feeder visits, we present results for the number of visits rather than for transience.

Individual consistency and state-dependent differences in foraging patterns

Individuals showed significantly 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 the number of daily visits to feeders (*r* ranging from 0.45 to 0.60 within winters and from 0.47 to 0.51 between winters; Fig. 3b). Great tits binged to a greater extent (Figs 4a & 4b; estimated mean GT PC1: 0.48, BT PC1: -0.16, SE=0.04, t=17.53, P<0.001, n=24,345) and visited feeders more times per day than blue tits (Figs 4c & 4d; estimated mean GT daily visits: 39.44, BT daily visits: 29.96, SE=0.45, t=21.10, p<0.001, n=24,345).

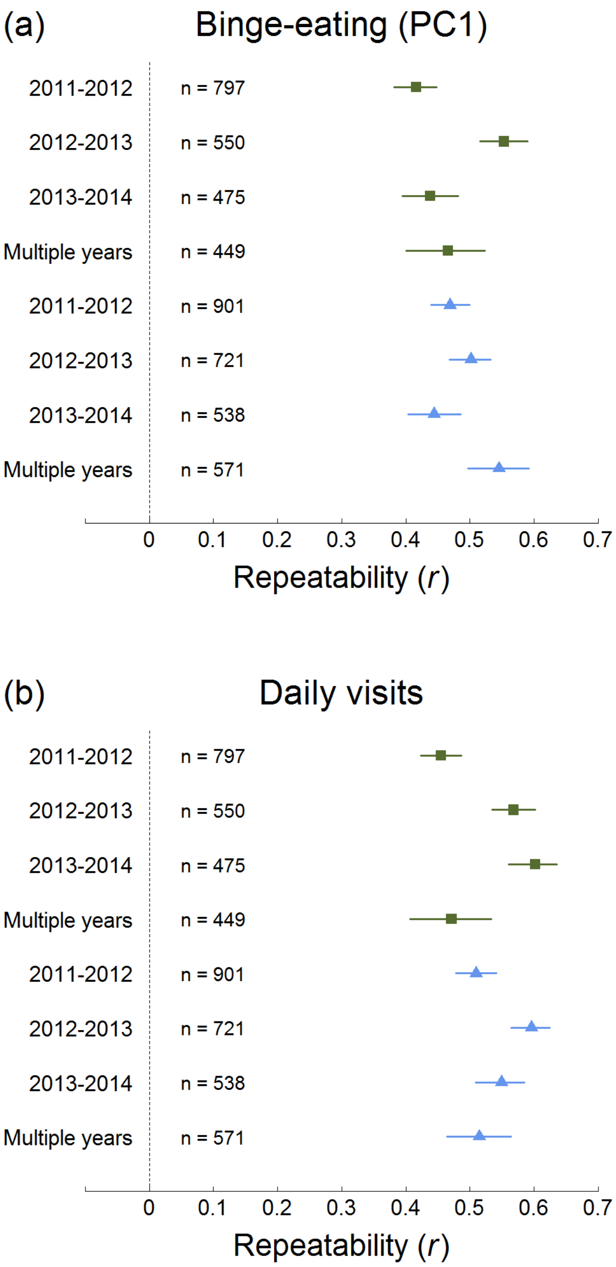


Fig. 3. Repeatability r ± 95% CI of (a) binge-eating and (b) daily number of visits by winter; great tits: green squares, blue tits: blue triangles. Estimates with confidence intervals that do not cross the dotted line at r=0 are significantly repeatable at the α=0.05 level; n=number of individuals with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

Overall, individuals of both species with subsequent breeding territories further from feeding stations binged more (Figs 4a & 4b) and visited feeders fewer times per day (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 increasing distance to territory, males increased binge-eating more than females and adults increased binge-eating more than juveniles, i.e. adult males had the most positive slopes with DTT and juvenile females had the least positive slopes with DTT (Figs 4a & 4b; see Table 1 for model estimates). Males visited feeders more per day than females in both species and juveniles visited feeders more per day than adults in great tits only (Figs 4c & 4d; see Table 2 for model estimates).

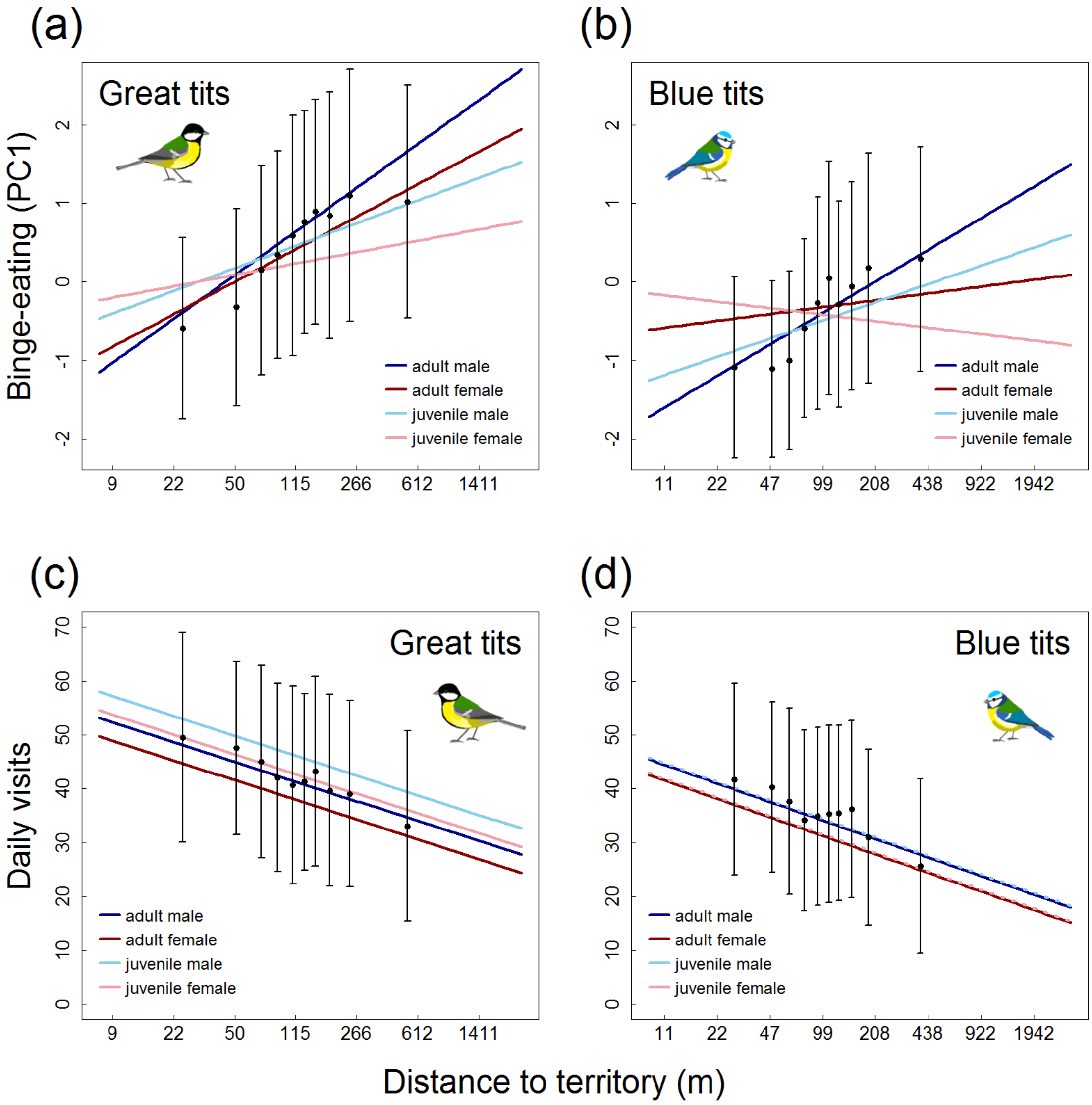


Fig. 4. Mean level of binge-eating (PC1) ± 1 SD for (a) great tits and (b) blue tits and mean daily number of visits ± 1 SD for (c) great tits and (d) blue tits with increasing distance to subsequent breeding territory; data were binned into tenths by distance to territory. Lines show fitted model effects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

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.

	great tits					blue tits				
Fixed effect	Coefficient	SE	*t*	d.f.	P	Coefficient	SE	*t*	d.f.	P
daily visits	−0.38	0.02	−16.39	345	<0.001	−0.72	0.02	−33.48	310	<0.001
age (juvenile)	−0.18	0.06	−3.13	345	0.002	−0.10	0.06	−1.57	310	0.118
sex (male)	0.23	0.07	3.08	345	0.002	−0.07	0.07	−0.94	310	0.346
distance to territory	0.41	0.05	9.20	345	<0.001	0.09	0.05	1.89	310	0.060
average competition	0.00	0.05	0.04	345	0.970	0.05	0.05	1.11	310	0.267
deviation from average competition	−0.32	0.04	−8.13	345	<0.001	−0.27	0.04	−6.30	310	<0.001
age * distance to territory	−0.27	0.05	−5.46	345	<0.001	−0.17	0.05	−3.45	310	0.001
sex * distance to territory	0.14	0.05	2.68	345	0.008	0.31	0.05	5.82	310	<0.001

	great tits			blue tits		
Random term	Variance	SD	n	Variance	SD	n
individual ID	0.64	0.80	623	0.44	0.66	504
individual ID with random slope for competition deviation	0.10	0.31	623	0.14	0.37	504
site	0.18	0.43	64	0.11	0.33	63
date	0.07	0.26	30	0.06	0.25	30
residual	1.06	1.03		0.66	0.81	

Table 2. Linear mixed model on factors affecting the daily number of visits to feeders. Number of observations: great tit n=4895; blue tit n=3405.

	great tits					blue tits				
Fixed effect	Coefficient	SE	*t*	d.f.	P	Coefficient	SE	*t*	d.f.	P
age (juvenile)	4.81	0.64	7.51	100	<0.001	0.30	0.86	0.35	167	0.724
sex (male)	3.40	0.81	4.22	100	<0.001	2.85	1.11	2.58	167	0.011
distance to territory	-3.67	0.32	-11.31	100	<0.001	-3.44	0.39	-8.75	167	<0.001
average competition	6.17	0.54	11.33	100	<0.001	4.87	0.65	7.50	167	<0.001
deviation from average competition	8.40	0.45	18.87	100	<0.001	6.85	0.57	11.96	167	<0.001

	great tits			blue tits		
Random term	Variance	SD	n	Variance	SD	n
individual ID	78.63	8.87	623	107.69	10.38	504
individual ID with random slope for competition deviation	20.42	4.52	623	27.36	5.23	504
site	38.01	6.17	64	22.78	4.77	63
date	25.48	5.05	30	7.45	2.73	30
residual	125.47	11.20		116.61	10.80	

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 have a significant effect on the level of binge-eating (β=0.03, SE=0.03, t=1.18, P=0.24, df=460) or on the number of daily visits (β=-0.34, SE=0.26, t=-1.31, p=0.19, df=115) when added to the respective models.

Effects of change in local competition on foraging strategies

The extent of binge-eating by an individual was not predicted by the mean level of competition experienced, but was predicted by the daily deviation from its mean level of competition (Table 1): individuals binged less on days when feeders were more busy than they normally experienced (Fig. 5a). Both the average competition and deviation from average competition experienced predicted the daily number of feeder visits by individuals (Table 2), with individuals making more daily visits when feeders were busy (Fig. 5b).

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

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 the daily number of visits to feeders with r above 0.4 for all within-year and between-year estimates. Moreover, individuals shifted their foraging patterns with a change in local competition, binge-eating less and visiting 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 wild populations, 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, binge-eating and transience (Fig. 1). The binge-eating axis quantified how clustered an individual's feeding was while transience related to the number of daily visits to a feeder.

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), binge-eat more than blue tits, juveniles and females (age and sex were only significant in great tits), 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 (Kluijver 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 strategy 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 a significant interaction between age/sex class and distance to territory explained some of the variation in foraging strategy: with greater distance to territory, males and adults binge-eat more than females and juveniles to a greater extent (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 visit less often than those with closer territories (Figs 4c & 4d).

Males of both species made more daily visits to feeders 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. In great tits but not blue tits, juveniles visited feeders more times per day 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.

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 significant relationship between either the clustering, or the daily number, of feeder visits 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 significant repeatability in both binge-eating and the daily number of feeder visits across the study period – i.e. both within and between years (Fig. 3). With values between 0.4 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 strategy with change in local competition: individuals binged less when feeders were busier than they usually experienced (Fig. 5a). This suggests that a binge-eating strategy may be the preferred strategy 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 strategy than grazing by reducing the total daily time spent near feeders. Reducing the number of feeding bouts by binge-eating to a greater extent could also make it a more efficient strategy by reducing longer-distance travel, or ‘commuting’, costs and increasing the amount of time available for rest and other behaviours.

To investigate the consequences of foraging patterns, it would be useful to test whether foraging strategy has an effect on survival, recruitment to the breeding population, or reproductive success in the future. Late winter measures of foraging strategy would likely have a stronger effect on reproductive success than the midwinter measures reported here. However, the number of visits to feeders over the whole winter has no effect on these measures of fitness (Crates *et al.* 2016). 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 visited feeders more times per day 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 strategies 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 and daily number of feeder visits. In addition, individuals reduced the temporal clustering of their visits as local competition increased. These individual-level findings give a more complete description of the timing of foraging in these species than previously reported. This level of detail will enable the foraging dynamics of the population to be more accurately modelled in the future, which may give rise to considerably different predictions than population-level analyses. For example, it would be interesting to investigate whether individual foraging strategies affect flock structure or pair bonds. Adaptive variation in foraging strategies may have important implications for survival and reproductive success; therefore future studies should also explore their fitness consequences.

ACKNOWLEDGEMENTS

We thank Lucy Aplin for providing personality data, the social network group for help with collecting winter logger data, catching and tagging birds during the winter, and all the Wytham tit fieldworkers for assistance in catching and tagging birds during the spring. We are also grateful to Lucy Aplin and Josh Firth for helpful comments on the manuscript. This work was funded by a European Research Council (ERC) grant to B.C.S (AdG 250164).

REFERENCES

Alanärä, A., M. D. Burns and N. B. Metcalfe (2001). Intraspecific resource partitioning in brown trout: the temporal distribution of foraging is determined by social rank. *Journal of Animal Ecology* **70**(6): 980-986.

Bednekoff, P. A. and A. I. Houston (1994). Avian daily foraging patterns: effects of digestive constraints and variability. *Evolutionary Ecology* **8**(1): 36-52.

Bednekoff, P. A. and J. R. Krebs (1995). Great tit fat reserves: effects of changing and unpredictable feeding day length. *Functional Ecology* **9**(3): 457-462.

Bell, A. M., S. J. Hankison and K. L. Laskowski (2009). The repeatability of behaviour: a meta-analysis. *Animal Behaviour* **77**(4): 771-783.

Bonter, D. N. and E. S. Bridge (2011). Applications of radio frequency identification (RFID) in ornithological research: a review. *Journal of Field Ornithology* **82**(1): 1-10.

Bonter, D. N., B. Zuckerberg, C. W. Sedgwick and W. M. Hochachka (2013). Daily foraging patterns in free-living birds: exploring the predation-starvation trade-off. *Proceedings of the Royal Society B: Biological Sciences* **280**(1760): 20123087.

Bouwhuis, S., B. C. Sheldon and S. Verhulst (2011). Basal metabolic rate and the rate of senescence in the great tit. *Functional Ecology* **25**(4): 829-838.

Brittingham, M. C. and S. A. Temple (1992). Use of winter bird feeders by black-capped chickadees. *Journal of Wildlife Management* **56**(1): 103-110.

Brodin, A. (2007). Theoretical models of adaptive energy management in small wintering birds. *Philosophical Transactions of the Royal Society B: Biological Sciences* **362**(1486): 1857-1871.

Broggi, J., E. Hohtola, K. Koivula, M. Orell and J. A. Nilsson (2010). Idle slow as you grow old: longitudinal age-related metabolic decline in a wild passerine. *Evolutionary Ecology* **24**(1): 177-184.

Broggi, J., E. Hohtola, K. Koivula, M. Orell, R. L. Thomson and J. A. Nilsson (2007). Sources of variation in winter basal metabolic rate in the great tit. *Functional Ecology* **21**(3): 528-533.

Castellano, S., B. Cuatto, R. Rinella, A. Rosso and C. Giacoma (2002). The advertisement call of the European treefrogs (*Hyla arborea*): A multilevel study of variation. *Ethology* **108**(1): 75-89.

Cole, E. F. and J. L. Quinn (2012). Personality and problem-solving performance explain competitive ability in the wild. *Proceedings of the Royal Society B: Biological Sciences* **279**(1731): 1168-1175.

Crates, R. A., J. A. Firth, D. R. Farine, C. J. Garroway, L. R. Kidd, L. M. Aplin, R. Radersma, N. D. Milligan, B. Voelkl, A. Culina, B. L. Verhelst, C. A. Hinde and B. C. Sheldon (2016). Individual variation in winter supplementary food consumption and its consequences for reproduction in wild birds. *Journal of Avian Biology*. doi: 10.1111/jav.00936.

Dall, S. R. X. and M. S. Witter (1998). Feeding interruptions, diurnal mass changes and daily routines of behaviour in the zebra finch. *Animal Behaviour* **55**(3): 715-725.

De Laet, J. (1984). Site-related dominance in the great tit *Parus major major*. *Ornis Scandinavica* **15**(2): 73-78.

De Laet, J. F. (1985). Dominance and anti-predator behavior of great tits *Parus major*: a field study. *Ibis* **127**(3): 372-377.

Desrochers, A. (1992). Age and foraging success in European blackbirds - variation between and within individuals. *Animal Behaviour* **43**(6): 885-894.

Dingemanse, N. J. and N. A. Dochtermann (2013). Quantifying individual variation in behaviour: mixed-effect modelling approaches. *Journal of Animal Ecology* **82**(1): 39-54.

Dingemanse, N. J. and D. Réale (2005). Natural selection and animal personality. *Behaviour* **142**(9-10): 1159-1184.

English, S., S. Nakagawa and T. H. Clutton-Brock (2010). Consistent individual differences in cooperative behaviour in meerkats (*Suricata suricatta*). *Journal of Evolutionary Biology* **23**(8): 1597-1604.

Enoksson, B. (1988). Age- and sex-related differences in dominance and foraging behavior of nuthatches *Sitta europaea*. *Animal Behaviour* **36**(1): 231-238.

Gosler, A. (1993). The great tit. London, Hamlyn.

Gosler, A. and T. Carruthers (1999). Body reserves and social dominance in the great tit *Parus major* in relation to winter weather in southwest Ireland. *Journal of Avian Biology* **30**(4): 447-459.

Gosler, A. G. (1987). Pattern and process in the bill morphology of the great tit *Parus major*. *Ibis* **129**(4): 451-476.

Greig, S. A., J. C. Coulson and P. Monaghan (1983). Age-related differences in foraging success in the herring gull (*Larus argentatus*). *Animal Behaviour* **31**(4): 1237-1243.

Heath, J. P., H. G. Gilchrist and R. C. Ydenberg (2010). Interactions between rate processes with different timescales explain counterintuitive foraging patterns of arctic wintering eiders. *Proceedings of the Royal Society B: Biological Sciences* **277**(1697): 3179-3186.

Hegner, R. E. (1985). Dominance and anti-predator behavior in blue tits (*Parus caeruleus*). *Animal Behaviour* **33**(3): 762-768.

Herborn, K. A., B. J. Heidinger, L. Alexander and K. E. Arnold (2014). Personality predicts behavioral flexibility in a fluctuating, natural environment. *Behavioral Ecology* **25**(6): 1374-1379.

Hinde, R. A. (1952). The behaviour of the great tit (*Parus major*) and some other related species. *Behaviour (Supplement)* **2**: 1-201.

Houston, A. and J. McNamara (1982). A sequential approach to risk-taking. *Animal Behaviour* **30**(4): 1260-1261.

Houston, A. I. and J. M. McNamara (1993). A theoretical investigation of the fat reserves and mortality levels of small birds in winter. *Ornis Scandinavica* **24**(3): 205-219.

Houston, A. I., J. M. McNamara and J. M. C. Hutchinson (1993). General results concerning the trade-off between gaining energy and avoiding predation. *Philosophical Transactions of the Royal Society B: Biological Sciences* **341**(1298): 375-397.

Kenward, M. G. and J. H. Roger (1997). Small sample inference for fixed effects from restricted maximum likelihood. *Biometrics* **53**(3): 983-997.

Kluijver, H. N. (1951). The population ecology of the great tit, *Parus m. major* L. *Ardea* **39**(1): 1-135.

MacLeod, R., A. G. Gosler and W. Cresswell (2005). Diurnal mass gain strategies and perceived predation risk in the great tit *Parus major*. *Journal of Animal Ecology* **74**(5): 956-964.

McCleery, R. H., R. A. Pettifor, P. Armbruster, K. Meyer, B. C. Sheldon and C. M. Perrins (2004). Components of variance underlying fitness in a natural population of the great tit *Parus major*. *American Naturalist* **164**(3): E62-E72.

McNamara, J. M., Z. Barta, A. I. Houston and P. Race (2005). A theoretical investigation of the effect of predators on foraging behaviour and energy reserves. *Proceedings of the Royal Society B: Biological Sciences* **272**(1566): 929-934.

McNamara, J. M., A. I. Houston and S. L. Lima (1994). Foraging routines of small birds in winter: a theoretical investigation. *Journal of Avian Biology* **25**(4): 287-302.

Missoweit, M., S. Engels and K. P. Sauer (2007). Foraging ability in the scorpionfly *Panorpa vulgaris*: individual differences and heritability. *Behavioral Ecology and Sociobiology* **61**(3): 487-492.

Moe, B., B. Rønning, S. Verhulst and C. Bech (2009). Metabolic ageing in individual zebra finches. *Biology Letters* **5**(1): 86-89.

Newton, I. (1986). The Sparrowhawk. Calton, Poyser.

Oberski, I. M. and J. D. Wilson (1991). Territoriality and site-related dominance: on two related concepts in avian social organization. *Ethology* **87**(3-4): 225-236.

Olsson, O., U. Wiktander and S. G. Nilsson (2000). Daily foraging routines and feeding effort of a small bird feeding on a predictable resource. *Proceedings of the Royal Society B: Biological Sciences* **267**(1451): 1457-1461.

Parker, G. A. and R. A. Stuart (1976). Animal behavior as a strategy optimizer: evolution of resource assessment strategies and optimal emigration thresholds. *American Naturalist* **110**(976): 1055-1076.

Patrick, S. C., S. Bearhop, D. Grémillet, A. Lescroël, W. J. Grecian, T. W. Bodey, K. C. Hamer, E. Wakefield, M. Le Nuz and S. C. Votier (2014). Individual differences in searching behaviour and spatial foraging consistency in a central place marine predator. *Oikos* **123**(1): 33-40.

Perrins, C. M. (1979). British Tits. London, Collins.

Piersma, T. and J. Drent (2003). Phenotypic flexibility and the evolution of organismal design. *Trends in Ecology & Evolution* **18**(5): 228-233.

Polo, V. and L. M. Bautista (2006). Daily routines of body mass gain in birds: 2. An experiment with reduced food availability. *Animal Behaviour* **72**(3): 517-522.

Quinn, J. L., E. F. Cole, J. Bates, R. W. Payne and W. Cresswell (2012). Personality predicts individual responsiveness to the risks of starvation and predation. *Proceedings of the Royal Society B: Biological Sciences* **279**(1735): 1919-1926.

Quinn, J. L., S. C. Patrick, S. Bouwhuis, T. A. Wilkin and B. C. Sheldon (2009). Heterogeneous selection on a heritable temperament trait in a variable environment. *Journal of Animal Ecology* **78**(6): 1203-1215.

R Development Core Team (2014). R: A language and environment for statistical computing. Vienna, R Foundation for Statistical Computing.

Ratikainen, I. I. and J. Wright (2013). Adaptive management of body mass by Siberian jays. *Animal Behaviour* **85**(2): 427-434.

Savill, P. S., C. M. Perrins, K. J. Kirby and N. Fisher (2010). Wytham Woods: Oxford's ecological laboratory. Oxford, Oxford University Press.

Schoener, T. W. (1974). Resource partitioning in ecological communities. *Science* **185**(4145): 27-39.

Sih, A., A. Bell and J. C. Johnson (2004). Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution* **19**(7): 372-378.

Smith, B. R. and D. T. Blumstein (2008). Fitness consequences of personality: a meta-analysis. *Behavioral Ecology* **19**(2): 448-455.

Steinmeyer, C., J. C. Mueller and B. Kempenaers (2013). Individual variation in sleep behaviour in blue tits *Cyanistes caeruleus*: assortative mating and associations with fitness-related traits. *Journal of Avian Biology* **44**(2): 159-168.

Stephens, D. W., J. S. Brown and R. C. Ydenberg (2007). Foraging: behavior and ecology. Chicago, University of Chicago Press.

Stephens, D. W. and J. R. Krebs (1986). Foraging theory. Princeton, Princeton University Press.

Svensson, L. (1992). Identification guide to European passerines. Thetford, British Trust for Ornithology.

Wilson, D. S. (1998). Adaptive individual differences within single populations. *Philosophical Transactions of the Royal Society B: Biological Sciences* **353**(1366): 199-205.

APPENDIX

Supplementary Figures

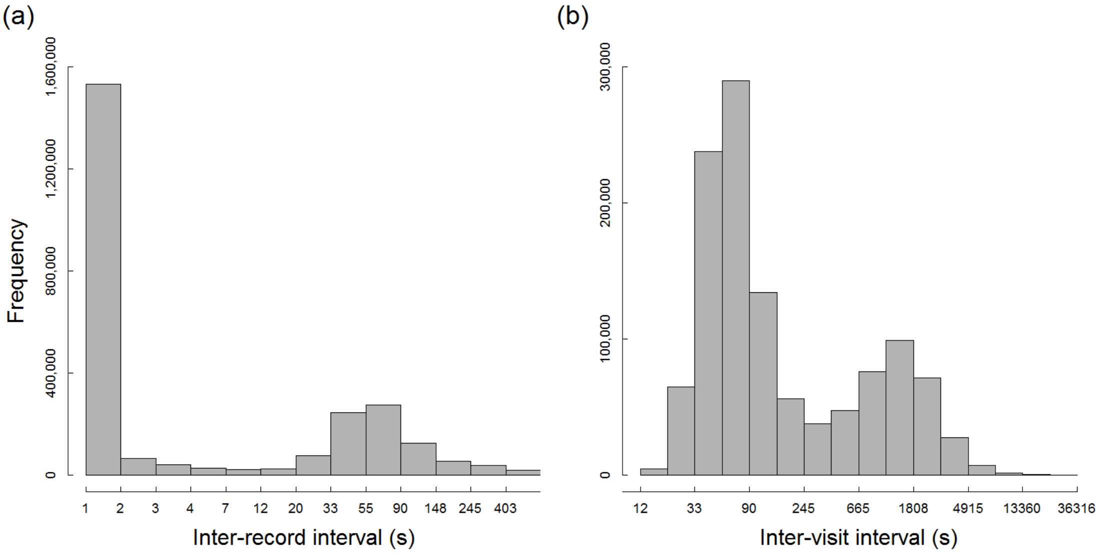


Fig. S1. Histogram on a log scale of (a) inter-record intervals less than 514s and (b) inter-visit intervals for great and blue tits, recorded over five consecutive midwinter weekends from three consecutive years between December 2011 and January 2014.

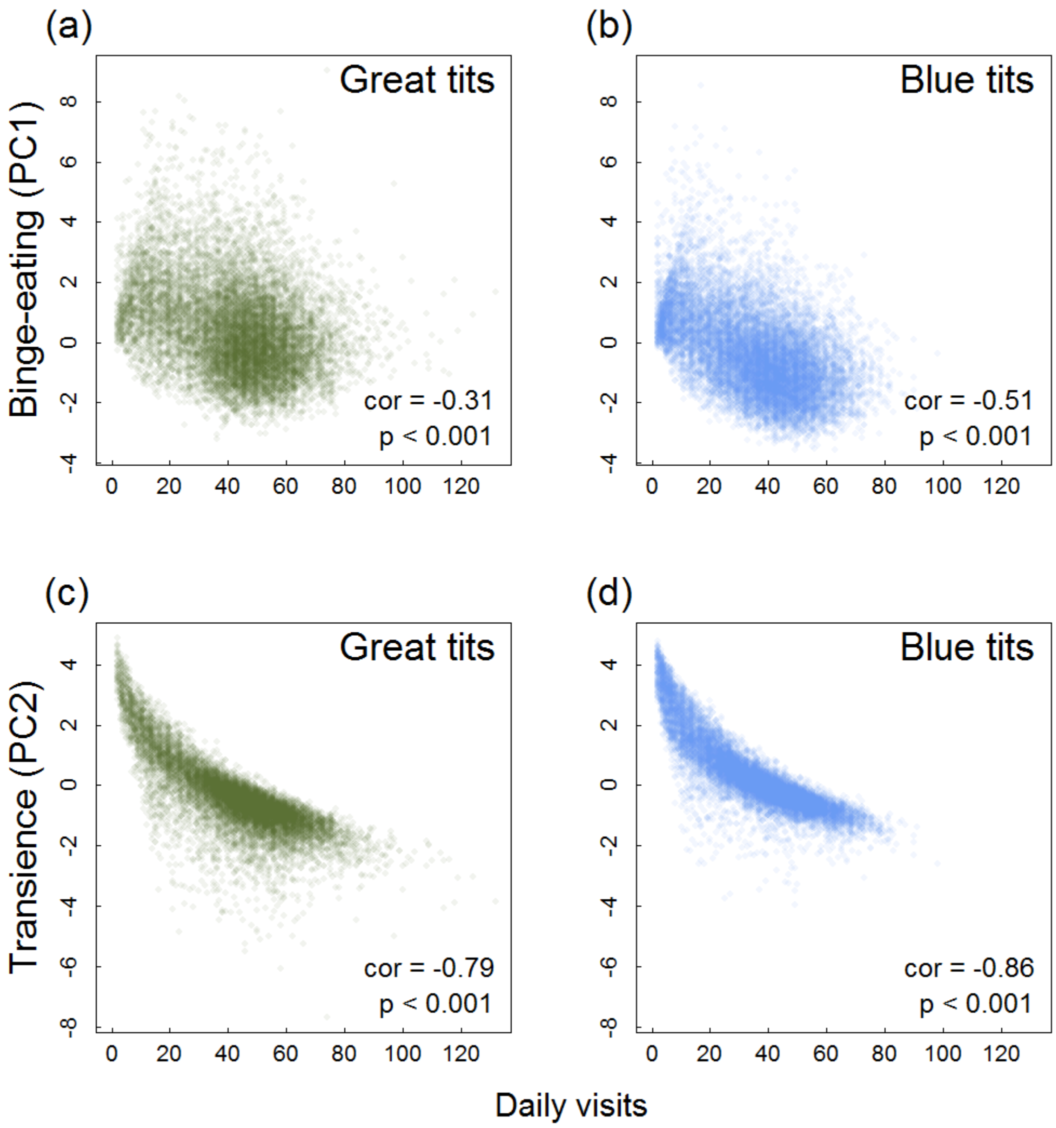


Fig. S2. Level of binge-eating (PC1) and number of visits at feeder per day for (a) great tits and (b) blue tits; level of transience (PC2) and number of visits at feeder per day for (c) great tits and (d) blue tits; one point per individual per date. Data cover five consecutive midwinter weekends from three consecutive years between December 2011 and January 2014.

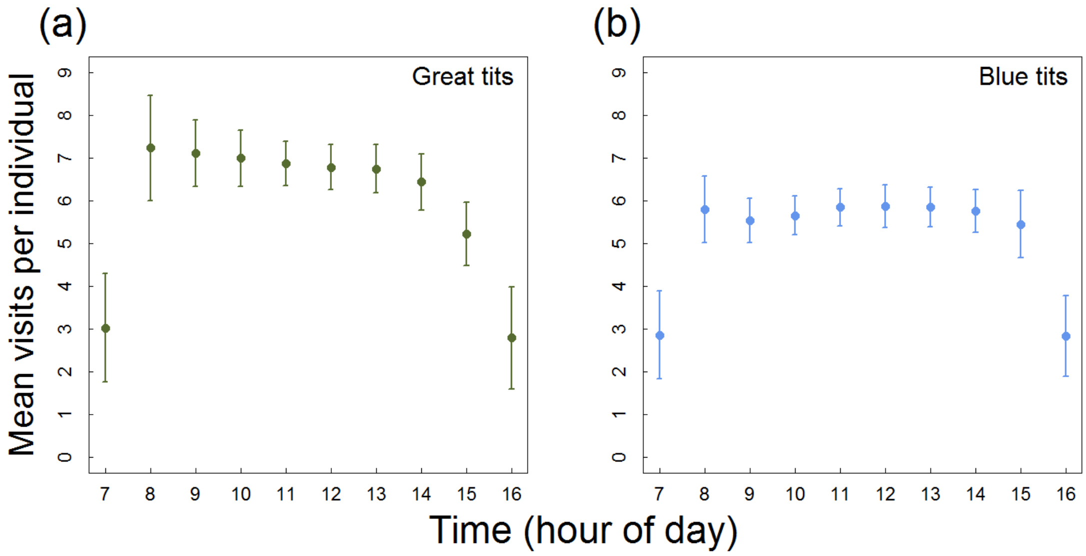


Fig. S3. Mean ± 1 SD individual hourly feeder visit rates of (a) great tits and (b) blue tits recorded during five consecutive midwinter weekends from three consecutive years between December 2011 and January 2014.

Supplementary Tables

Table S1. Number of visits recorded and analysed per site and date.

Site	10/12/11	11/12/11	17/12/11	18/12/11	24/12/11	25/12/11	31/12/11	01/01/12	07/01/12	08/01/12
1A	1650	1188	832	2200	2491	2373	1755	2127	862	1306
1B	1104	1094	815	1139	N/A	N/A	500	991	151	206
1C	1850	1158	1310	2247	1622	1504	2195	1538	2230	1806
1D	595	349	742	826	1295	927	1004	799	1527	1048
1E	7	145	N/A	N/A	176	102	87	N/A	N/A	13
1F	39	16	137	86	N/A	163	15	166	288	236
1G	N/A	357	180	381	271	628	314	532	127	88
1H	48	529	43	N/A	0	N/A	301	236	361	353
2A	0	0	N/A	3	N/A	N/A	0	69	N/A	119
2B	2130	2526	2151	3477	3034	3250	3243	2467	3461	2893
2C	1943	2017	1642	1436	1435	1334	1598	1442	1753	1604
2D	244	337	223	622	1152	692	412	448	600	274
2E	1420	1668	719	1198	656	1659	1414	1596	2045	2142
2F	760	910	728	521	592	390	642	566	1102	818
2G	0	N/A	0	0	48	77	985	405	85	133
2H	N/A	24	0	42	N/A	3	17	18	70	N/A
2I	0	0	0	121	407	358	267	72	14	119
3A	70	28	87	119	0	126	N/A	91	0	N/A
3B	108	207	520	279	428	122	50	131	87	112
3C	7	34	276	44	N/A	N/A	N/A	N/A	154	86
3D	45	286	385	295	407	331	623	333	208	202
3E	1122	17	461	427	1182	689	686	12	675	670
3F	928	1533	N/A	N/A	1817	2216	378	1761	1202	419
3G	N/A	N/A	767	746	347	276	434	705	643	469
3H	389	89	1025	467	53	164	298	419	473	302
4A	794	941	286	480	980	1039	973	720	559	619
4B	446	80	629	705	296	413	338	295	187	337
4C	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
4D	801	1676	474	727	2107	2077	N/A	N/A	292	253
4E	71	N/A	37	48	N/A	N/A	N/A	111	5	N/A
4F	42	84	63	128	0	0	N/A	N/A	11	163
4G	500	262	584	808	802	1181	768	931	914	721
4H	629	196	738	576	N/A	7	469	404	1453	1118
4I	1872	1692	1529	1791	1512	1950	1207	2062	1942	1850
5A	99	92	0	N/A	N/A	30	N/A	142	127	144
5B	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
5C	620	673	1333	1742	1164	1706	1801	2061	1318	1715
5D	13	N/A	82	82	0	N/A	0	6	N/A	11
5E	370	340	896	877	1652	424	0	N/A	549	479
5F	367	11	192	273	N/A	N/A	1290	957	187	341
5G	N/A	213	26	29	406	522	310	176	434	147
5H	212	198	N/A	0	11	20	103	197	6	0
5I	1199	2078	1382	1323	832	1121	1587	1902	1150	1956
6A	0	0	N/A	0	0	0	0	0	0	0
6B	0	0	3	N/A	24	48	0	0	42	124
6C	11	13	79	45	227	439	556	N/A	57	370
6D	0	0	N/A	N/A	N/A	0	0	N/A	N/A	10
6E	109	32	N/A	3	N/A	N/A	0	N/A	184	110
6F	1370	124	1420	1578	1610	1641	1891	1600	2476	1473
6G	149	423	11	309	898	953	1030	614	N/A	156
6H	182	27	10	138	381	150	287	356	N/A	172
6I	0	30	N/A	82	81	30	0	0	0	52
7A	1477	885	1190	1874	1126	729	330	1220	1424	1218
7B	1732	2157	1347	1744	1554	2109	1791	11	2460	2179
7C	1802	1455	1478	2195	1750	1666	N/A	N/A	N/A	N/A
7D	9	251	275	613	863	1250	1090	1199	1601	1157
7E	304	1836	1281	1120	1391	1394	1117	898	1218	926
7F	671	773	15	636	715	652	117	636	799	581
7G	1595	2336	2075	1570	2296	2139	1549	1778	1731	1991
7H	N/A	N/A	1877	2350	1730	1070	1003	1321	2660	2205
8B	64	N/A	35	N/A	0	0	0	38	38	8
8C	1218	596	691	1573	1165	1045	834	973	1327	1064
8D	329	312	277	338	310	250	327	273	N/A	0
8E	784	140	674	2221	1865	1684	105	685	1051	796
8F	31	0	N/A	N/A	0	0	40	48	110	278

Table S1. Continued.

Site	08/12/12	09/12/12	15/12/12	16/12/12	22/12/12	23/12/12	29/12/12	30/12/12	05/01/13	06/01/13
1A	1804	1794	1422	1604	216	1374	862	1551	579	1113
1B	804	1106	1023	981	488	960	876	676	781	797
1C	1898	1723	1528	1756	344	883	1612	1594	1374	1352
1D	784	815	1125	1135	529	846	815	1058	821	844
1E	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
1F	99	125	66	159	N/A	53	132	114	N/A	N/A
1G	1495	1454	1514	1071	689	1405	1029	1102	1143	1062
1H	141	393	N/A	13	0	N/A	120	173	118	80
2A	361	344	106	9	88	17	199	253	402	27
2B	1872	2353	2647	2459	1822	2155	2363	2723	2611	2074
2C	1785	1925	1598	1522	1780	1772	1713	1706	2184	1586
2D	340	213	403	466	51	446	686	380	256	194
2E	1837	1774	1920	N/A	867	1425	1940	1960	1906	1450
2F	309	695	632	485	303	612	704	643	764	343
2G	253	122	47	187	42	N/A	167	148	N/A	N/A
2H	2	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	4
2I	94	54	94	N/A	36	44	N/A	43	38	65
3A	10	147	14	227	0	N/A	0	N/A	2	3
3B	224	134	40	178	180	143	180	20	6	N/A
3C	95	15	149	6	201	124	9	N/A	2	13
3D	335	214	192	192	0	66	254	209	125	177
3E	516	786	635	466	697	627	633	700	N/A	N/A
3F	497	458	669	442	168	480	343	352	450	300
3G	696	369	223	362	270	416	395	587	401	324
3H	288	156	162	206	43	86	187	217	200	145
4A	273	444	332	276	238	106	418	478	234	272
4B	707	657	610	760	552	855	622	864	538	720
4C	336	419	694	729	94	698	429	458	681	525
4D	377	441	222	299	153	127	158	221	229	188
4E	264	71	234	121	0	63	194	201	43	49
4F	604	447	362	371	242	397	401	549	83	481
4G	446	729	907	513	79	726	842	519	715	479
4H	97	93	298	78	48	105	189	173	111	76
4I	1756	1623	N/A	N/A	23	1256	1018	1315	1406	1347
5A	300	54	95	92	5	33	0	0	N/A	39
5B	1620	1646	1136	1458	611	1281	892	1364	N/A	N/A
5C	432	664	611	381	5	227	0	700	0	593
5D	18	16	12	13	0	2	N/A	82	27	21
5E	150	N/A	200	92	0	164	16	126	218	197
5F	67	42	194	59	0	N/A	N/A	0	0	0
5G	41	353	254	146	227	199	278	242	147	278
5H	372	18	150	184	120	26	43	319	N/A	N/A
5I	1004	1065	1608	1504	418	1522	1643	1685	1605	1742
6A	350	159	273	138	10	56	39	95	157	N/A
6B	125	28	N/A	145	0	N/A	N/A	51	98	119
6C	199	615	287	263	125	455	549	316	530	539
6D	N/A	49	107	82	0	71	0	45	N/A	N/A
6E	187	136	N/A	85	0	0	41	107	94	106
6F	523	613	605	455	493	590	670	639	697	591
6G	593	411	817	405	364	32	145	242	N/A	131
6H	221	48	154	N/A	256	265	410	252	339	105
6I	91	469	205	270	167	270	177	160	176	102
7A	1567	1671	1287	1445	763	1268	890	1477	1078	1444
7B	1529	1560	1568	1222	528	1351	1319	1672	1412	1671
7C	2188	1964	1394	1469	908	1524	1334	1229	1438	1754
7D	442	546	868	562	273	295	215	593	409	343
7E	428	597	391	543	0	149	192	488	424	563
7F	298	166	420	255	322	100	221	127	159	101
7G	843	1371	1069	992	585	1080	939	1030	949	1118
7H	2052	1744	2078	1858	281	1070	186	1512	1867	1759
8B	149	N/A	192	176	N/A	21	0	149	0	55
8C	653	428	386	389	216	309	8	290	289	63
8D	635	477	608	614	522	423	291	557	437	523
8E	1487	1080	1466	1341	298	1307	737	1382	N/A	N/A
8F	305	297	216	212	282	182	379	354	263	302

Table S1. Continued.

Site	07/12/13	08/12/13	14/12/13	15/12/13	21/12/13	22/12/13	28/12/13	29/12/13	04/01/14	05/01/14
1A	349	653	753	723	500	962	1493	1522	1301	1312
1B	545	656	533	544	916	851	1161	1112	520	611
1C	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
1D	694	N/A	892	909	893	865	852	1208	581	539
1E	N/A	N/A	27	N/A	6	110	N/A	N/A	N/A	29
1F	N/A	N/A	N/A	40	N/A	N/A	N/A	27	103	N/A
1G	122	501	339	197	224	704	440	471	124	687
1H	218	38	N/A	162	179	114	8	209	292	393
2A	190	48	169	N/A	28	4	107	74	N/A	52
2B	989	1173	1422	1614	2451	2134	1912	1740	1794	1934
2C	801	739	592	838	986	781	499	931	816	966
2D	29	N/A	359	276	N/A	N/A	N/A	N/A	35	N/A
2E	1306	1302	N/A	837	885	827	1462	1539	1198	1557
2F	N/A	11	136	N/A	100	N/A	101	90	77	242
2G	135	207	31	251	68	399	123	238	99	262
2H	14	15	12	N/A	20	98	8	8	N/A	N/A
2I	0	48	262	204	N/A	64	N/A	115	N/A	36
3A	N/A	N/A	N/A	N/A	N/A	N/A	34	53	0	58
3B	15	61	57	64	56	45	46	55	53	34
3C	N/A	N/A	0	19	N/A	N/A	94	N/A	28	95
3D	204	78	283	N/A	311	279	253	158	370	169
3E	137	351	329	419	832	558	69	318	781	396
3F	304	302	262	493	172	894	520	415	891	720
3G	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
3H	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
4A	301	266	69	390	301	268	317	214	192	123
4B	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
4C	381	383	576	255	N/A	N/A	587	952	1340	1301
4D	256	191	591	315	N/A	423	376	398	317	943
4E	0	91	0	36	0	62	19	54	0	41
4F	119	96	98	7	14	66	49	100	80	142
4G	100	217	736	632	N/A	166	254	N/A	560	938
4H	163	47	N/A	N/A	0	91	130	51	0	N/A
4I	650	1597	2228	1854	1904	2677	2565	2099	2131	2373
5A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
5B	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
5C	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
5D	N/A	N/A	11	49	N/A	N/A	56	197	80	67
5E	105	399	201	61	215	472	224	66	706	145
5F	108	137	297	75	160	202	201	204	N/A	224
5G	131	257	192	188	278	148	N/A	N/A	337	235
5H	N/A	6	N/A	71	0	N/A	302	302	N/A	191
5I	749	1223	1790	1386	1703	609	1134	1152	1362	1212
6A	N/A	4	35	163	151	143	445	308	109	316
6B	N/A	33	21	7	62	165	76	108	139	93
6C	260	264	178	190	107	429	131	218	466	550
6D	0	7	15	N/A	N/A	18	13	10	0	0
6E	63	34	N/A	0	0	N/A	29	30	0	24
6F	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
6G	0	92	262	N/A	0	316	404	396	N/A	N/A
6H	N/A	N/A	N/A	N/A	0	98	35	61	0	43
6I	10	82	N/A	11	N/A	54	24	166	N/A	43
7A	58	159	N/A	191	609	N/A	935	1242	334	1076
7B	1342	1135	1266	1238	932	1712	456	425	1288	1084
7C	1363	1413	1184	1453	875	1413	1319	1601	1260	1590
7D	48	19	623	511	N/A	548	415	655	28	171
7E	0	148	251	180	N/A	276	267	332	358	226
7F	110	95	N/A	82	274	238	192	N/A	49	N/A
7G	958	889	859	451	666	831	998	1117	1116	N/A
7H	N/A	N/A	1899	1639	846	1496	N/A	N/A	1215	N/A
8B	14	110	89	N/A	16	36	151	54	N/A	16
8C	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
8D	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
8E	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
8F	180	127	191	147	109	163	180	180	165	144

Table S2. Summary of the number of individuals, visits, and bouts.

Species	Winter	Individuals	Individuals: First two winters	Individuals: Last two winters	Individuals: All three winters	Visits	Bouts
P. major	2011-2012	853	370	195	130	210343	52071
	2012-2013	591				168270	43067
	2013-2014	541				98723	25445
C. caeruleus	2011-2012	1012	417	313	166	188637	61260
	2012-2013	827				166122	56962
	2013-2014	626				100991	32173
total *P. major*		1406				477336	120583
total *C. caeruleus*		1728				455750	150395
grand total		3134	787	508	296	933086	270978

CHAPTER 3

Great tits and blue tits shift their daily foraging routines with seasonal changes in temperature and day length

Great tits and blue tits shift their daily foraging routines with seasonal changes in temperature and day length

Nicole D. Milligan, Reinder Radersma, Ella F. Cole and Ben C. Sheldon

1. Animals are faced with a wide range of conditions across seasons and should shift their behaviour accordingly in order to maximize fitness. At high latitudes, energetic requirements and day length vary greatly over the course of the year, with strong effects on foraging behaviour. This is particularly relevant during the winter when time and energy constraints are likely to be operating. Previous studies on seasonal foraging patterns in birds have focussed on population-level trends or individual fattening strategies but little is known of how individuals vary in the way that they adjust their behaviour with changing environmental conditions.

2. In this chapter I investigate how individual great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*) in a wild population shift their foraging behaviour across the non-breeding season, using a grid of 65 automated feeding stations coupled with RFID-detectors over three years. I explore how the daily (i) fine-scale timing of visits, (ii) number of visits, and (iii) arrival time at feeders change with environmental factors including temperature, day length and time of year. I then explore how variation in these behavioural measures is linked to key state differences (species, sex and age).

3. Analysis of 4,024,990 feeder visits by 4,408 individuals revealed seasonal differences in all three measures of feeding behaviour. Visits were more clustered on short days while birds visited feeders more on cold and long days. Birds arrived at feeders earlier relative to sunrise on short days. I further tested whether dominance-linked attributes (species, sex, and age) were associated with different seasonal changes in foraging pattern, since

social dominance is expected to be linked to priority access at feeders in these species.

4. Great tits increased the temporal clustering of feeder visits more on short days than blue tits; great tits arrived at feeders later than blue tits early in winter. Males of both species clustered their feeder visits more than females early in winter and arrived later than females when days were long. Juvenile great tits increased the number of daily visits on cold days more than adults, whereas adult blue tits increased the number of daily visits on cold days more than juveniles.

5. These dominance-related differences in seasonal feeding patterns were small relative to the overall seasonal shift in foraging behaviours, suggesting that dominance rank does not severely restrict the ability of individuals to adjust their feeding behaviour across seasons. Overall, these analyses shed light on the extent to which individuals vary their foraging behaviour with an increase in daily time constraints and energy requirements, with likely consequences for survival rates.

INTRODUCTION

Many animals live in seasonal environments and the fluctuating conditions that result from these will impose different pressures on behaviour at different times. Adjusting behaviour appropriately in a changing environment may be important for an individual’s survival and reproductive prospects. Individuals are likely to have different energy requirements due to differences in state, while social status can restrict access to resources and so may also play a role in determining how individuals behave over time (subordinate trout shift foraging behaviour to become more diurnal when energetic requirements are increased while dominant individuals remain nocturnal: Alanärä *et al.* 2001; manipulating energetic demands on sparrows caused dominant individuals to change their use of scrounging more than subordinates: Lendvai *et al.* 2006). In some species, the two sexes exhibit different strategies for coping with seasonal food availability (sexually size-dimorphic grey seals use different spatial foraging strategies across seasons: Breed *et al.* 2009). The adaptiveness of some foraging patterns is only apparent when different timescales are investigated (foraging eider ducks respond to the timing of both tidal currents and digestion to increase long-term energy gain despite avoiding foraging at the most profitable foraging time window in the short-term: Heath *et al.* 2010).

Many cases of seasonal foraging patterns have been documented in a wide range of taxa, including mammals (seasonal predation patterns in wolves; Metz *et al.* 2012), fish (seasonal feeding rates in salmon; Amundsen *et al.* 1999), insects (seasonal foraging activity in ants; Bernstein 1979) and birds (seasonal foraging routines in geese; Cope 2003). Seasonal shifts in behaviour can be linked to changes in the physical environment such as temperature (temperature-dependent switch in timing of foraging in salmon; Fraser *et al.* 1993) and day length (effect of photoperiod on winter fattening strategies of coal tits; Polo *et al.* 2007) which often influence an individual's energetic requirements and the time available to forage. Food availability can also be very seasonal, leading to large shifts in foraging behaviour (effect of manipulating food availability on activity patterns in salmon: Orpwood *et al.* 2006; seasonal food availability causes mice to shift their home feeding ranges: Schradin and Pillay 2006; fur seals alter foraging intensity with seasonal changes in prey abundance: Boyd *et al.* 1994).

Individuals with different physiological requirements and behavioural limitations may use alternative strategies to overcome these seasonal pressures since they are likely to face different selection pressures. There is little existing work on fine-timescale individual foraging patterns over a long timescale. Since so many aspects of the environment change seasonally, most studies on foraging routines have aimed to reduce their effects by recording behaviour in the controlled conditions of captivity, or over a relatively short timescale in the wild. For example, Dall and Witter (1998) investigated the effect of manipulating food availability on daily routines in captive zebra finch; Brandt and Cresswell (2009) studied the effects of temperature and predation risk on daily foraging routines in rock finches, and Van der Veen (1999) manipulated perceived predation risk to test its effect on the daily foraging routines of yellowhammers. In wild populations, Bonter *et al.* (2013) studied feeder visitation rates over two months in midwinter in passerines, while Heath *et al.* (2010) studied diving routines of eider ducks during one tidal cycle on one date. Previous studies on seasonal foraging patterns have focussed on population-level behavioural trends (daily foraging routines of unmarked geese: Cope 2003; seasonal feeding patterns in untagged salmon: Blyth *et al.* 1999) or individual fattening strategies (daily pattern of weight gain in marsh tits in response to supplemental feeding: Koivula *et al.* 1995; Beck *et al.* 2003 recorded sex-specific patterns in seasonal weight gain in seals; MacLeod *et al.* 2005 manipulated perceived predation risk and recorded the effect on daily mass gain patterns of individual great tits). To gain a better understanding of how individuals adapt their foraging behaviour seasonally, and to identify the use of potential alternative strategies, many individuals should be monitored at a fine temporal scale over a long period.

Passive integrated transponder (PIT) technology allows the automated collection of feeder visit data from a large number of individuals simultaneously (Bonter *et al.* 2011). In chapter 2, I demonstrated that individual great tits and blue tits differ consistently in their daily foraging patterns in the short term, both in the temporal clustering of foraging behaviour and in the number of feeder visits. In this chapter, in order to investigate how individuals adapt to the changing seasonal environment, I monitored feeder visits by the same population of great tits and blue tits during the non-breeding season over three years. Here I investigate seasonal trends in the daily clustering of feeder visits, number of visits, and arrival time of individuals. Specifically: (i) whether there is a shift in foraging behaviour related to the change in day length, average daytime temperature, or time of year over the non-breeding season and (ii) whether there are species, age or sex differences in these seasonal foraging patterns.

METHODS

Study system and automated data collection

This study was conducted over three consecutive non-breeding seasons: from late August 2011 to late February 2012 and from early September to early March in 2012-2013 and 2013-2014. Automated data loggers (see chapter 2 for more details on equipment) were set up at 65 feeding stations across Wytham Woods, positioned in a grid with approximately 250m spacing between sites. Each feeding station supplied black sunflower seeds *ad libitum* when open. Great tits and blue tits were tagged with metal BTO rings and unique passive integrated transponder (PIT) tags (IB Technology), either at nest boxes during the spring breeding season or at mist nets during autumn and winter. Age and sex were determined using methods described in Svensson (1992). Feeding stations were programmed to open at least one hour before sunrise and close at least one hour after sunset, two days per week (Saturdays and Sundays), except before December 2011 when they were set to open and record one day per week (Thursdays). When open, the two radio frequency identification (RFID) antennae at each station scanned for PIT-tags three times per second and an attached data logger recorded the PIT-tag code, time and location whenever a tagged bird landed on an antenna to access seed. Further details of the data logging process are given in chapter 2. To reduce the effect of different schedules of feeder opening on foraging behaviour, only data collected from December 2011 onwards were analysed for this chapter, i.e. whole-weekend data. The remaining five days per week when no supplemental food was provided should minimize the carry-over effects of supplemental feeding (Crates *et al.* 2016). Data from a subset of date and site combinations were excluded from the analyses for this chapter due to other experiments being conducted which either altered the accessibility of food or provided supplemental food every day of the week.

Seasonal environment

I tested three seasonally-changing factors for their effects on daily foraging patterns. Firstly, day length was calculated as the time to the nearest minute between sunrise and sunset, as reported for Oxford (timeanddate.com). The short days in midwinter will place additional time pressure on diurnal animals to conduct their daily activities. Furthermore, the correspondingly long nights will require more energy stores to be built up prior to roosting. Secondly, hourly dry bulb temperature records taken at the Upper Seeds site near the centre of Wytham (data provided by the Environmental Change Institute, Oxford, UK) were used to calculate the mean daytime temperature per recording date. Only temperatures for hours between sunrise and sunset inclusive were used in these calculations. Low temperatures will increase the energy required to maintain body temperature, especially when active, increasing energy constraints. Moreover, low temperatures may also increase the difficulty of finding invertebrate prey (Avery & Krebs 1984) and reduce territoriality in tits (Perrins 1979). Thirdly, the day of year was defined as the number of days after the winter solstice. Thus, the day before the winter solstice = -1, day of winter solstice = 0, day after winter solstice = 1, and so on. This variable may capture temporal variation at either end of the winter, e.g. the ending of moult or approach to the breeding season.

Data handling and statistical analysis

All data were analysed using R 3.2.0 (R Core Team 2015). I used the bimodal distribution of raw data record intervals and of inter-visit intervals of individual birds to set thresholds for allocating (i) raw records to feeder visits and (ii) visits to feeding bouts (Fig. 1). The threshold interval separating visits was 17 seconds and separating feeding bouts was 514 seconds. Further details of data processing are given in chapter 2.

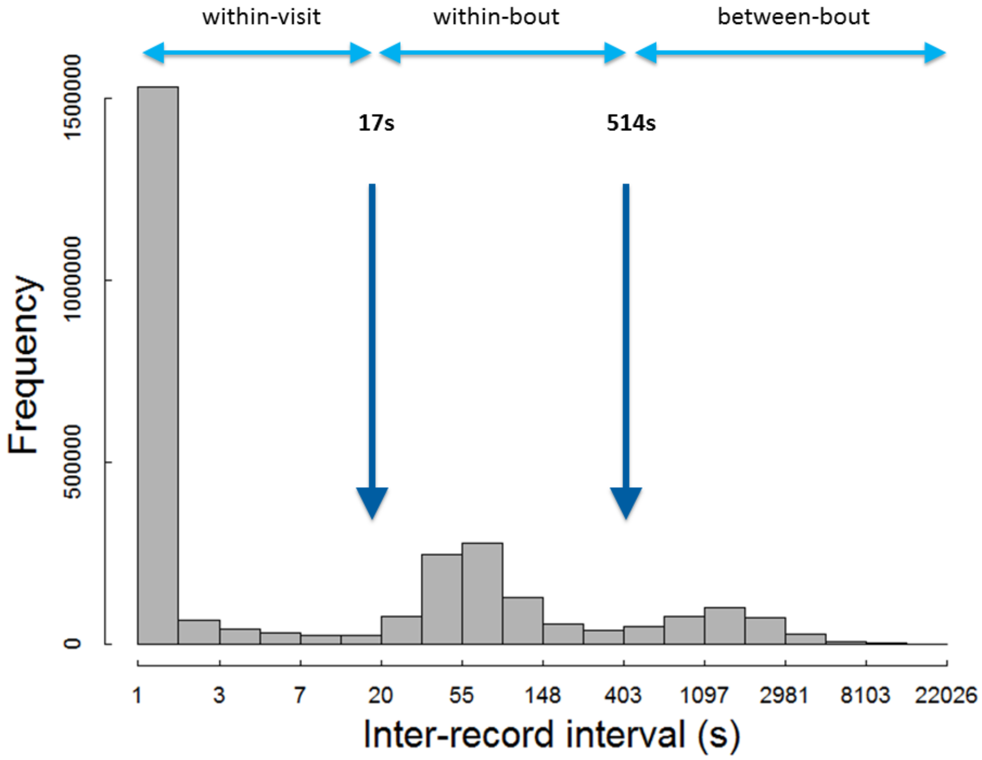


Fig. 1. Inter-record intervals of individual great tits and blue tits visiting feeders. Threshold values for minimum inter-visit intervals and minimum inter-bout intervals shown in dark blue.

A principal component analysis (PCA) was used to describe the temporal clustering of visits by individuals within a day. Six parameters associated with the timing of feeder visits and foraging bouts were calculated per individual per recording day: time of first visit, time of last visit, number of bouts, mean length of bout, mean inter-bout interval, and mean number of visits per bout. The first principal component gave an axis of variation indicating the extent to which individuals ‘binge-eat’ (high PC1) or ‘graze’ (low PC1), i.e. a measure of the clustering of feeder visits within a day. More detailed information on this PCA can be found in chapter 2. To check that the PCA was robust to seasonal change, I ran a separate PCA for the dates in each quartile of day length and temperature. The plots of PC1 against PC2 are very similar for each set of quartiles (Fig. S1), supporting the use of PC1 derived from all of the data as a measure of binge-eating across the study period.

Generalized linear mixed-effect models (GLMMs) were fitted to determine the effects of day length, temperature and time of year on (i) the daily clustering of feeder visits (PC1), (ii) the daily number of visits by individuals, and (iii) the daily arrival time, relative to sunrise, of individuals at feeders. Individual ID, feeder site, and date were included as random terms; species, age, sex, distance between the feeder and the subsequent breeding territory, and a measure of local competition (the daily total number of visits by all other tagged individuals at a site) were included as fixed effects since they were all shown to have an effect on daily foraging patterns in chapter 2. To normalize the distribution of distances, I took the logarithm of distance to territory. I also added two fixed effect terms to the models for competition: one for the mean competition experienced by an individual and another for the deviation from its mean for each date. Winter year was also included as a factor in predicting the daily number of visits since many aspects of the environment will vary annually. For example, there was variation in the amount of beechmast available in each winter (good crop produced in the first and third years of this study, but not in the second) and tits tend to visits feeders more in poor beechmast years (Perrins 1979). Since the daily number of visits by an individual is correlated with the level of binge-eating (chapter 2), I added the number of daily visits as a fixed effect to the model predicting clustering (PC1). To investigate whether birds use alternative foraging strategies when adjusting to seasonal change, I added interaction terms to the models for [species, age, or sex] x [day length, average daytime temperature, or day of winter]. Akaike's information criterion (AIC) was used in model selection (Burnham & Anderson 2002). I then used the Kenward-Roger approximation to calculate approximate degrees of freedom which, in combination with the t-distribution, I used to calculate p-values for each fixed effect. Interaction terms with significant (<0.05) p-values were kept in the models.

RESULTS

A total of 14,321,739 raw data records were logged across the study period. Individuals used an average of 3.1 different feeding stations within a winter. I excluded visits by individuals for the dates on which they moved between feeding stations within the same day from further analyses. This affected 21.6% of recorded visits and resulted in 2.1% of individuals being entirely excluded from analyses. However, these visits by within-day movers were included in the measure of local competition. Since inter-bout interval was used as a parameter in the PCA, I also 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 9.2% of individuals from further analyses; however, these visits also contributed to the measure of local competition.

Once data filtering was complete and visits and bouts allocated for 1820 great tits and 2588 blue tits, I analysed the 4,024,990 feeder visits made in 1,224,560 foraging bouts. A summary of the numbers of individuals, visits and bouts by species and year is given in Table S1. The mean daily number ± 1SD of visits per individual was 35 ± 15 and of bouts was 11 ± 4. Having run the PCA on 6 parameters, the clustering of feeder visits within a day (PC1) explained 37% of the total variation. Three GLMMs were fitted for each of the three dependent variables (clustering, number of visits, and arrival time) – one model including data from both species for between-species comparisons and additional models for each species separately to make within-species comparisons.

Temporal clustering of feeder visits within a day

Models predicting the level of binge-eating showed similar support for the factors tested in chapter 2 (see Tables S2 and S3 for model estimates). There were also significant interactions between day length and species (Table S2) and between day of winter and sex (Table S3). Great tits binged more than blue tits but also increased the level of binge-eating more than blue tits on shorter days (Fig. 3). Males binged more than females early in the season and this difference decreased over winter (Fig. S2). There was no difference in the behaviour of adults and juveniles as day length changed.

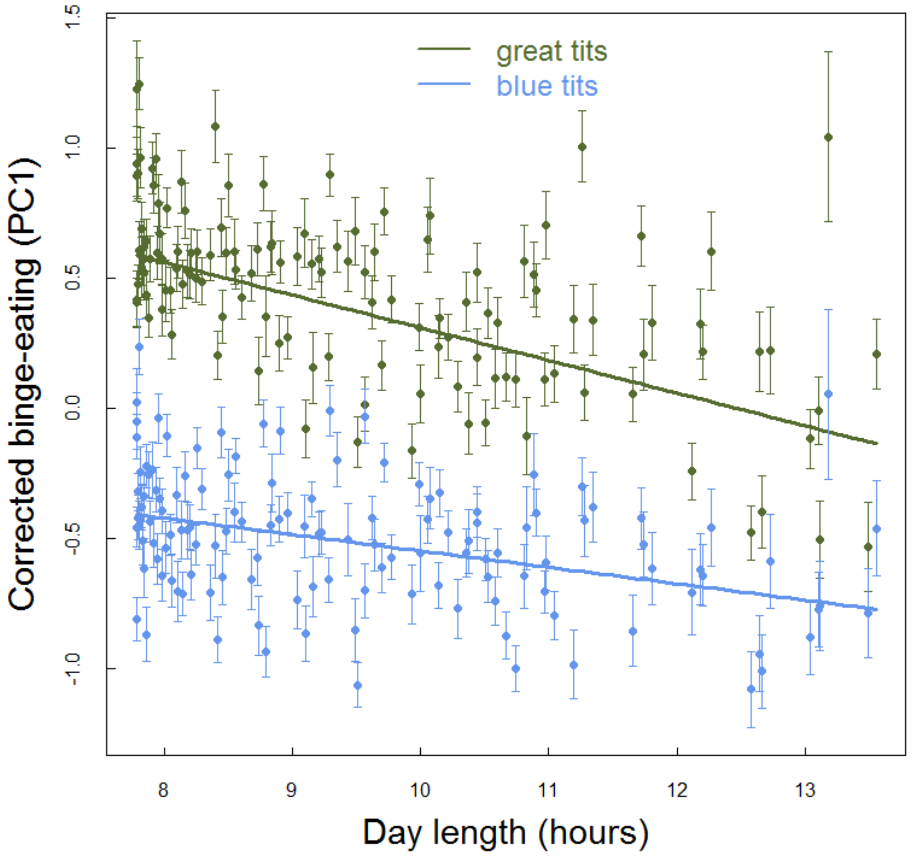


Fig. 3. Level of binge-eating (PC1) by individual great tits and blue tits on days of different length. Points are mean ± SE per date, corrected for the time of year, daily number of visits, age, sex, distance to territory, and competition. Lines indicate the predicted level of binge-eating.

Daily number of visits at feeders

Results of the models predicting the daily number of feeder visits were also consistent with those from chapter 2 (model estimates provided in Tables S4 and S5). Great tits visited feeders approximately 10 times more per day than blue tits while both species increased the number of visits to a similar extent as temperature decreased (Fig. 4). In great tits, juveniles increased the number of feeder visits more than adults with decreasing daytime temperatures while adult blue tits increased their daily visit rates more than juvenile blue tits on cold days (Fig. S3). In addition, there was an interaction between mean daytime temperature and age (Table S5).

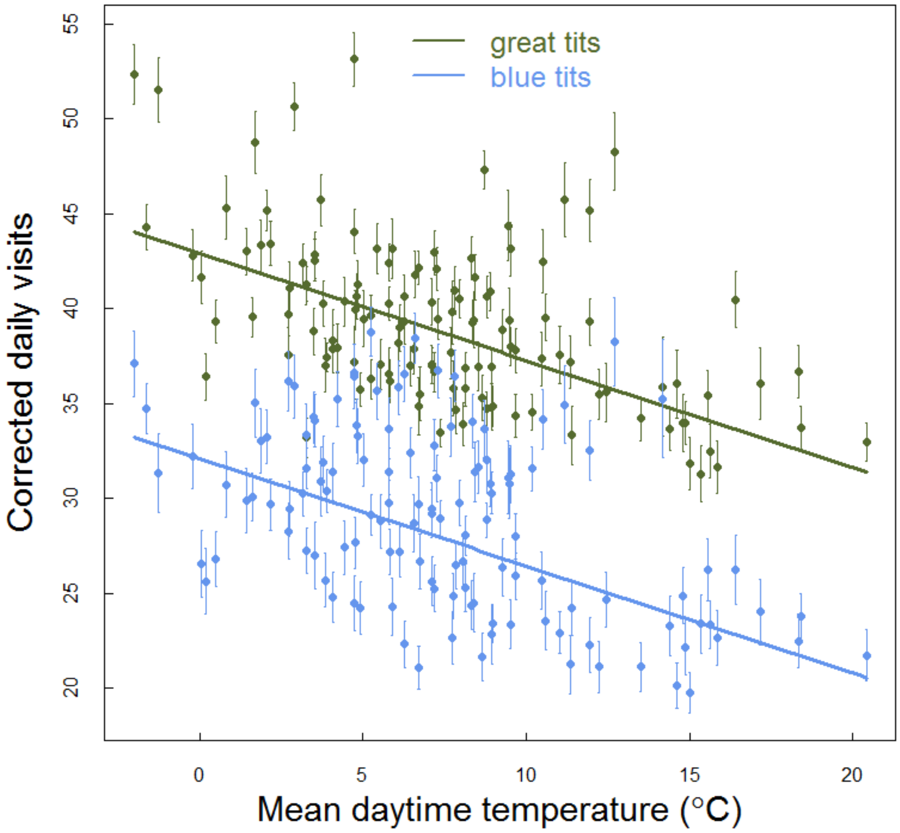


Fig. 4. Daily number of feeder visits made by individual great tits and blue tits on days of different average daytime temperature. Points are mean ± SE per date, corrected for day length, winter, age, sex, distance to territory, and competition. Lines indicate the predicted number of visits per day.

Arrival time at feeders relative to sunrise

Birds arrived at feeders earlier relative to sunrise when days were short (Fig. 5). Blue tits tended to arrive at feeders earlier in the day than great tits in autumn but this difference decreased over winter and was not apparent in late winter (Fig. S4). The later arrival of birds on long days was more pronounced in males than in females (Fig. S5). The distance between a feeding station and an individual's subsequent breeding territory was linked to the arrival time at feeders, with those individuals, especially adults, with large distances to travel between territory and feeder arriving later at feeders than those with nearby territories (see model estimates in Tables S6 and S7).

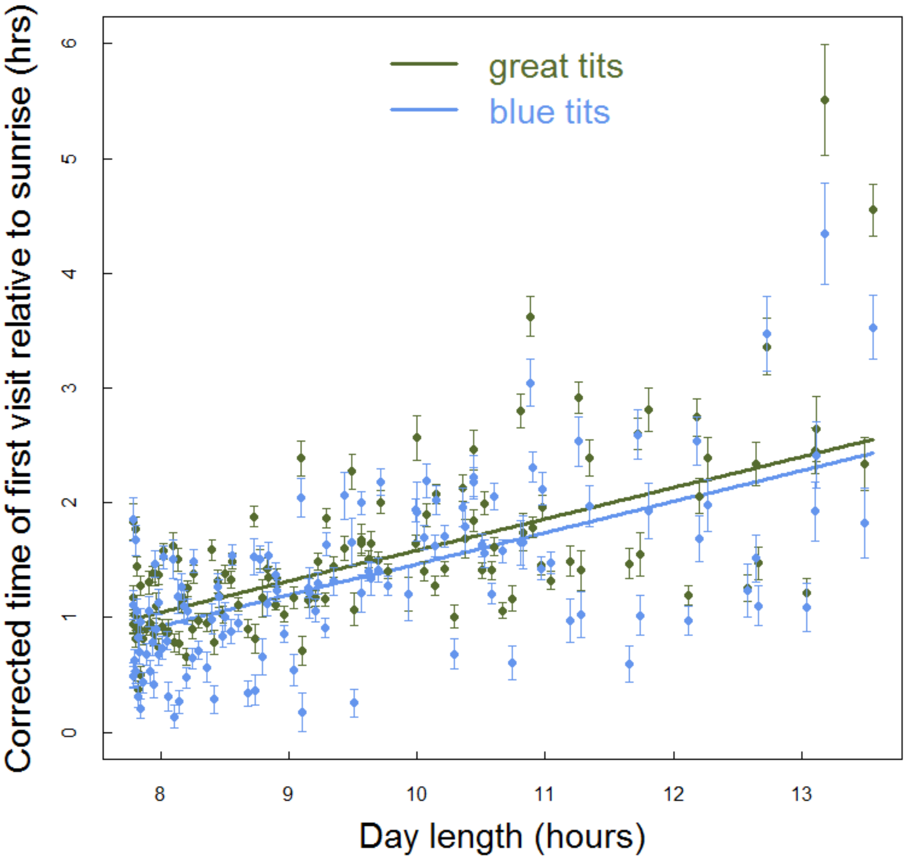


Fig. 5. Daily arrival time of individual great tits and blue tits on days of different length. Points are mean ± SE per date, corrected for time of year, temperature, age, sex, distance to territory, and competition. Lines indicate the predicted arrival time at a feeder.

Mean hourly visit rates of individual great tits and blue tits are shown for each calendar month in Fig. S6. These visit rates peaked in December and January for both species. The hourly number of individuals visiting feeders also increased from autumn to winter, peaking slightly later in February (Fig. S7). The mean level of binge-eating, daily number of visits, and arrival time relative to sunrise on each recording date of the study period are illustrated in Fig. S8; the day length and mean daytime temperature for the same dates are shown in Fig. S9.

A summary of general seasonal shifts, general dominance-related differences, and specific dominance-related seasonal shifts in foraging behaviour are summarized in Table 1.

Table 1. Summary of the general and seasonal patterns in feeder visits by great tits and blue tits.

Behavioural measure	Pattern	Dominance-related attribute					
		Species		Age		Sex	
		Great tit	Blue tit	Adult	Juvenile	Male	Female
Binge-eating (PC1)	**General seasonal trend**	**Birds binge-eat more on short days**					
	General dominance-related trend	GTs binge-eat more than BTs		adults binge-eat more than juveniles		males binge-eat more than females (in GTs only)	
	Dominance-related seasonal shift	*GTs increase binge-eating more than BTs on short days*				*males binge-eat more than females early in winter*	
Number of visits	**General seasonal trend**	**Birds visit feeders more on cold days**					
	General dominance-related trend	GTs visit feeders more than BTs		juveniles visit feeders more than adults		males visit feeders more than females	
	Dominance-related seasonal shift			*juvenile GTs increase visits more than adults on cold days* *adult BTs increase visits more than juveniles on cold days*			
Arrival time at feeder (relative to sunrise)	**General seasonal trend**	**Birds arrive earlier on short days**					
	General dominance-related trend	BTs arrive earlier than GTs				males arrive later than females	
	Dominance-related seasonal shift	*BTs arrive earlier than GTs early in winter*				*males arrive later than females on long days*	

DISCUSSION

In this chapter I have demonstrated that both great tits and blue tits exhibit seasonality in their daily foraging patterns. All three daily measures of foraging behaviour (the temporal clustering of feeder visits, number of visits, and arrival time at feeder) of over 4000 individuals recorded at automated feeders shifted during the autumn and winter study period over three consecutive years. Overall, birds arrived at feeders earlier and binged more on short days (Figs 5 and 3) whereas they visited feeders more often when it was cold (Fig. 4). In addition, there were differences between individuals across a dominance-related attribute (species, age or sex) in the seasonal shift of all three behavioural measures (Table 1). These alternative shifts in seasonal behaviour suggest that a change in climate, either in a certain direction or in variability, will have an impact on how different individuals in a population will be able to adapt their behaviour in the future.

Seasonal shifts in behaviour

I found two density-independent factors that affected the seasonality of foraging behaviour: day length and temperature. There are likely to be multiple mechanisms involved.

Energy requirements

Both day length and temperature are critical factors in determining the daily energy requirements of a small diurnal bird in winter (Kendeigh 1949). When days are short in midwinter, there is relatively little time to find enough food to fuel the bird through the long night. Great tits can lose 10-15% of their body mass overnight (Owen 1954). Also, birds require more energy to maintain body temperature when the air temperature is low. My results show that birds are able to shift their foraging behaviour to fulfil both of these demands, by binge-eating to a greater extent on short days and visiting feeders more on cold days. Hourly visit rates also peak in midwinter when days are short (Fig. S6). A manipulation of feeding day length by Bednekoff and Krebs (1995) showed that great tits were able to gain mass more on short days despite eating less, suggesting that they reduced energy expenditure. Binge-eating is likely to be a more efficient foraging tactic than grazing since it allows more food to be consumed in a short period of time, allowing more time for rest which could reduce overall daily energy requirements.

Great tits at five study locations in the Netherlands emerged from their roosting sites on average half an hour before sunrise during winter months (Kluijver 1950) while in this study, with birds at a similar latitude to Kluijver's study, I have shown that they typically arrive at feeders at least 1 hour after sunrise in midwinter (Fig. 5). This supports Kluijver's statement that "in the early morning, the birds do not in general seem hungry." Great tits experiencing the very short days of arctic winter, however, start feeding well before sunrise (Franz 1943). Conditions in Wytham are less extreme, with a minimum day length of around 8 hours and a minimum average daytime temperature around -3˚C during this study (Fig. S9).

Food availability

Tits are omnivorous, being mainly insectivorous during spring and summer while relying more on seeds in autumn and winter (Perrins 1979), with up to 70-90% of the diet coming from plants in midwinter (Veľký *et al.* 2011; Van Balen 1980). Invertebrate availability decreases with falling air temperature (Gibb 1960) and it has been shown that great tits find invertebrates at a slower rate when temperatures are lower (Avery and Krebs 1984). Tits visit artificial feeders more when it is cold (Perrins 1979), which is supported by my results (Fig. 4). When available, beechmast forms a large part of the natural diet of tits during winter and the amount available has a direct effect on the annual survival of great tits (Perdeck *et al.* 2000). However, beech trees only produce mast at most once every other year and tend to synchronize with neighbouring trees (Perrins 1965; Perrins 1966). It follows that birds should also visit feeders more in years when there is no beech crop. Over the course of this study, birds visited feeders more in the second winter than in the first or third (Table S1). This coincided with an absent beech crop in the second winter while there were heavy crops the year before and after. However, our ability to infer a pattern is weak since N=3 years.

Territoriality

After the breeding season and post-breeding moult, most adult tits resume territorial behaviour; however, territory defence is weaker in cold weather and often ceases in midwinter to allow more time for foraging (Perrins 1979). My results suggest that the distance between an individual's territory and a feeding station affects the daily foraging pattern, with long commutes linked to more binge-eating and later arrival, especially in adults. However, I did not detect any seasonal shifts in feeding behaviour related to the distance to territory in addition to the general seasonal shifts reported.

Local competition

I found that the level of local competition, a density-dependent factor, affected daily foraging routines as shown in chapter 2. Although I have not explicitly tested for seasonal shifts in behaviour related to competition levels, the number of individuals recorded at feeding stations did vary month by month (Fig. S7). Numbers were lowest in September and increased until they peaked in February. Although some individuals die over the course of winter, the tagged population density in Wytham can increase through the capture and tagging of immigrants during the winter season and through the return of birds that left the woods after the breeding season.

Alternative strategies

In addition to the overall seasonal trends in foraging behaviour, I found several factors that were involved in the differential shift of foraging behaviour in different individuals over time: species, age and sex. Again, these factors likely affect foraging behaviour through multiple mechanisms.

Dominance

In this system, social dominance affects priority access at feeders, with great tits, males and adults typically being dominant over blue tits, females and juveniles respectively (Perrins 1979). In support of this, I have shown that individuals in the dominant classes can apparently cluster their feeder visits more than subordinate classes, which may be more important on short days when feeding time is more limited. Holding a territory close to a feeding station can also increase dominance status (De Laet 1984) but my results suggest that the cost of long distance commutes to feeders plays a stronger role in determining the level of binge-eating than site-related dominance.

Social status can play a role when modelling the use of alternative foraging tactics (producer versus scrounger in Barta and Giraldeau 1998), while it has been shown in fish (by McLaughlin *et al.* 1999) that individuals with different levels of aggression foraging under competition pressure use alternative foraging tactics. Aggressive individuals use a combination of high and low feeding activity levels while nonaggressive individuals use an intermediate level of feeding activity; these are similar tactics to binge-eating and grazing.

Great tits, as the largest tit species in the UK, have the largest daily energy requirements. In outdoor aviaries, great tits consumed on average 19.7 calories daily while blue tits only 10.8 (Gibb 1957), giving the same energy requirement per unit body mass. My results show that the average daily number of visits made by great tits is around 40 and blue tits 29. Husked sunflower seeds weigh on average 0.055g each and with a caloric content of 584 calories per 100g (USDA National Nutrient Database for Standard Reference: http://ndb.nal.usda.gov/), each seed contains approximately 0.32 calories. Assuming each feeder visit results in one seed being consumed, great tits were gaining, on average, 65% of their daily energy expenditure (DEE) from feeders while blue tits gained 86% of their DEE.

With access to food most limited when competition is high and days short, fighting for food is most common in midwinter and is mostly intraspecific (Gibb 1954). At feeders, dominant individuals can supplant subordinates, so that some individuals lose much food due to fighting. In observations of unmarked individuals, great tits were supplanted 5 times per hour while blue tits were attacked more often at 15 times per hour (Gibb 1954); Sasvári (1988) also found that blue tits were supplanted more often than great tits. Therefore it is likely in this study that great tits were obtaining slightly less than 12.8 calories while blue tits were consuming much less than 9.3 calories daily from feeders, so that the energy gained would be similar per unit body mass as described in a previous study (Gibb 1957).

State/condition

As the breeding season approaches, individuals may have different needs. For example, female great tits may need up to 45% more food to form their eggs (Royama 1966). My results show that females binge-eat less than males but this difference decreases towards the end of winter (Fig. S2).

Morphology

Great tits, with larger beaks than blue tits, are able to open seeds more efficiently. This potentially reduces the handling time of each seed, the inter-visit interval, and thus increases the level of binge-eating a bird is capable of achieving. When days are short and the time available for feeding more limited, great tits do increase the level of binge-eating more than blue tits (Fig. 3). Within great tits, there are also beak shape differences between the sexes with males better adapted to open seeds quickly (Gosler 1987) and males exhibit the highest levels of binge-eating relative to females (Fig. S2a).

Body size affects the length of foraging day, with smaller species requiring relatively more energy to maintain body temperature than larger species and thus spending a greater proportion of the day feeding; in midwinter, great tits spend on average 75% of the day feeding while blue tits spend 85% feeding (Gibb 1954). My results show that, except in late winter, blue tits arrive at feeders earlier than great tits. This difference in feeding day length means that species can differentially allocate time to other activities; for example, great tits spend 6.4% of their day resting or preening while blue tits only allocate 2.9% (Gibb 1954). Therefore I suggest that binge-eating is a more efficient foraging tactic than grazing, since it allows more time between bouts for other activities.

Conclusions and implications

The results presented in this study show that individuals, based on their species, age and sex, adopt different seasonal foraging strategies to cope with changing biotic and abiotic conditions. These alternative shifts in seasonal behaviour suggest that long term changes in environmental conditions, either in direction or in variance, will affect how different individuals in a population will adapt their behaviour in the future. It will be helpful to determine the survival and fitness consequences of the alternative foraging routines, which could then clarify how supplemental feeding affects individuals either beneficially or detrimentally and then how it affects the population as a whole.

The effect sizes of dominance-related attributes in predicting seasonal shifts in foraging behaviour were relatively small compared to the shift in behaviour exhibited by the average individual. This suggests that dominance status is not a strongly limiting factor in how individuals shift their foraging behaviour seasonally. Competition with other individuals, however, is more likely to constrain an individual's ability to gain access to feeders; thus I will focus on the effects of local competition in the following chapter.

ACKNOWLEDGEMENTS

Temperature data were provided by the Environmental Change Institute, Oxford, UK. We thank the social network group for help with collecting winter logger data, catching and tagging birds during the winter, and all the Wytham tit fieldworkers for assistance in catching and tagging birds during the spring. This work was funded by a European Research Council (ERC) grant to B.C.S (AdG 250164).

REFERENCES

Alanärä, A., M. D. Burns and N. B. Metcalfe (2001). Intraspecific resource partitioning in brown trout: the temporal distribution of foraging is determined by social rank. *Journal of Animal Ecology* **70**(6): 980-986.

Amundsen, P. A., R. Bergersen, H. Huru and T. G. Heggberget (1999). Diel feeding rhythms and daily food consumption of juvenile Atlantic salmon in the River Alta, northern Norway. *Journal of Fish Biology* **54**(1): 58-71.

Avery, M. I. and J. R. Krebs (1984). Temperature and foraging success of great tits *Parus major* hunting for spiders. *Ibis* **126**(1): 33-38.

Barta, Z. and L. A. Giraldeau (1998). The effect of dominance hierarchy on the use of alternative foraging tactics: A phenotype-limited producing-scrounging game. *Behavioral Ecology and Sociobiology* **42**(3): 217-223.

Beck, C. A., W. D. Bowen and S. J. Iverson (2003). Sex differences in the seasonal patterns of energy storage and expenditure in a phocid seal. *Journal of Animal Ecology* **72**(2): 280-291.

Bednekoff, P. A. and J. R. Krebs (1995). Great tit fat reserves: effects of changing and unpredictable feeding day length. *Functional Ecology* **9**(3): 457-462.

Bernstein, R. A. (1979). Schedules of foraging activity in species of ants. *Journal of Animal Ecology* **48**(3): 921-930.

Blyth, P. J., S. Kadri, S. K. Valdimarsson, D. F. Mitchell and G. J. Purser (1999). Diurnal and seasonal variation in feeding patterns of Atlantic salmon, *Salmo salar* L., in sea cages. *Aquaculture Research* **30**(7): 539-544.

Bonter, D. N. and E. S. Bridge (2011). Applications of radio frequency identification (RFID) in ornithological research: a review. *Journal of Field Ornithology* **82**(1): 1-10.

Bonter, D. N., B. Zuckerberg, C. W. Sedgwick and W. M. Hochachka (2013). Daily foraging patterns in free-living birds: exploring the predation-starvation trade-off. *Proceedings of the Royal Society B: Biological Sciences* **280**(1760): 20123087.

Boyd, I. L., J. P. Y. Arnould, T. Barton and J. P. Croxall (1994). Foraging behavior of Antarctic fur seals during periods of contrasting prey abundance. *Journal of Animal Ecology* **63**(3): 703-713.

Brandt, M. J. and W. Cresswell (2009). Diurnal foraging routines in a tropical bird, the rock finch *Lagonosticta sanguinodorsalis*: how important is predation risk? *Journal of Avian Biology* **40**(1): 90-94.

Breed, G. A., I. D. Jonsen, R. A. Myers, W. D. Bowen and M. L. Leonard (2009). Sex-specific, seasonal foraging tactics of adult grey seals (*Halichoerus grypus*) revealed by state-space analysis. *Ecology* **90**(11): 3209-3221.

Burnham, K. P. and D. R. Anderson (2002). Model selection and multi-model inference: a practical information-theoretic approach. New York, Springer.

Cope, D. R. (2006). Variation in daily and seasonal foraging routines of non-breeding barnacle geese (*Branta leucopsis*): working harder does not overcome environmental constraints. *Journal of Zoology* **260**(1): 65-71.

Crates, R. A., J. A. Firth, D. R. Farine, C. J. Garroway, L. R. Kidd, L. M. Aplin, R. Radersma, N. D. Milligan, B. Voelkl, A. Culina, B. L. Verhelst, C. A. Hinde and B. C. Sheldon (2016). Individual variation in winter supplementary food consumption and its consequences for reproduction in wild birds. *Journal of Avian Biology*. doi: 10.1111/jav.00936.

Dall, S. R. X. and M. S. Witter (1998). Feeding interruptions, diurnal mass changes and daily routines of behaviour in the zebra finch. *Animal Behaviour* **55**(3): 715-725.

De Laet, J. (1984). Site-related dominance in the great tit *Parus major major*. *Ornis Scandinavica* **15**(2): 73-78.

Franz, J. (1943). Ueber Ernährung und Tagesrhythmus einiger Vögel im arktischen Winter. *Journal für Ornithologie* **91**(1): 154-165.

Fraser, N. H. C., N. B. Metcalfe and J. E. Thorpe (1993). Temperature-dependent switch between diurnal and nocturnal foraging in salmon. *Proceedings of the Royal Society B: Biological Sciences* **252**(1334): 135-139.

Gibb, J. A. (1954). Feeding ecology of tits, with notes on treecreeper and goldcrest. *Ibis* **96**(4): 513-543.

Gibb, J. A. (1957). Food requirements and other observations on captive tits. *Bird Study* **4**(4): 207-215.

Gibb, J. A. (1960). Populations of tits and goldcrests and their food supply in pine plantations. *Ibis* **102**(2): 163-208.

Gosler, A. G. (1987). Pattern and process in the bill morphology of the great tit *Parus major*. *Ibis* **129**(4): 451-476.

Grubb, T. C. (1978). Weather-dependent foraging rates of wintering woodland birds. *Auk* **95**(2): 370-376.

Heath, J. P., H. G. Gilchrist and R. C. Ydenberg (2010). Interactions between rate processes with different timescales explain counterintuitive foraging patterns of arctic wintering eiders. *Proceedings of the Royal Society B: Biological Sciences* **277**(1697): 3179-3186.

Kenward, M. G. and J. H. Roger (1997). Small sample inference for fixed effects from restricted maximum likelihood. *Biometrics* **53**(3): 983-997.

Kluijver, H. N. (1950). Daily routines of the great tit, *Parus m. major* L. *Ardea* **38**(3-4): 99-135.

Koivula, K., M. Orell, S. Rytkönen and K. Lahti (1995). Fatness, sex and dominance; seasonal and daily body-mass changes in willow tits. *Journal of Avian Biology* **26**(3): 209-216.

Lendvai, Á. Z., A. Liker and Z. Barta (2006). The effects of energy reserves and dominance on the use of social-foraging strategies in the house sparrow. *Animal Behaviour* **72**(4): 747-752.

MacLeod, R., A. G. Gosler and W. Cresswell (2005). Diurnal mass gain strategies and perceived predation risk in the great tit *Parus major*. *Journal of Animal Ecology* **74**(5): 956-964.

McLaughlin, R. L., M. M. Ferguson and D. L. G. Noakes (1999). Adaptive peaks and alternative foraging tactics in brook charr: evidence of short-term divergent selection for sitting-and-waiting and actively searching. *Behavioral Ecology and Sociobiology* **45**(5): 386-395.

Metz, M. C., D. W. Smith, J. A. Vucetich, D. R. Stahler and R. O. Peterson (2012). Seasonal patterns of predation for gray wolves in the multi-prey system of Yellowstone National Park. *Journal of Animal Ecology* **81**(3): 553-563.

Orpwood, J. E., S. W. Griffiths and J. D. Armstrong (2006). Effects of food availability on temporal activity patterns and growth of Atlantic salmon. *Journal of Animal Ecology* **75**(3): 677-685.

Owen, D. F. (1954). The winter weights of titmice. *Ibis* **96**(2): 299-309.

Perdeck, A. C., M. E. Visser and J. H. Van Balen (2000). Great Tit *Parus major* survival, and the beech-crop cycle. *Ardea* **88**(1): 99-108.

Perrins, C. M. (1965). Population fluctuations and clutch-size in the great tit, *Parus major* L. *Journal of Animal Ecology* **34**(3): 601-647.

Perrins, C. M. (1966). The effect of beech crops on great tit populations and movements. *British Birds* **59**(10): 419-432.

Perrins, C. M. (1979). British Tits. London, Collins.

Polo, V., L. M. Carrascal and N. B. Metcalfe (2007). The effects of latitude and day length on fattening strategies of wintering coal tits *Periparus ater* (L.): a field study and aviary experiment. *Journal of Animal Ecology* **76**(5): 866-872.

R Development Core Team (2015). R: A language and environment for statistical computing. Vienna, R Foundation for Statistical Computing.

Royama, T. (1966). A re-interpretation of courtship feeding. *Bird Study* **13**(2): 116-129.

Sasvári, L. (1988). Food selection by tits on an artificial winter food supply. *Journal of Applied Ecology* **25**(3): 807-817.

Schradin, C. and N. Pillay (2006). Female striped mice (*Rhabdomys pumilio*) change their home ranges in response to seasonal variation in food availability. *Behavioral Ecology* **17**(3): 452-458.

Svensson, L. (1992). Identification guide to European passerines. Thetford, British Trust for Ornithology.

Van Balen, J. H. (1980). Population fluctuations of the great tit and feeding conditions in winter. *Ardea* **68**(1-4): 143-164.

Van der Veen, I. T. (1999). Effects of predation risk on diurnal mass dynamics and foraging routines of yellowhammers (*Emberiza citrinella*). *Behavioral Ecology* **10**(5): 545-551.

Veľký, M., P. Kaňuch and A. Krištín (2011). Food composition of wintering great tits (*Parus major*): habitat and seasonal aspects. *Folia Zoologica* **60**(3): 228-236.

APPENDIX

Supplementary Figures

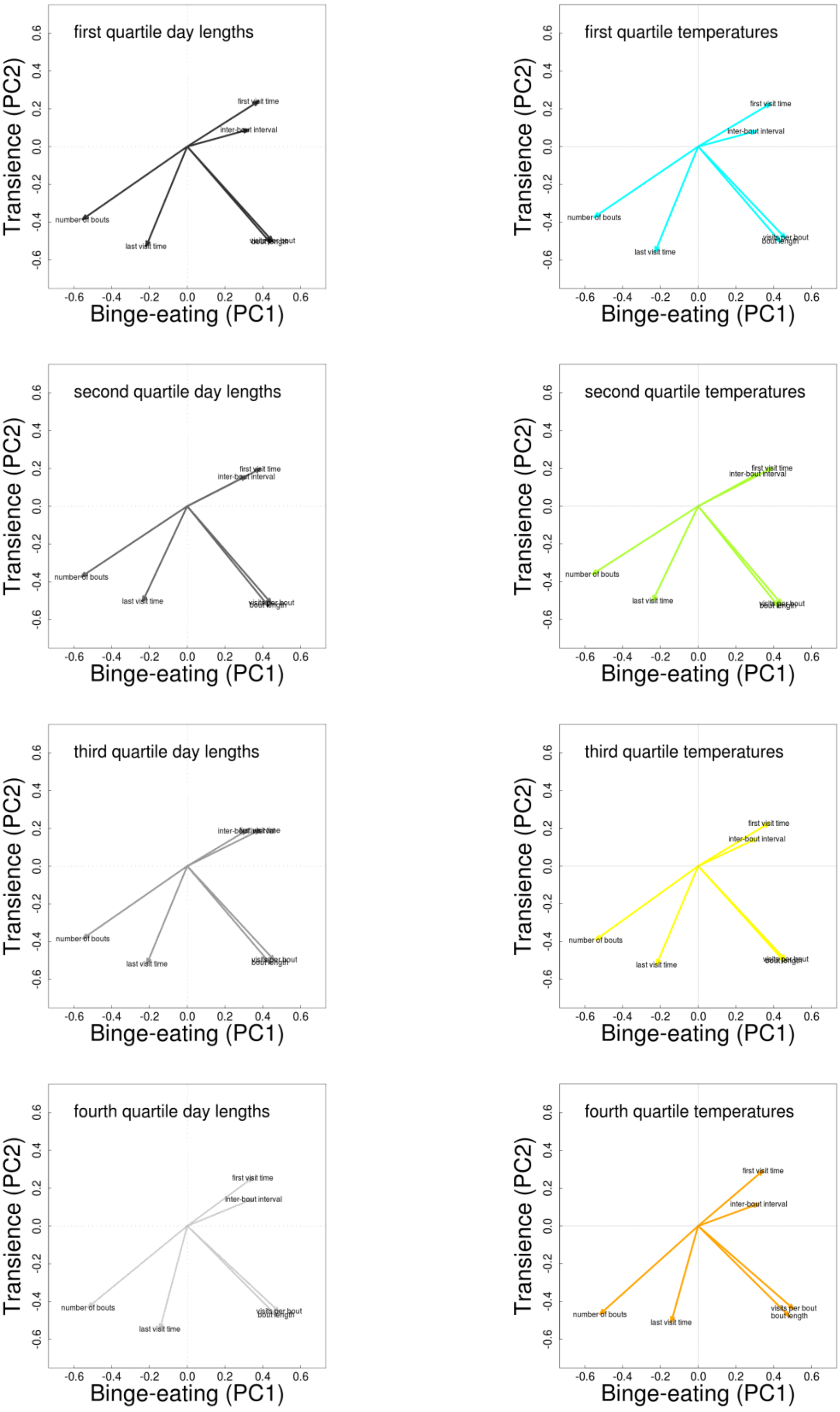


Fig. S1. Graphical representation of the degree to which different measures of the timing of feeding of individual great tits and blue tits load onto the first two axes of a principal component analysis; separate plots for each day length quartile and each average daytime temperature quartile.

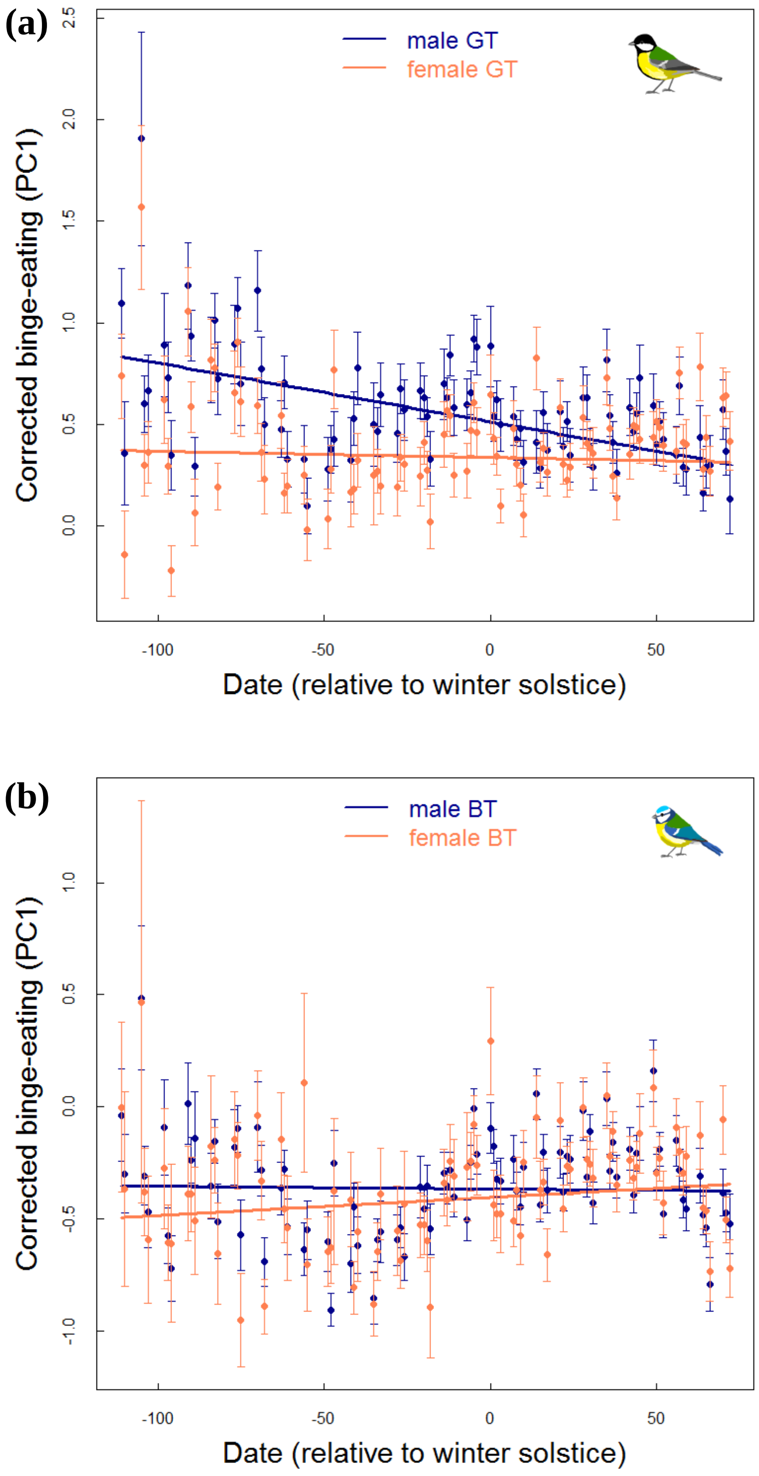


Fig. S2. Level of binge-eating (PC1) by male and female (a) great tits and (b) blue tits at different times of year. Points are mean ± SE per date, corrected for day length, the daily number of visits, age, distance to territory, and competition. Lines indicate the predicted level of binge-eating. (b) No significant sex difference.

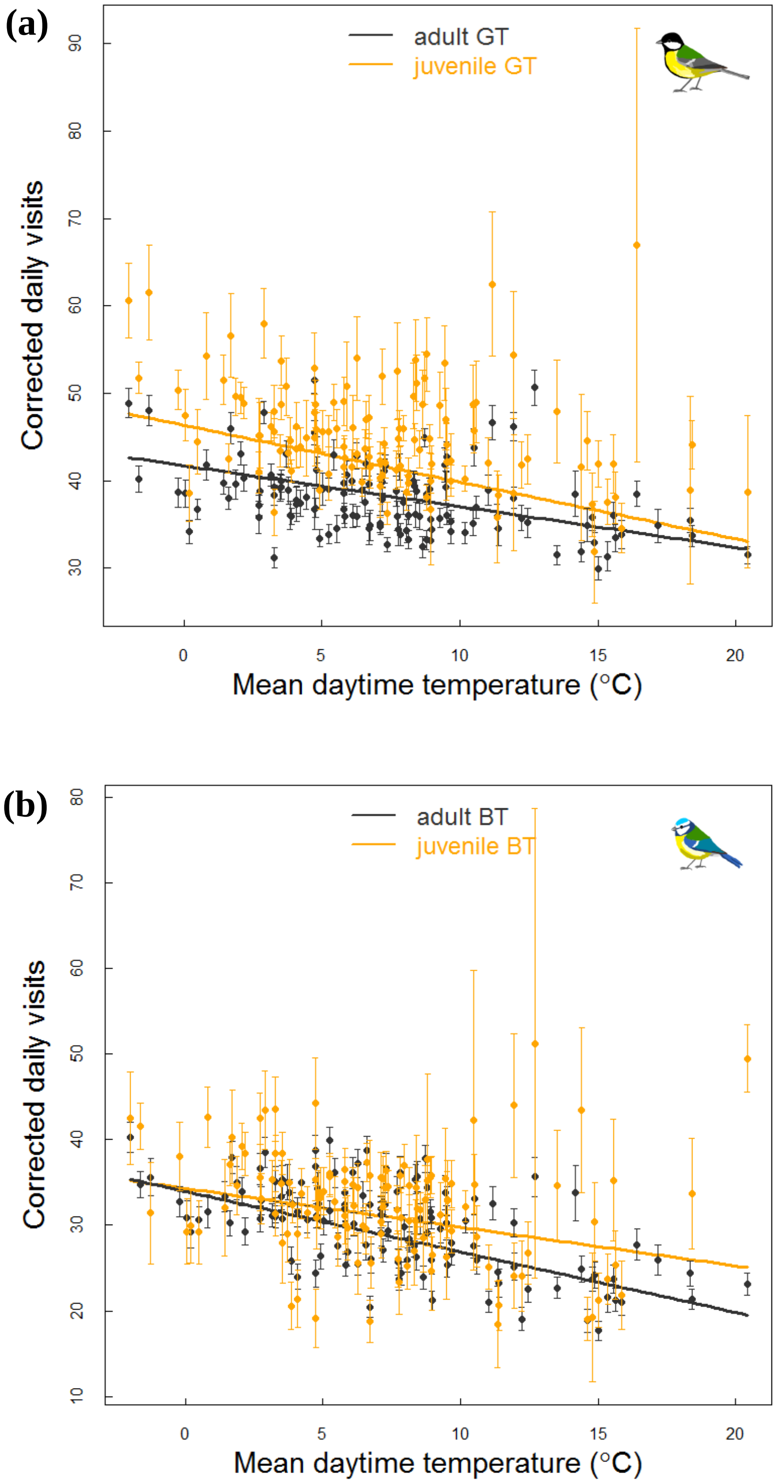


Fig. S3. Daily number of feeder visits by adult and juvenile (a) great tits and (b) blue tits on days of different average daytime temperature. Points are mean ± SE per date, corrected for day length, winter, sex, distance to territory, and competition. Lines indicate the predicted number of visits per day.

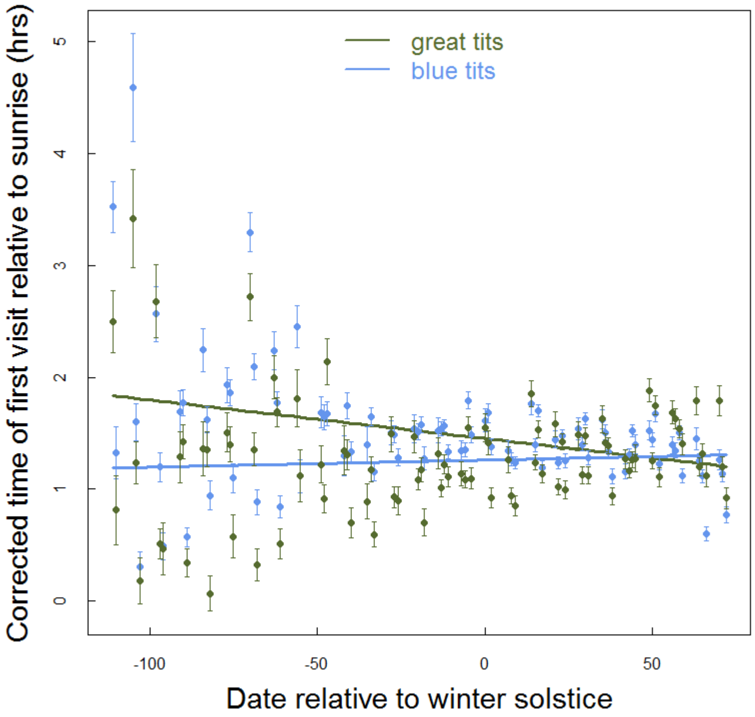


Fig. S4. Daily arrival time of individual great tits and blue tits at different times of year. Points are mean ± SE per date, corrected for the day length, temperature, daily number of visits, age, sex, distance to territory, and competition. Lines indicate the predicted arrival time at a feeder.

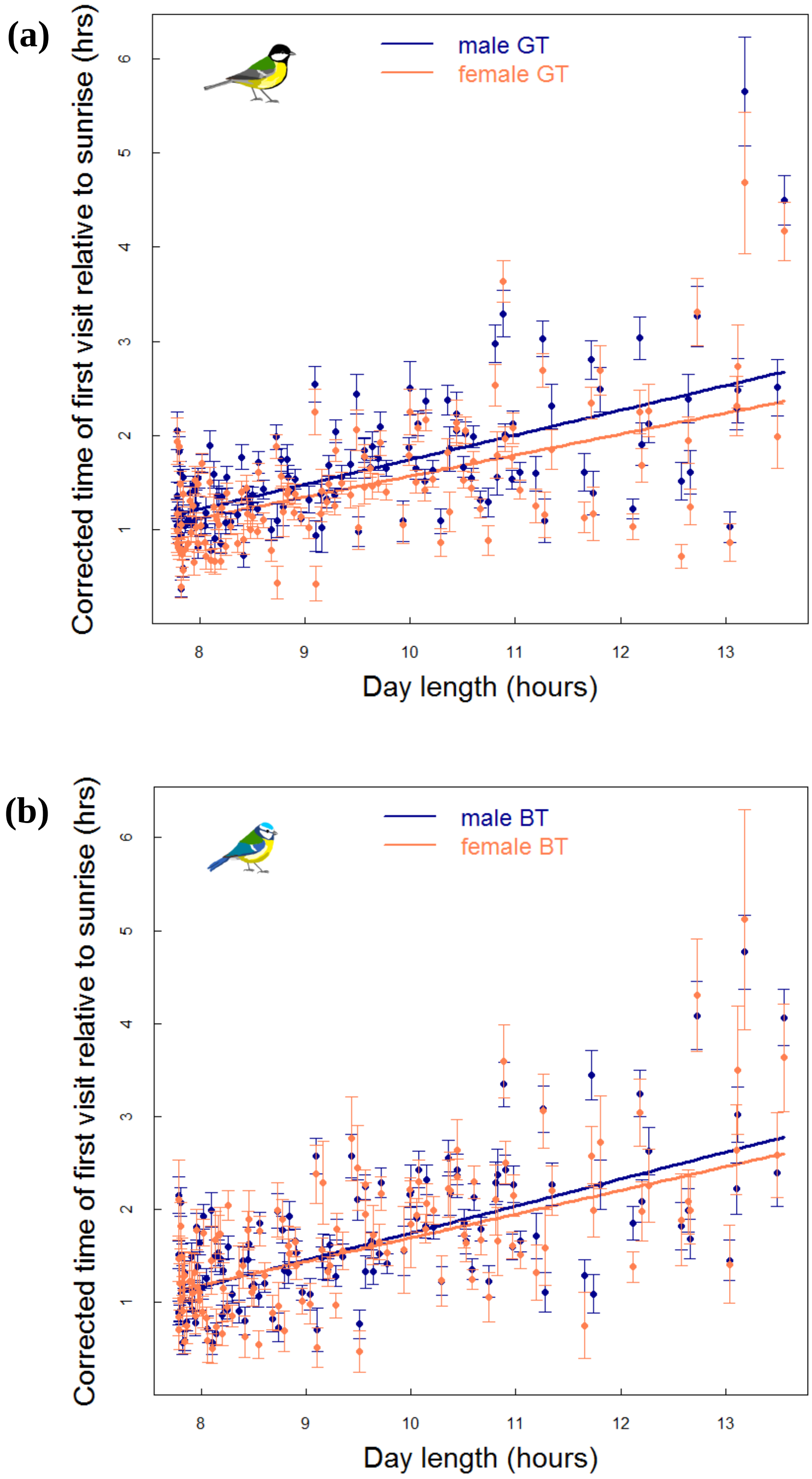


Fig. S5. Daily arrival time of male and female (a) great tits and (b) blue tits on days of different length. Points are mean ± SE per date, corrected for temperature, time of year, the daily number of visits, age, distance to territory, and competition. Lines indicate the predicted arrival time at a feeder.

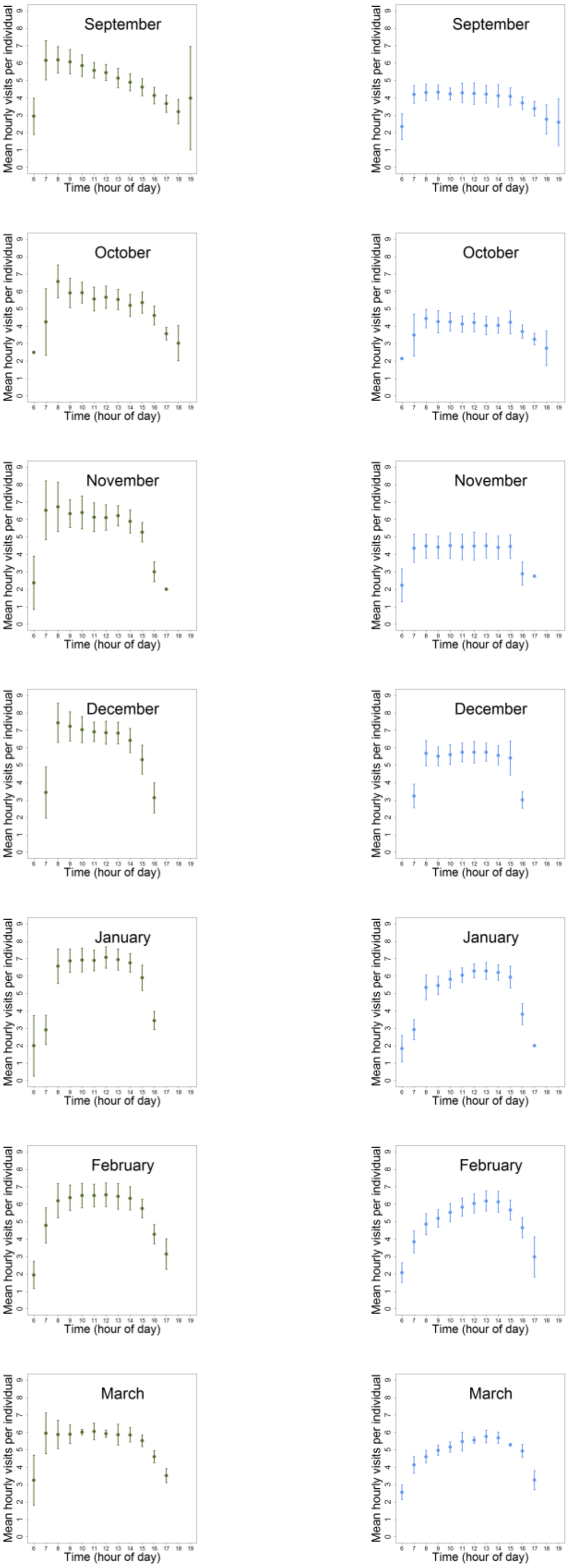


Fig. S6. Mean ± SD hourly visit rates per individual by month; great tits in green and blue tits in blue.

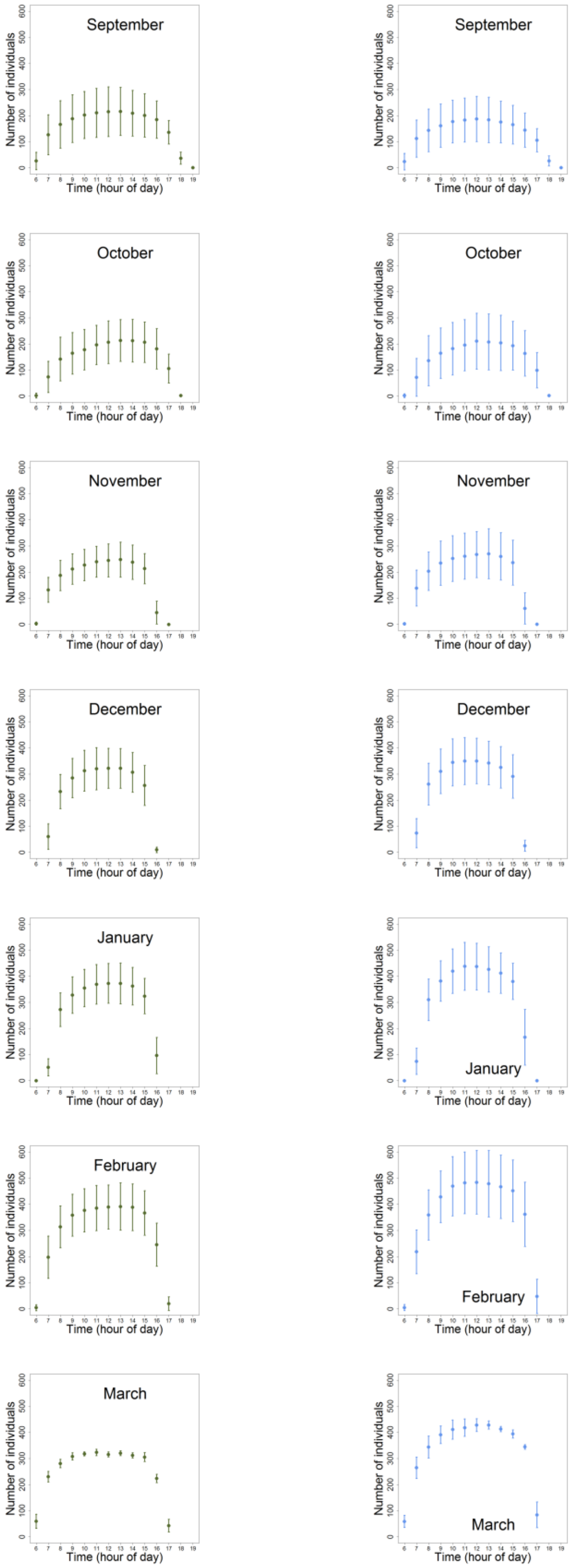


Fig. S7. Mean ± SD hourly number of recorded great tits (green) and blue tits (blue) by month.

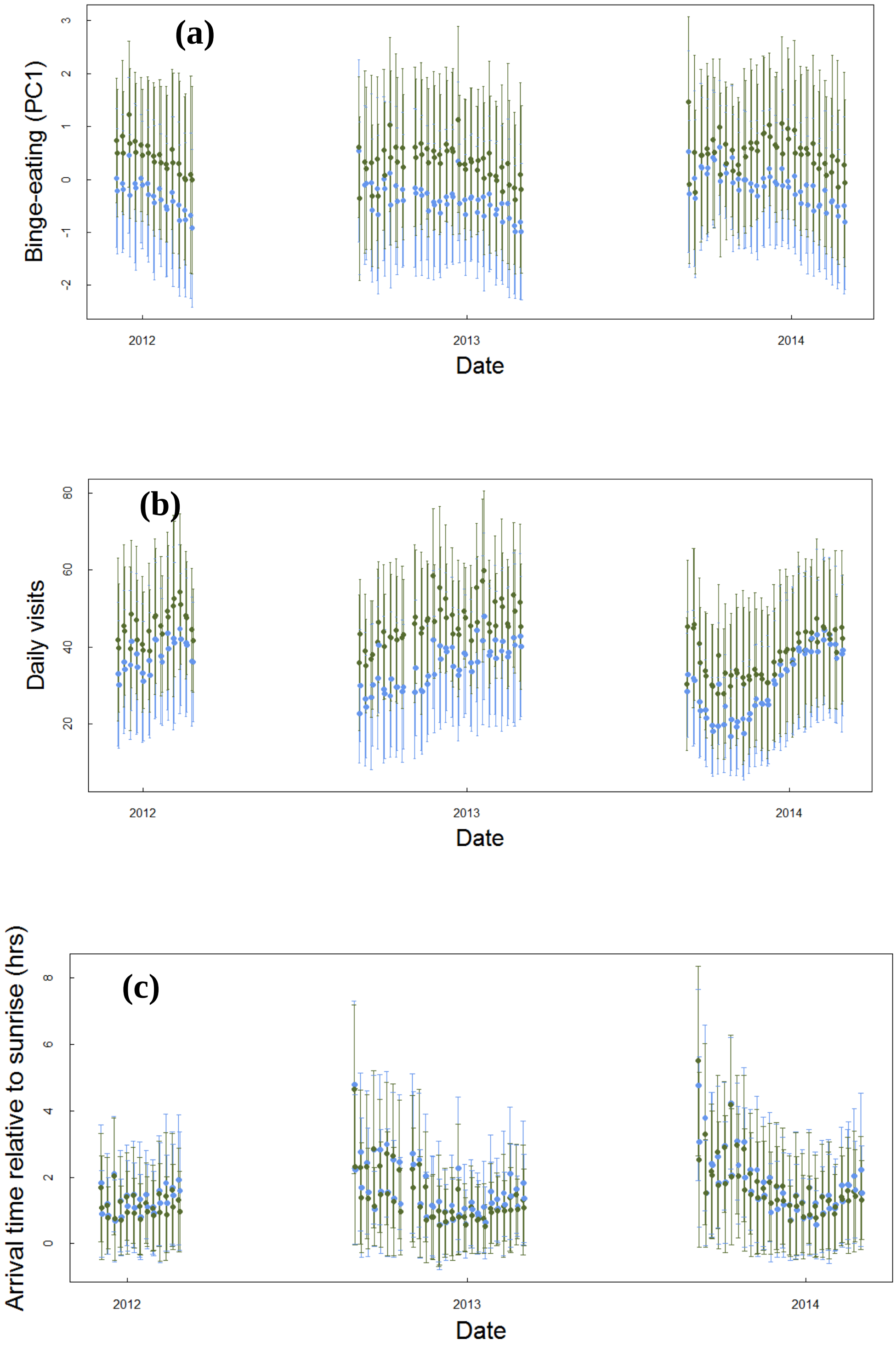


Fig. S8. Mean ± SD (a) level of binge-eating, (b) daily number of feeder visits, and (c) time of first feeder visit of day by individual birds on different dates over three winters; great tits in green, blue tits in blue.

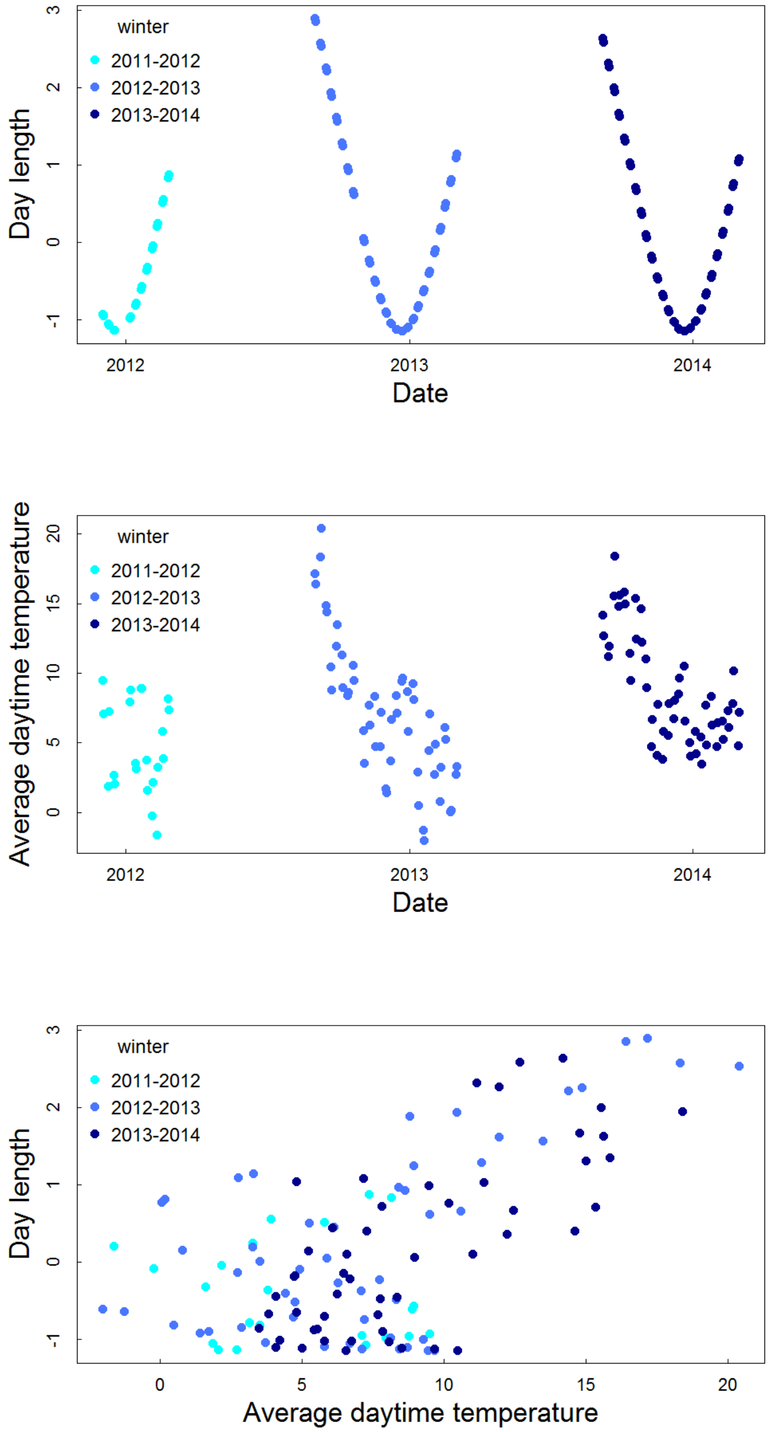


Fig. S9. Day length and average daytime temperature for each recording date across the study period.

Supplementary Tables

Table S1. Summary of the number of individuals, visits, and bouts by species and winter.

Species	Winter	Individuals	Individuals: First two winters	Individuals: Last two winters	Individuals: All three winters	Visits	Bouts
P. major	2011-2012	1,030	519		229	615,480	157,641
	2012-2013	817		340		852,536	227,229
	2013-2014	834				593,173	162,605
C. caeruleus	2011-2012	1,455	666		285	608,051	203,922
	2012-2013	1,227		516		792,005	281,357
	2013-2014	1,094				563,745	191,806
total *P. major*		1,820				2,061,189	547,475
total *C. caeruleus*		2,588				1,963,801	677,085
grand total		4,408	1,185	856	514	4,024,990	1,224,560

Table S2. Linear mixed model on factors affecting the level of binge-eating (PC1) by individual great tits and blue tits visiting feeders. 36,556 observations of both species.

Fixed effect	Coefficient	SE	t	*P*
day length	-0.06	0.02	-3.91	<0.001
day of winter	0.00	0.00	-0.03	0.976
daily visits	-0.51	0.01	-65.32	<0.001
species (GT)	1.49	0.09	17.13	<0.001
age (juvenile)	-0.13	0.03	-5.10	<0.001
sex (male)	0.10	0.04	2.45	0.014
distance to territory	0.26	0.01	19.72	<0.001
average competition	-0.02	0.02	-0.76	0.445
deviation from average competition	-0.19	0.02	-10.99	<0.001
age (juvenile) * distance to territory	-0.08	0.02	-4.70	<0.001
day of winter * sex (male)	0.00	0.00	-7.07	<0.001
day length * species (GT)	-0.06	0.01	-7.69	<0.001

Random term	Variance	SD	n
individual ID	0.54	0.73	1508
individual ID with random slope for competition deviation	0.14	0.37	1508
date	0.16	0.40	130
site	0.05	0.23	65
residual	0.98	0.99	

Table S3. Linear mixed models on factors affecting the level of binge-eating (PC1) by individual great tits and blue tits visiting feeders; one model per species. 20,969 observations of great tits; 15,587 observations of blue tits.

	great tits				blue tits			
Fixed effect	Coefficient	SE	*t*	*P*	Coefficient	SE	*t*	*P*
day length	-0.14	0.02	-8.11	<0.001	-0.05	0.02	-2.96	0.003
day of winter	0.00	0.00	-0.55	0.579	0.00	0.00	1.41	0.159
daily visits	-0.38	0.01	-35.53	<0.001	-0.67	0.01	-65.15	<0.001
age (juvenile)	-0.24	0.04	-6.69	<0.001	-0.02	0.04	-0.53	0.598
sex (male)	0.18	0.06	3.00	0.003	0.04	0.05	0.73	0.463
distance to territory	0.27	0.02	14.18	<0.001	0.24	0.02	13.79	<0.001
average competition	-0.04	0.03	-1.19	0.236	0.03	0.03	1.07	0.283
deviation from average competition	-0.18	0.02	-8.04	<0.001	-0.19	0.02	-7.81	<0.001
age (juvenile) * distance to territory	-0.09	0.02	-3.51	<0.001	-0.10	0.03	-3.67	<0.001
day of winter * sex (male)	0.00	0.00	-7.37	<0.001	0.00	0.00	-2.37	0.018

	great tits			blue tits		
Random term	Variance	SD	n	Variance	SD	n
individual ID	0.61	0.78	765	0.41	0.64	743
individual ID with random slope for competition deviation	0.12	0.35	765	0.16	0.39	743
date	0.23	0.48	130	0.11	0.33	130
site	0.06	0.24	65	0.05	0.23	65
residual	1.13	1.06		0.72	0.85	

Table S4. Linear mixed model on factors affecting the daily number of feeder visits by individual great tits and blue tits. 35,118 observations of both species.

Fixed effect	Coefficient	SE	t	*P*
average daytime temperature	−0.47	0.07	−6.60	<0.001
winter (2nd)	5.25	0.90	5.81	<0.001
winter (3rd)	0.03	0.97	0.03	0.978
species (GT)	10.83	0.53	20.59	<0.001
age (juvenile)	2.74	0.33	8.28	<0.001
sex (male)	3.52	0.52	6.78	<0.001
distance to territory	−3.37	0.14	−23.97	<0.001
average competition	6.66	0.31	21.38	<0.001
deviation from average competition	9.21	0.24	37.61	<0.001

Random term	Variance	SD	n
individual ID	85.14	9.23	1507
individual ID with random slope for competition deviation	33.58	5.79	1507
date	19.79	4.45	126
site	10.55	3.25	65
residual	160.40	12.66	

Table S5. Linear mixed models on factors affecting the daily number of feeder visits by individual great tits and blue tits; one model per species. 20,070 observations of great tits; 15,048 observations of blue tits.

	great tits				blue tits			
Fixed effect	Coefficient	SE	*t*	*P*	Coefficient	SE	*t*	*P*
average daytime temperature	-0.47	0.09	-5.05	<0.001	-0.71	0.10	-6.74	<0.001
day length	0.50	0.25	1.99	0.046	0.30	0.28	1.06	0.290
winter (2nd)	6.40	0.95	6.74	<0.001	3.07	1.11	2.76	0.006
winter (3rd)	-1.40	1.02	-1.37	0.170	1.99	1.22	1.64	0.102
age (juvenile)	4.64	0.56	8.31	<0.001	0.35	0.70	0.50	0.615
sex (male)	2.89	0.65	4.42	<0.001	3.66	0.79	4.64	<0.001
distance to territory	-3.04	0.18	-16.53	<0.001	-3.61	0.22	-16.33	<0.001
average competition	7.23	0.39	18.46	<0.001	5.88	0.48	12.20	<0.001
deviation from average competition	9.33	0.30	30.96	<0.001	8.78	0.38	23.07	<0.001
average daytime temperature * age (juvenile)	-0.18	0.06	-2.88	0.004	0.25	0.08	3.10	0.002

	great tits			blue tits		
Random term	Variance	SD	n	Variance	SD	n
individual ID	69.50	8.34	765	99.73	9.99	742
individual ID with random slope for competition deviation	25.86	5.08	765	39.79	6.31	742
date	21.57	4.64	126	22.04	4.69	126
site	10.85	3.29	65	13.76	3.71	65
residual	159.61	12.63		153.45	12.39	

Table S6. Linear mixed model on factors affecting the daily arrival time of individual great tits and blue tits at feeders. 35,118 observations of both species.

Fixed effect	Coefficient	SE	t	*P*
day length	946.11	129.80	7.29	<0.001
day of winter	5.15	3.98	1.29	0.196
daily visits	-3116.55	33.84	-92.10	<0.001
species (GT)	691.17	126.62	5.46	<0.001
age (juvenile)	131.05	94.77	1.38	0.167
sex (male)	300.19	121.59	2.47	0.014
distance to territory	1302.81	53.18	24.50	<0.001
average competition	-129.46	92.29	-1.40	0.161
deviation from average competition	-171.37	74.40	-2.30	0.021
age (juvenile) * distance to territory	-529.10	73.55	-7.19	<0.001
day of winter * species (GT)	-14.68	1.15	-12.80	<0.001

Random term	Variance	SD	n
individual ID	3966332.10	1991.57	1507
individual ID with random slope for competition deviation	2139040.66	1462.55	1507
date	1431419.33	1196.42	126
site	3872691.96	1967.92	65
residual	18503663.82	4301.59	

Table S7. Linear mixed models on factors affecting the daily arrival time of individual great tits and blue tits at feeders; one model per species. 20,070 observations of great tits; 15,048 observations of blue tits.

	great tits				blue tits			
Fixed effect	Coefficient	SE	*t*	*P*	Coefficient	SE	*t*	*P*
day length	802.09	140.94	5.69	<0.001	918.14	149.13	6.16	<0.001
day of winter	-13.65	4.76	-2.87	0.004	7.88	4.88	1.61	0.107
average daytime temperature	-96.83	60.52	-1.60	0.110	-78.62	61.94	-1.27	0.204
daily visits	662.40	234.19	2.83	0.005	995.05	313.05	3.18	0.001
age (juvenile)	196.93	115.65	1.70	0.089	-132.51	160.06	-0.83	0.408
sex (male)	-784.35	428.50	-1.83	0.067	-1073.16	620.75	-1.73	0.084
distance to territory	1374.07	68.78	19.98	<0.001	1206.45	82.33	14.65	<0.001
average competition	-98.08	111.26	-0.88	0.378	-143.12	144.36	-0.99	0.321
deviation from avg competition	106.30	88.52	1.20	0.230	-548.72	120.79	-4.54	<0.001
age (juvenile) * dist to territory	-655.12	89.70	-7.30	<0.001	-171.05	124.89	-1.37	0.171
day length * daily visits	-315.97	26.87	-11.76	<0.001	-329.64	34.86	-9.45	<0.001
avg daytime temp * daily visits	-136.63	9.03	-15.12	<0.001	-156.61	12.20	-12.84	<0.001
day length * sex (male)	140.94	42.87	3.29	0.001	126.03	62.73	2.01	0.045

	great tits			blue tits		
Random term	Variance	SD	n	Variance	SD	n
individual ID	3129523.02	1769.05	765	4731225.43	2175.14	742
individual ID with random slope for competition deviation	1584015.45	1258.58	765	2644437.57	1626.17	742
date	1572912.95	1254.16	126	1981142.98	1407.53	126
site	3678360.05	1917.91	65	3763051.79	1939.86	65
residual	16295775.67	4036.80		19822213.42	4452.21	

CHAPTER 4

Foraging in the face of competition: an experimental manipulation of access to food

Foraging in the face of competition: an experimental manipulation of access to food

Nicole D. Milligan, Reinder Radersma, Ella F. Cole and Ben C. Sheldon

1. Foraging in groups can reduce the risk of predation for individuals. However, competition will increase with group size, potentially limiting individual foraging efficiency. Efficiency is usually quantified by feeding rates or net food gained but, as shown in previous chapters, other measures such as the timing of feeding within a day can explain a large amount of variation in foraging patterns. Here we describe the relationship between competition level, both natural and experimentally manipulated, and daily foraging patterns of wild great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*) at feeders during the winter, and explore how these relationships vary with dominance-related traits such as age, sex and species.

2. 65 automated feeding stations were set up in a grid across Wytham Woods, recording visits by tagged individuals over three winters. Natural levels of competition – the daily number of visits by other individuals at a given feeder, termed ‘feeder traffic’, varied between sites and over time. In addition to this background variation, we manipulated competition levels at four of the feeding stations by introducing a second feeder. At these experimental sites, feeders alternated between one and two feeders open each day. We predicted that the constraint of interference competition would be greater in the one-feeder treatment by limiting individuals’ levels of ‘binge-eating’ (temporal clustering of feeder visits) and their daily visit rates, while also causing them to spend a larger proportion of the day at feeders. We further predicted that subordinate classes of individuals (i.e. blue tits, yearlings and females) would be affected more negatively by an increase in competition. That is, with increasing background level of competition (feeder traffic), subordinates would binge-eat less, visit feeders less often and spend a larger proportion of the day at feeders, relative to dominants.

3. We found effects of both manipulated and natural levels of competition on all three measures of foraging behaviour. An increase in manipulated competition caused: (i) a decrease in binge-eating, (ii) an increase in the proportion of day spent at feeders, and (iii) a reduction in daily visit rate, but only when feeders were busy with background competition. With increasing natural competition: (i) binge-eating increased in dominants relative to subordinates, (ii) the proportion of day spent at feeders decreased, but only in dominants, and (iii) overall daily visit rates increased.

4. Binge-eating more and spending a smaller proportion of the day at feeders can lead to more time being available for other activities. Therefore we conclude that maximizing binge-eating and minimizing the time spent at feeders improved foraging efficiency. The behavioural responses to a manipulation of feeder access suggest that interference competition can limit the efficiency of feeding at busy sites. In addition, dominance status and feeder traffic interact so that subordinate individuals are more susceptible to the negative effects of local competition. Thus, the costs of group foraging differ between individuals, with potential consequences for survival patterns within the population and for community composition.

INTRODUCTION

Foraging to fulfil daily energy and nutrient requirements is essential for survival, but so is the need to avoid predation. Since an increase in foraging rate tends to increase the probability of being predated (Stephens *et al.* 2007), animals often face a trade-off between acquiring food and maintaining safety (Lima & Dill 1990). For this reason, individuals of many species forage in groups. Group formation has many benefits, including increased probability of predator detection, sharing of vigilance, food-finding efficiency, spread of information, and mate choice (Krause & Ruxton 2002; Clark & Mangel 1986; Pulliam 1973; Cresswell 1994). However, grouping also incurs costs, through increased competition, aggression, spread of disease, or as a larger target for predators (Krause & Ruxton 2002; Cresswell 1997). Interference competition is the depression of feeding rates resulting from the proximity or behaviour of other individuals (Krause & Ruxton 2002, Sutherland 1996; Goss-Custard 1980). Typically, when feeding on limited resources, the larger the group, the greater the competition (Barton *et al.* 1996; Ekman & Rosander 1987; Clark & Mangel 1986). However, there may also be inequalities between individuals in competitive ability. Social dominance is often a strong determinant of foraging success, with dominants tending to feed at higher rates than subordinates (Metcalfe 1986; Baker *et al.* 1981; Ekman & Askenmo 1984; Kotrschal *et al.* 1993; Vervaecke *et al.* 1999). In some cases, competitive inequalities can also be due to individuals trading-off the costs and benefits of competitiveness in different ways with alternative behavioural strategies. In great tits (*Parus major*), for example, good competitors were bad problem-solvers, while individuals with low competitive ability were better problem solvers (Cole & Quinn 2012). Furthermore, individuals may handle the trade-off between resource acquisition and safety differently. For instance, proactive individuals tend to prioritize productivity while reactive individuals prioritize survival (Biro & Stamps 2008; Quinn *et al.* 2012). Thus, the consequences of competition will vary among individuals.

In some species, individuals reduce the risk of predation by taking food to the safety of nearby cover for consumption, especially when the perceived risk is high. For instance, chickadees (*Parus atricapillus*) were more likely to carry food to safety after a model sparrowhawk flew by (Lima 1985). Individuals can also minimize the time they spend exposed to predators, an example being the reduction of foraging day length in juncos under higher risk of predation (*Junco hyemalis*; Lima 1988) or great tits (Krams 2000). Density dependence will play a role in how competition affects foraging behaviour, along with the state of an individual, such as its hunger level or social rank (Kotrschal *et al.* 1993; Dill & Fraser 1984; McNamara & Houston 1990). Mass-dependent costs, anti-predation behaviour, and group size can also influence the safety-feeding trade-off (Stephens *et al.* 2007). Under high competition, individuals can partition resources by segregating across habitats, food types, methods of food acquisition, or time (Schoener 1974, Ziv *et al.* 1993). For example, brown trout (*Salmo trutta*) separate temporally under high competition, with subordinates shifting to forage at more dangerous times of day (Alanärä *et al.* 2001).

The temporal scales at which behaviours are evaluated are key in making conclusions about optimality, as demonstrated in foraging eiders (*Somateria mollissima*) which trade-off the different timescales of tidal and digestive constraints (Heath *et al.* 2010). It is also important to quantify appropriate measures, or currencies, of behaviour in order to determine efficiency (Houston & McNamara 2014). In previous studies, currencies have included rate maximization (Schmid-Hempel *et al.* 1985; Cuthill *et al.* 1990) and energy-expenditure minimization (Charlton & Houston 2010). When the risk of predation whilst foraging is high, safety-maximization may also play a role in what is optimal (Gilliam & Fraser 1987; Kotler *et al.* 2002). Group foraging confers advantages to individual members in foraging and safety. However, variation in feeding efficiency between individuals tends to reduce survival and reproduction in subordinates which, through interference competition, typically face higher risks of starvation and predation than dominants (Rutten *et al.* 2010). Foraging decisions made by individuals will have implications for group size and composition (Sutherland 1996).

Of the investigations on interference competition in the wild, few studies have manipulated the number of competitors, with most relying on natural variation in competitor density and/or manipulating resource density (e.g. Cresswell 1998, Dolman 1995; Kotrschal *et al.* 1993). An exception is a study on oystercatchers (*Haematopus ostralegus*) that manipulated competitor density in the wild, demonstrating interference competition (Rutten *et al.* 2010). As shown in previous chapters, the temporal clustering of feeder visits explains a considerable proportion of the individual variation in daily foraging routines in both great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*). Additionally, the level of ‘binge-eating’ (the extent of temporal clustering of feeder visits within a day) by individuals varied with a measure of competitor density. Here, we combine natural levels of competitor density (‘feeder traffic’, defined as the total number of visits by non-focal individuals at a given feeder on a given day) with a manipulation of access to food at supplemental feeders to test the effects of interference competition on foraging behaviour in great tits and blue tits. We also investigate whether dominance-related factors such as species, age and sex class influence the relationship with competition. We use three measures of foraging behaviour: the level of binge-eating, the daily number of feeder visits, and the proportion of daytime spent at feeders.

We predicted that, at high feeder traffic, experimentally reducing the effect of interference competition by increasing access to food would (i) allow a greater level of binge-eating, (ii) allow more daily feeder visits per individual, and (iii) decrease the proportion of day spent at feeders. In addition, we expected dominant classes of individual (great tits, adults or males) to feed more efficiently (i.e. binge-eat more and spend a smaller proportion of day visiting feeders) than subordinate classes (blue tits, juveniles or females) with increasing competition. That is, subordinates should be more susceptible to interference competition.

METHODS

Study system and automated data collection

Fieldwork was conducted in a 385-ha mixed woodland, Wytham Woods (51˚46′N, 1˚20′W; Savill *et al.* 2010) in Oxfordshire, between 2011 and 2014. This study took place in the context of an ongoing long-term population study of tits (Perrins 1979; McCleery *et al.* 2004). Great tits (GTs) and blue tits (BTs) were caught and marked either at nest boxes during the spring breeding season or with mist nets at artificial feeders throughout the woodland during the non-breeding season. Each individual was marked with a metal British Trust for Ornithology (BTO) ring and a plastic passive integrated transponder (PIT) tag (IB Technology, Aylesbury, UK). Biometric data were recorded, with age and sex determined by plumage (Svensson 1992) and, during the breeding season, by the presence or absence of a brood patch. Great tits are typically dominant over blue tits and, within-species, males over females and adults over juveniles (Perrins 1979).

65 feeding stations were set up in a grid with 250m spacing. Each station contained an artificial bird feeder with two seed access points. A radio-frequency identification (RFID) antenna was positioned in front of each access point so that a tagged bird landing on it would be detected. Both antennae were connected to an automated data logger (Dorset ID, Aalten, The Netherlands) which recorded the ID, time and location up to 3 times per second whenever the feeder was open and a PIT-tag was detected. Feeders supplied black sunflower seeds *ad libitum* when open. Equipment at each site was housed in a $1m^3$ heavy duty mesh cage 1m above ground to exclude squirrels and large birds; mesh spacing was 5cm.

The feeding stations were programmed to open access to seed pre-dawn and close post-dusk every Saturday and Sunday[*] from September to February inclusive in 2011-2012, 2012-2013 and 2013-2014. This work was undertaken as part of a larger project investigating the social ecology of tits (Aplin *et al.* 2015, Farine *et al.* 2015). In order to minimize the effect of change in day length on feeding behaviour, for this study we restrict analysis to the five weekends surrounding the winter solstice in December and early January of each of the three winters.

Experimental protocol

Four of the 65 logger sites were selected as experimental sites. They were spaced evenly across Wytham Woods (approximately 1km apart; map in Fig. S2) and attracted different numbers of birds, spanning a large part of the observed range of feeder traffic (Fig. S3a). In order to manipulate access to food, a second feeder-logger-cage unit was introduced at each of the four sites, 1m from the original unit (layout in Fig. S1). For each day of experimental data collection, either one feeder or both feeders were programmed to open at each site. Experimental data were collected over three consecutive days midweek over eight weeks from December 2013 to February 2014 (24 days, totalling 96 days' worth of data across the 4 locations), alternating between the one-feeder and two-feeder treatments (see Table S13 for the experimental schedule – the same for all four sites). One feeder at each experimental site was programmed to open, as usual, at the weekends and

---

[*] Except prior to December 2011, when feeding stations were programmed to open on Thursdays only.

the particular feeder that opened alternated every two weeks. This schedule maintained the winter weekend observational protocol and allowed one ‘closed’ day between weekends and experimental days, thus preventing continuous food supplementation.

Data handling and statistical analysis

In the raw data, the inter-record intervals of individuals formed a tri-modal distribution, corresponding to within-visit intervals, within-bout intervals, and between-bout intervals. A foraging bout is a temporal cluster of feeder visits. We used the two troughs in the distribution to determine the thresholds with which to allocate consecutive records of an individual to the same visit (records less than 17s apart), to the same bout (visits up to 514s apart) or to different bouts (visits greater than 514s apart). Data for individuals that were recorded at more than one feeding station within a day were excluded from analyses for that date. This did not affect the experimental dataset (where feeding stations were 1km apart) and only 15 individuals moved between experimental feeding stations over the course of the 8-week food access manipulation. More details of record allocation and data filtering are given in chapter 2. Within-day movers were excluded from analyses as focal individuals, but still counted towards the measures of feeder traffic and group size which are described below.

The number of visits recorded at a feeding station in a day was highly correlated with the number of individuals recorded there on that day (Fig. S3a; Pearson’s $r=0.92$, $df=1459$, $p<0.001$) and also strongly predicted a measure of mean group size (Figs S5 & S6; model estimates in Tables S8 & S4). We used a sliding-window method to quantify group size, i.e. the number of other individuals present when a focal individual visits a feeder. To achieve this we calculated the number of unique individuals (of either species) that visited the same feeder within 514s before or after the focal individual’s visit, for every visit. Daily mean group size was then calculated for each individual. Of the three measures we chose to use the total number of visits as a daily measure of local competition, since individuals and flocks may vary considerably in number over a day. We define the term feeder traffic as the number of visits recorded of both great tits and blue tits at a feeding station in one day. Thus, the feeder traffic experienced by a focal individual is the feeding station's daily total visits minus the focal individual's daily total visits.

In order to investigate how competition affects feeding behaviour, we quantified three aspects of foraging. Firstly, as described in Chapter 2, we ran a principal component analysis (PCA) on six measures of the daily timing of feeder visits to characterize the temporal pattern of foraging behaviour. The first principal component, PC1, captures the extent to which individuals cluster their feeder visits into foraging bouts. This axis of variation covers a spectrum, with binge-eaters at one end exhibiting highly clustered visits and grazers at the other end with periodic visits throughout the day. Secondly we summed the total number of feeder visits by each individual per day. Thirdly we calculated the proportion of daytime spent at feeders. For this purpose we define daytime as the length of time between sunrise and sunset, and the time spent at feeders as the daily sum of an individual's bout lengths. The length of a bout is the sum of the inter-visit intervals of the constituent visits plus 513s. The addition of 513s prevents one-visit bouts from having zero length but does not cause consecutive bouts to overlap in time.

Feeder traffic data were square-root-transformed to normalize the distribution. This measure of local competition was also split into two factors: between-individual variation (the mean feeder traffic experienced by an individual across a winter) and within-individual variation (the daily deviation in feeder traffic experienced from the individual's winter mean). This accounts for individuals being unevenly sampled across recording dates and competition levels (i.e. feeder traffic) and also enables the use of mixed models which fit random slopes for individuals.

We fitted generalized linear mixed-effect models (GLMMs) to test the effect of local competition on feeding patterns, with separate terms for mean feeder traffic experienced and daily deviation. Individual ID, site and date were included as random effects, with a random slope within individual for deviation from mean feeder traffic experienced. Models were fitted to both the 4-site experimental dataset and 65-site observational dataset. Three types were fitted: (i) for each species under experimental conditions (N=4 sites), (ii) for each species in the observational dataset (N=65 sites), and (iii) for both species in the observational dataset (to compare species). Site was not included as a random effect in the experimental models due to low sample size. Treatment (one feeder or two feeders open) was added as a categorical fixed effect to experimental models, along with an interaction term between treatment and mean feeder traffic experienced. Species or age (first year or adult) and sex class were added as categorical fixed effects to type (ii) and type (iii) models, along with an interaction term between the category and mean feeder traffic experienced. (Age and sex interactions were not added to experimental models due to limited sample size.) A list of *a priori* models was compiled for each of the three behavioural measures (binge-eating, daily visits and proportion of day) for each dataset type. Initial data exploration and the results of previous chapters were used to list additional variables likely to affect each behavioural measure. Akaike's information criterion (AIC) was used in model selection (Burnham & Anderson 2002). We used the Kenward-Roger approximation to calculate approximate degrees of freedom, and along with the t-distribution, calculated p-values for each fixed effect (Kenward & Roger 1997). When there is a significant covariate interaction term (e.g. between treatment and feeder traffic), it is inappropriate to immediately conclude that the factor has an effect over the entire range of the continuous variable (Engqvist 2005); here the continuous variable acts as a moderator on the predictor factor. The Johnson-Neyman procedure for determining regions of significance can estimate the values of the continuous variable for which the factor has a significant effect (Johnson & Neyman 1936; Huitema 1980). Model tables, including Johnson-Neyman regions of significance where appropriate, are given in the appendix for types (i) Tables S1-S3, (ii) Tables S5-S7, and (iii) Tables S9-S11. All statistical analyses were conducted using R 3.2.0 (R Core Team 2015).

RESULTS

Over 24 experimental dates (3 days in each of 8 weeks), 184 individual great tits and 267 individual blue tits were recorded across four experimental sites; the daily total number of individuals at a site ranged between 27 and 112. The mean ± 1SD daily number of visits per individual was 34.6±14.7 and there was no significant difference in this measure between the one-feeder and two-feeder treatments (Welch's two-sample t-test: $t_{(834)}$=-1.43, p=0.154).

Over 30 observational dates (5 midwinter weekends in each of 3 winters), 1296 individual great tits and 916 individual blue tits were recorded across 65 sites (including the four experimental sites); the daily total number of individuals (of both species) at a site ranged between 0 and 108. The mean ± 1SD daily number of visits per individual was 35.6±15.0. There was no significant difference in the number of daily visits per individual across the four experimental sites between the experimental dataset and the observational dataset (Welch's two-sample t-test: $t_{(181)}$=0.83, p=0.405). Summaries of the experimental and observational datasets are given in Table S12.

Daily feeder traffic at a site was positively correlated with the number of unique individuals recorded at that site on that date (Fig. S3; experimental dataset: r=0.89, df=94, p<0.001). The proportion of daytime spent at feeders was negatively correlated with the level of binge-eating in both species in the observational dataset (Fig. S4; GTs: Pearson's r=-0.66, df=1294, p<0.001; BTs: r=-0.78, df=914, p<0.001) and in the experimental dataset (GTs: Pearson's r=-0.51, df=182, p<0.001; BTs: r=-0.71, df=265, p<0.001).

The effects of manipulating access to food are summarized in Table 1, along with the relationship of each dependent variable with daily feeder traffic.

Table 1. Summary of relationships between individual feeding behaviours and levels of interference competition (both experimentally manipulated and background levels)

Behavioural measure	**Effect of manipulation (increased interference)** *(experimental dataset)*	**Effect of (increasing) natural competition** *(observational dataset)*	**Dominance-related effect of (increasing) natural competition** *(observational dataset)*
Binge-eating (PC1)	🟥 decreases (only in GTs at high feeder traffic)		🟨 no change in GTs; decreases in BTs 🟧 GTs: decreases more in juveniles & females than in adults & males 🟩 BTs: greater in adults (only at low feeder traffic)
Daily number of visits	🟥 decreases (only in BTs at high feeder traffic)	increases	🟨 increases more in GTs than in BTs
Proportion of day at feeder	🟥 increases (only at high feeder traffic)		🟨 decreases in GTs; increases in BTs 🟧 decreases in males; no change in females

KEY:

🟥	supports **experimental constraint of competition** hypothesis
🟧	dominants better off than subordinates at **high feeder traffic**
🟨	dominants better off than subordinates
🟩	dominants better off than subordinates at **low feeder traffic**

Within-day visit clustering

Experimental data

Great tits binged more (high values of PC1) when there were two feeders open than when one feeder was open, above a mean daily feeder traffic threshold of 3343 daily feeder visits by other individuals; however, there was no significant relationship between PC1 and experimental treatment in blue tits (Fig. 1; model estimates in Table S1).

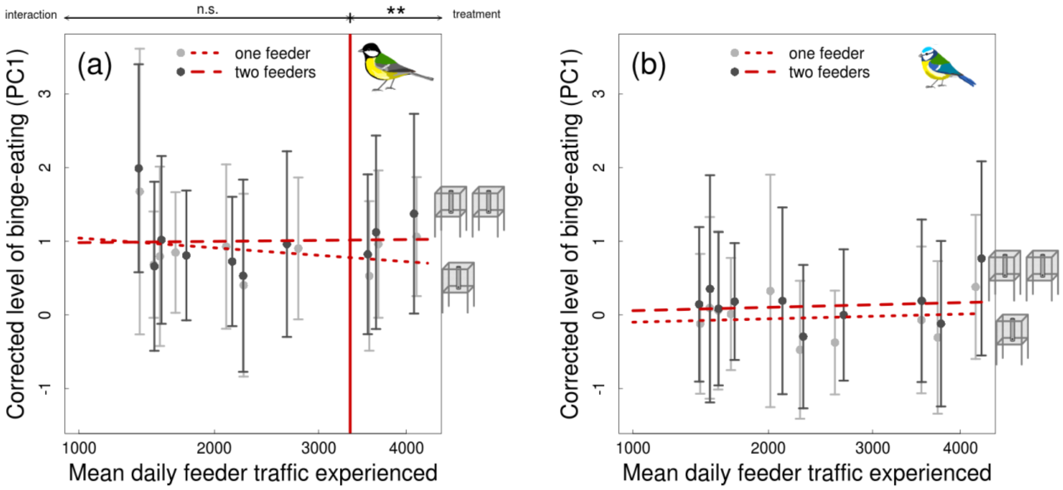


Fig. 1. Level of binge-eating (PC1; corrected for age and daily number of visits) by mean daily feeder traffic experienced in (a) great tits and (b) blue tits under a one- or two-feeder treatment. Points show means ± 1 SD, with data binned into tenths. Dotted lines indicate the model prediction of the relationship for each experimental treatment (either one feeder open or two feeders open at a feeding station). The vertical bar delineates the Johnson-Neyman region of significance for the treatment × traffic interaction.

Observational data

Great tits binged more than blue tits and this difference increased with mean feeder traffic experienced (Fig. 2a; model estimates in Table S9).

In great tits, above a traffic threshold of 777, adults binged more than juveniles; above at threshold of 770, males binged more than females (Fig. 2b; model estimates in Table S5a). In blue tits, adults binged more than juveniles, but only below a traffic threshold of 1270 (Fig. 2c; model estimates in Table S5b).

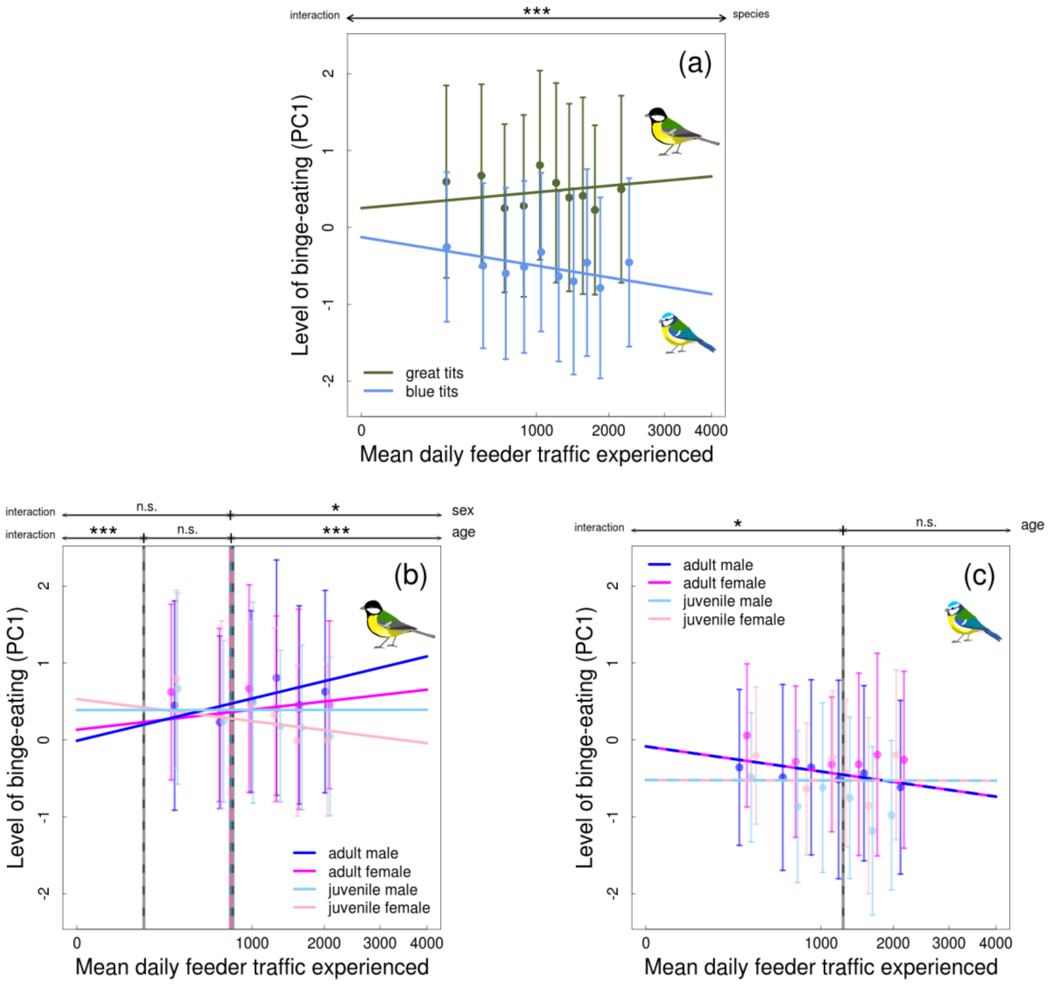


Fig. 2. Level of binge-eating (PC1) by mean daily feeder traffic experienced in (a) great tits and blue tits, (b) great tits and (c) blue tits; species or age-sex classes are plotted separately. Points show means ± 1 SD, with data binned into tenths (species) or sixths (age-sex). Lines indicate the model prediction of the relationship for each species or age-sex class. Vertical bars delineate Johnson-Neyman regions of significance for class × traffic interactions.

Daily visits

Experimental data

Blue tits visited feeders more times per day when there were two feeders open than when one feeder was open, above a mean daily feeder traffic threshold of 2474 daily feeder visits by other individuals; however, there was no significant relationship between daily visits and experimental treatment in great tits (Fig. 3; model estimates in Table S2).

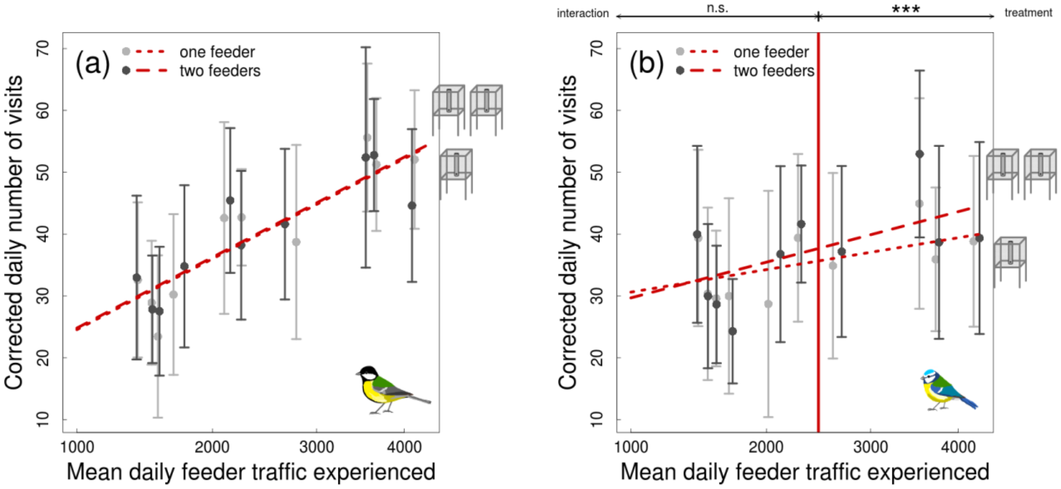


Fig. 3. Daily number of feeder visits by mean daily feeder traffic experienced in (a) great tits and (b) blue tits under a one- or two-feeder treatment. Points show means ± 1 SD, with data binned into tenths; data were corrected for age in both species and also for day length in great tits. Dotted lines indicate the model prediction of the relationship for each experimental treatment (either one feeder open or two feeders open at a feeding station). The vertical bar delineates the Johnson-Neyman region of significance for the treatment × traffic interaction.

Observational data

Great tits visited feeders more times per day than blue tits and this difference increased with mean feeder traffic experienced, with both species visiting more with increasing feeder traffic (Fig. 4a; model estimates in Table S10). In great tits, juveniles visited more often than adults and, below a traffic threshold of 1856, males visited more often than females (Fig. 4b; model estimates in Table S6a). In blue tits, below a traffic threshold of 2457, males visited more often than females (Fig. 4c; model estimates in Table S6b). In addition, juveniles visited more than adults at low feeder traffic (fewer than 492 feeder visits by other individuals) but less than adults at high feeder traffic (above threshold of 1340).

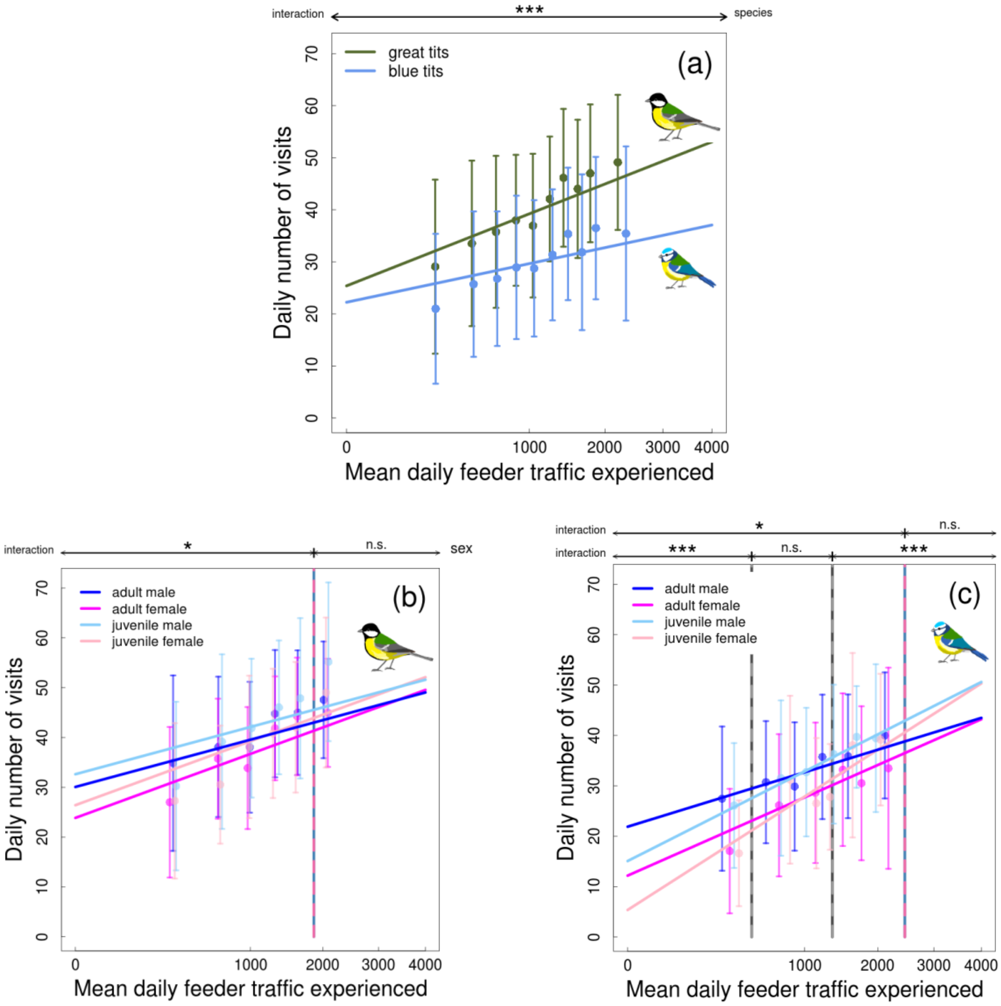


Fig. 4. Daily number of feeder visits by mean daily feeder traffic experienced in (a) great tits and blue tits, (b) great tits and (c) blue tits; species or age-sex classes are plotted separately. Points show means ± 1 SD, with data binned into tenths (species) or sixths (age-sex). Lines indicate the model prediction of the relationship for each species or age-sex class. Vertical bars delineate Johnson-Neyman regions of significance for class × traffic interactions.

Proportion of day at feeder

Experimental data

Both great tits and blue tits spent a smaller proportion of the day visiting feeders when there were two feeders open than when one feeder was open, above a mean daily feeder traffic threshold of 3880 (GTs) and 3760 (BTs) daily feeder visits by other individuals (Fig. 5; model estimates in Table S3).

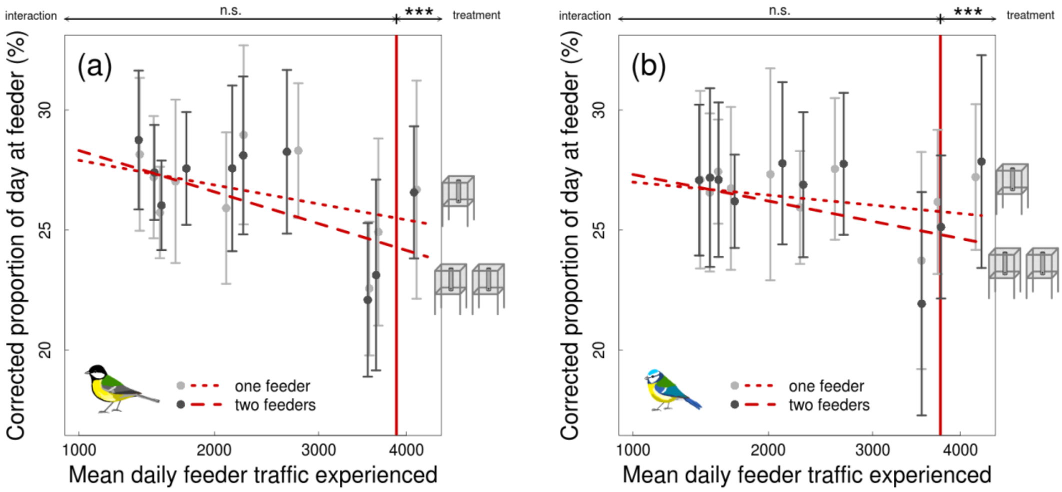


Fig. 5. Proportion of day spent at feeder by mean daily feeder traffic experienced in (a) great tits and (b) blue tits under a one- or two-feeder treatment. Points show means ± 1 SD, with data binned into tenths; data were corrected for age (in BTs only), daily number of visits, level of binge-eating (PC1) and day length. Dotted lines indicate the model prediction of the relationship for each experimental treatment (either one feeder open or two feeders open at a feeding station). Vertical bars delineate Johnson-Neyman regions of significance for treatment × traffic interactions.

Observational data

Great tits spent a larger proportion of the day visiting feeders than blue tits, with great tits decreasing the proportion and blue tits increasing the proportion with increasing feeder traffic below a threshold of 2163 visits by other individuals. Above this level of feeder traffic, there was no difference between species in the proportion of day spent at feeders (Fig. 6a; model estimates in Table S11).

In great tits, above a traffic threshold of 229, males spent a smaller proportion of the day visiting feeders than females and this difference increased with increasing feeder traffic (Fig. 6b; model estimates in Table S7a); the same pattern was observed in blue tits, above a traffic threshold of 689 (Fig. 6c; model estimates in Table S7b). Adults spent a smaller proportion of the day at feeders than juveniles in both species regardless of feeder traffic.

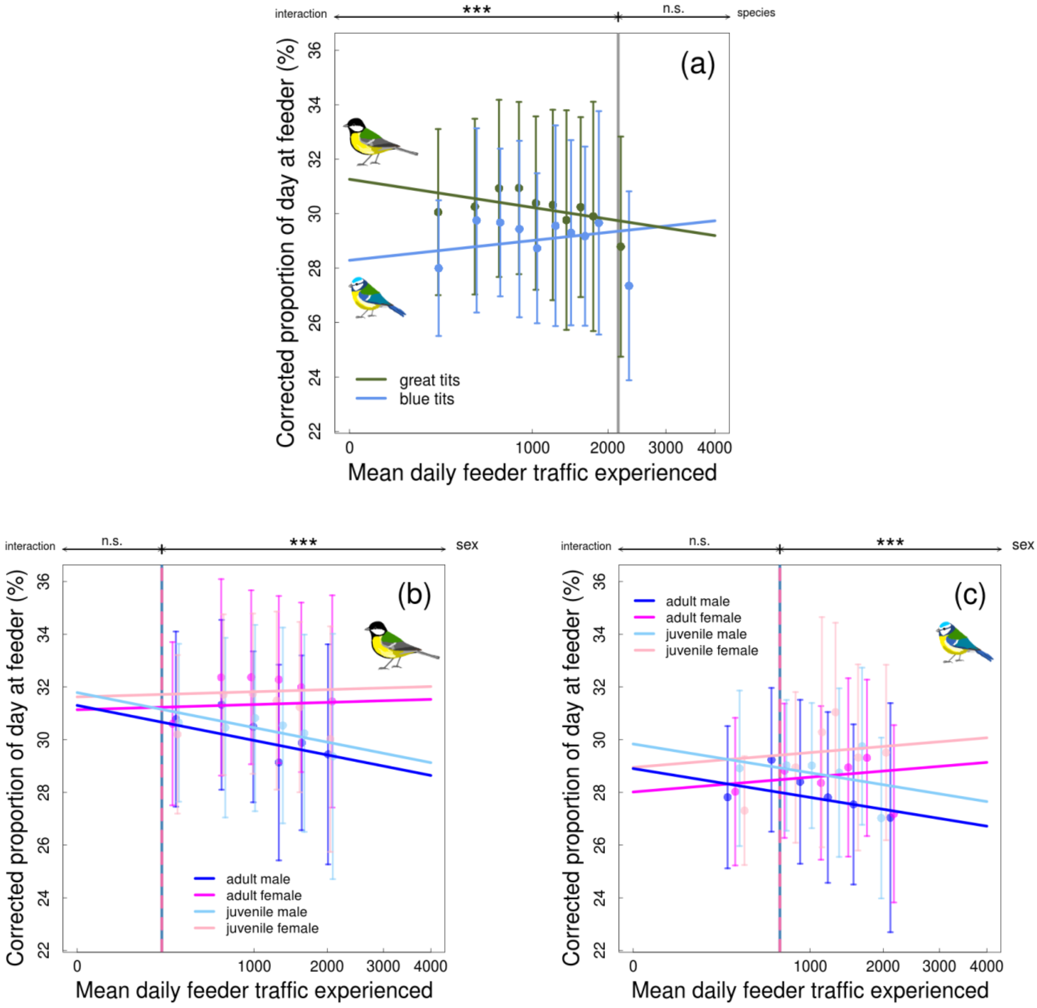


Fig. 6. Proportion of daytime spent at feeder by mean daily feeder traffic experienced in (a) great tits and blue tits, (b) great tits and (c) blue tits; species or age-sex classes are plotted separately. Points show means ± 1 SD, with data binned into tenths (species) or sixths (age-sex); data were corrected for each individual's daily number of feeder visits and level of binge-eating (PC1). Lines indicate the model prediction of the relationship for each category (species or age-sex class). Vertical bars delineate Johnson-Neyman regions of significance for category × traffic interactions.

DISCUSSION

The findings from this study suggest that interference competition affected great tits and blue tits visiting feeders, but that it only constrained feeding behaviour when competitor density was particularly high. When access to food was doubled during high feeder traffic, the constraint of competition was relaxed and some individuals were able to feed more efficiently by binge-eating more and spending a smaller proportion of the day at feeders while some visited feeders more often. Our analyses also demonstrated that dominance status was linked to foraging efficiency, with dominant classes of individual (great tits, adults or males) typically feeding more efficiently than subordinate classes, especially with increasing competitor density.

Foraging efficiency and susceptibility to interference

The negative relationship between the level of binge-eating and the proportion of day spent at feeders (Fig. S4) supports our assumption that binge-eating is a more efficient foraging strategy than grazing. Adult male great tits, the highest-ranking individuals in the dominance hierarchy in this study system, were predicted to be the least affected by interference competition. They should gain the most benefit (reduced time spent being vigilant) with the least cost (interference) with increasing group size and feeder traffic. Indeed, they binged more (Fig. 2b) and spent a smaller proportion of the day at feeders (Fig. 6b) as traffic increased, relative to females. As dominance rank decreased, down to juvenile females at the bottom of the hierarchy, this gain of efficiency with feeder traffic decreased (Figs 2b & 6b). Moreover, blue tits, which are typically subordinate to great tits, generally binged less (Fig. 2a) and spent a larger proportion of the day at feeders (Fig. 6a) with increasing traffic. This suggests an overall negative effect of competitor density on foraging efficiency in blue tits, in contrast to the overall positive effect in great tits (Figs 2a & 6a). These differences between species imply that when access to food is limited, the benefits of mixed-species flocking (reduced vigilance and increased foraging efficiency) outweigh the costs (competition) in great tits, whereas the costs may outweigh the benefits in blue tits. Moreover, there were also age and sex differences within blue tits. As in great tits, male blue tits spent a smaller proportion of the day visiting feeders as traffic increased (Fig. 6c). Dominant blue tits (in this case adults), however, only binged more than juveniles when feeder traffic was low. This suggests that blue tits, as the subordinate species, are all limited in how much they can binge-eat during high feeder traffic; and this constraint of competition is released in adults during low feeder traffic (Fig. 2c). These results suggest that blue tits are more susceptible to interference competition than great tits. Also in support of this, the lowest Johnson-Neyman threshold for an effect of treatment was observed in the daily number of feeder visits by blue tits (Fig. 3b) while interference does not appear to constrain visit rates at all in great tits (Fig. 3a). Furthermore, it has been shown in a previous study that great tits were able to feed more quickly in mixed-species flocks than in single-species flocks and were attracted to heterospecifics (Sasvári 1992, Farine *et al.* 2014).

There are multiple potential sources of interference including fighting, prey disturbance and kleptoparasitism (Sutherland 1996). In great tits and blue tits, conflict rarely escalates into fighting and rather than stealing seeds from subordinates, dominant individuals can supplant them from the food source (Perrins 1979, Gosler 1993). Thus, queueing is likely the main source of interference in this system, with dominant individuals able to jump the queue and subordinates being supplanted before re-joining the queue. Individuals often waited their turn whilst perching on the mesh of a feeding station cage, i.e. within 1m of the feeder, or in nearby natural cover. While queueing is not a natural phenomenon in tits (natural seed resources such as beechmast are more dispersed than supplemental food in feeders), supplanting behaviour is relatively common (Gibb 1954). Moreover, since search times for seed at feeders are small compared to those for beechmast which is often hidden under leaf litter (Perrins 1979), queueing time could be regarded as a proxy for search time in natural foraging: time and effort lost when supplanted by a more dominant individual.

When individuals differ in competitive ability, they can differ in either intercept or slope with an increase in competitor density (Caldow *et al.* 1999); differences in intercept indicate different absolute foraging efficiencies while individuals with different slopes differ in their susceptibility to interference (illustrated in Fig. 7; Sutherland 1996).

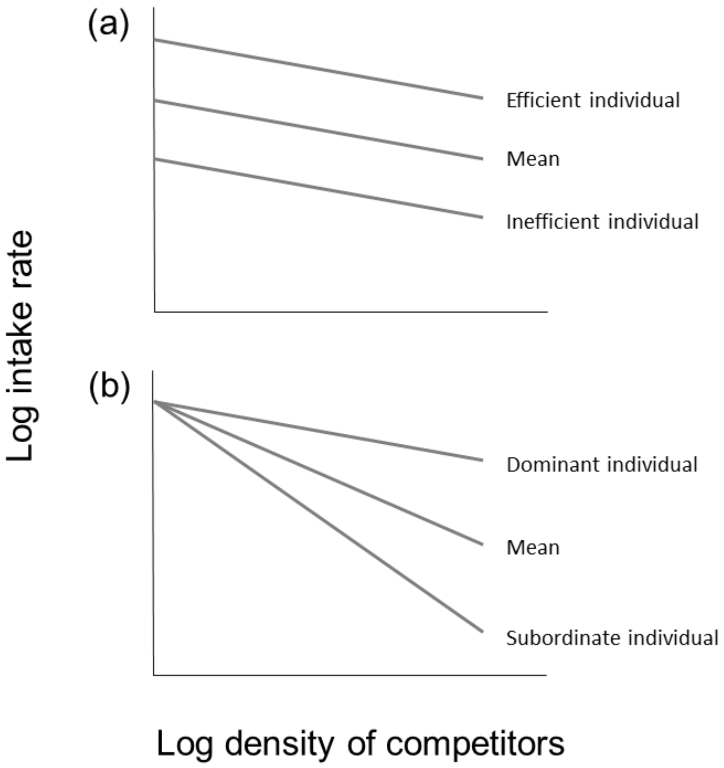


Fig. 7. Individual differences in competitive ability on food intake rate when individuals differ in (a) foraging efficiency and (b) susceptibility to interference (adapted from Sutherland 1996).

We have evidence of differences in both absolute foraging efficiency and susceptibility to interference competition. Our results show, for instance, that adults spend a consistently smaller proportion of the day at feeders than juveniles (having corrected for the daily number of visits) while males spend an increasingly smaller proportion relative to females with increasing feeder traffic (Figs 6b & 6c). That is, age affects foraging efficiency while sex affects the susceptibility to interference. Possible mechanisms include handling time and priority access to food; age affects foraging experience (Enoksson 1988; Desrochers 1992) so handling time may differ between adults and juveniles, contributing to the differences in bout lengths and thus feeding efficiency. In contrast, if sex is a stronger determinant of dominance and supplanting rates, then females will suffer more from interference competition than males. Furthermore, subordinates may need to invest time in avoiding displacement by dominants, reducing their foraging efficiency with increasing competition (Vines 1980; Beauchamp 1998, Slotow & Rothstein 1995; Smith *et al.* 2001).

Since seed was provided *ad libitum* in this study, we were only able to investigate the effects of interference competition. However, the depletion of resources over time is more likely than continuous input in nature (Sutherland 1996). This can lead to density-dependent exploitation competition over time (Alatalo *et al.* 1987). The combination of interference and depletion will increase the costs of competition and, as a consequence, some individuals will leave to find a new food patch or face a higher risk of starvation (Sutherland 1996). Thus, future studies on this topic should manipulate patch depletion. The costs and benefits of moving between patches are likely to vary among individuals. We predict that individuals with low competitive ability are more likely to move between patches than strong competitors and that this process will be density dependent.

Our experimental results suggest that access to food was not a strong constraint on foraging efficiency, as the Johnson-Neyman thresholds were high and since competitor density was higher during experimental manipulations than during the standard weekend protocol. (Experimental sites attracted individuals from neighbouring feeding stations on weekdays when non-experimental sites were closed.) However, even if interference competition does not have a strong effect on the risk of starvation, it may, through decreasing the efficiency of foraging, increase the risk of predation to a larger extent (Jansson *et al.* 1981, Minderman *et al.* 2006).

Foraging patterns and the starvation-predation risk trade-off

Our results suggest that binge-eating is a more efficient foraging strategy than grazing. It is also likely to be a safer strategy, under the assumption that the risk of predation is greatest when in the proximity of a feeder, since binge-eaters spend a smaller proportion of the day at feeders than grazers (Fig. S4). It was previously shown in tits that reducing search times, and therefore total time spent foraging, by providing supplemental food decreased the risk of predation (Jansson 1981). In this study we recorded a wide range of feeder traffic and group sizes (Figs S3, S5

& S6). At lower densities, more time should be allocated to vigilance in order to maintain a high probability of predator detection (Sansom *et al.* 2008); the proportion of time spent at feeders by males was indeed greater during low traffic (Figs 6b & 6c).

There was significant variation within sites in daily feeder traffic and number of individuals recorded (Fig. S3). These day to day fluctuations are likely due to variation in the general need of the population for supplemental food. Environmental conditions such as temperature will affect daily energy requirements and the risk of starvation, thus playing a role in determining daily feeder visit rates (as investigated in chapter 3). There were also consistent between-site differences in daily feeder traffic and number of individuals visiting feeders (Fig. S3). This variation likely contributed to the positive relationship between individual visit rates and daily feeder traffic (Figs 3 & 4). The positive relationship with background competition is somewhat counter-intuitive, given the prediction that competition will limit visit rates. The manipulation of interference competition did support our prediction. However, what caused some sites to be busier (or more ‘popular’) than others is not clear. Proximity to natural food sources is a potential factor; individuals visiting feeders near to natural food sources may rely on supplemental food less than those visiting more ‘isolated’ feeders. Isolated feeders may also attract (more) individuals from further afield.

In this study, great tits and blue tits spent, on average, less than a third of the daytime visiting feeders and, as shown in chapter 3, acquiring approximately two thirds of their daily energy requirements. This is a much higher rate of feeding than that reported for observations of foraging on natural resources, when tits spent 75-85% of the daytime foraging (Gibb 1954). While most individuals in our study population are also partly feeding on natural food sources, the high rate of visits at feeders suggests that their overall foraging efficiency is higher than under non-supplemented conditions. Since subordinates face a higher risk of starvation due to competition, they tend to return more quickly to feeders after a simulated predator visit (De Laet 1985; Hegner 1985). Thus dominants wait longer before returning and this could contribute to their smaller proportion of day spent at feeders.

Synchrony in time can dilute predator attacks, an extreme example being mayfly emergence (Sweeney & Vannote 1982). However, stationary food resources such as beechmast or supplemental feeders that are visited regularly by flocks will also attract predators. Little is known about the attack or success rates of sparrowhawks hunting tits foraging in winter (Gosler 1993). Future studies tracking wild sparrowhawks concurrently with tits would be worthwhile.

Higher mortality rates have been recorded in subordinate, especially juvenile, tits (Lack 1966) which face a higher risk of starvation than more dominant individuals due to the effects of competition. A previous study has shown that in willow tits (*Parus montanus*), subordinates spend more time being vigilant during foraging, having been relegated to more exposed areas of the foraging site (Ekman 1987), thus they also face a higher risk of predation.

General conclusions & implications

This is the first study to explore how competition influences patterns of fine temporal scale foraging behaviour in a wild population. We manipulated access to food at supplemental feeders to show that increasing interference competition could reduce foraging efficiency at busy sites by causing individuals to cluster their feeder visits to a lesser extent and to spend a larger proportion of the day at feeders. The daily visit rate could also be reduced by increasing interference at busy sites. Furthermore, we report dominance-related links between competition levels and foraging patterns; subordinate individuals tended to be more negatively affected by competition, typically foraging less efficiently than dominant individuals with increasing competition.

Variation in foraging efficiency and susceptibility to competition implies that the costs of flocking will vary among individuals which could ultimately have consequences for population patterns in survival. Understanding how dominance and competition interact to affect foraging efficiency potentially allows us to estimate how many individuals could be sustained at a site, with relevance for conservation. Moreover, differential effects of competition could influence the structuring of mixed-species communities (Dhondt 2012). Thus, competition should be taken into account when modelling the effects of climate change and supplemental feeding on community composition.

ACKNOWLEDGEMENTS

We thank Lucy Aplin for helpful comments on this paper, the social network group for help with collecting winter logger data, catching and tagging birds during the winter, and all the Wytham tit fieldworkers for assistance in catching and tagging birds during the spring. This work was funded by a European Research Council (ERC) grant to B.C.S (AdG 250164).

REFERENCES

Alanärä, A., M. D. Burns and N. B. Metcalfe (2001). Intraspecific resource partitioning in brown trout: the temporal distribution of foraging is determined by social rank. *Journal of Animal Ecology* **70**(6): 980-986.

Alatalo, R. V., D. Eriksson, L. Gustafsson and K. Larsson (1987). Exploitation competition influences the use of foraging sites by tits: experimental evidence. *Ecology* **68**(2): 284-290.

Aplin, L. M., J. A. Firth, D. R. Farine, B. Voelkl, R. A. Crates, A. Culina, C. J. Garroway, C. A. Hinde, L. R. Kidd, I. Psorakis, N. D. Milligan, R. Radersma, B. L. Verhelst and B. C. Sheldon (2015). Consistent individual differences in the social phenotypes of wild great tits, *Parus major*. *Animal Behaviour* **108**: 117-127.

Baker, M. C., C. S. Belcher, L. C. Deutsch, G. L. Sherman and D. B. Thompson (1981). Foraging success in junco flocks and the effects of social hierarchy. *Animal Behaviour* **29**(Feb): 137-142.

Barton, R. A., R. W. Byrne and A. Whiten (1996). Ecology, feeding competition and social structure in baboons. *Behavioral Ecology and Sociobiology* **38**(5): 321-329.

Beauchamp, G. (1998). The effect of group size on mean food intake rate in birds. *Biological Reviews* **73**(4): 449-472.

Biro, P. A. and J. A. Stamps (2008). Are animal personality traits linked to life-history productivity? *Trends in Ecology & Evolution* **23**(7): 361-368.

Burnham, K. P. and D. R. Anderson (2002). Model selection and multi-model inference: a practical information-theoretic approach. New York, Springer.

Caldow, R. W. G., J. D. Goss-Custard, R. A. Stillman, S. E. A. L. D. Durell, R. Swinfen and T. Bregnballe (1999). Individual variation in the competitive ability of interference-prone foragers: the relative importance of foraging efficiency and susceptibility to interference. *Journal of Animal Ecology* **68**(5): 869-878.

Charlton, N. L. and A. I. Houston (2010). What currency do bumble bees maximize? *PLoS ONE* **5**(8).

Clark, C. W. and M. Mangel (1986). The evolutionary advantages of group foraging. *Theoretical Population Biology* **30**(1): 45-75.

Cole, E. F. and J. L. Quinn (2012). Personality and problem-solving performance explain competitive ability in the wild. *Proceedings of the Royal Society B: Biological Sciences* **279**(1731): 1168-1175.

Cresswell, W. (1994). Flocking is an effective anti-predation strategy in redshanks, *Tringa totanus*. *Animal Behaviour* **47**(2): 433-442.

Cresswell, W. (1997). Interference competition at low competitor densities in blackbirds *Turdus merula*. *Journal of Animal Ecology* **66**(4): 461-471.

Cresswell, W. (1998). Variation in the strength of interference competition with resource density in blackbirds, *Turdus merula*. *Oikos* **81**(1): 152-160.

Cuthill, I. C., A. Kacelnik, J. R. Krebs, P. Haccou and Y. Iwasa (1990). Starlings exploiting patches: the effect of recent experience on foraging decisions. *Animal Behaviour* **40**: 625-640.

De Laet, J. F. (1985). Dominance and anti-predator behavior of great tits *Parus major*: a field study. *Ibis* **127**(3): 372-377.

Desrochers, A. (1992). Age and foraging success in European blackbirds - variation between and within individuals. *Animal Behaviour* **43**(6): 885-894.

Dhondt, A. A. (2012). Interspecific competition in birds. Oxford, Oxford University Press.

Dill, L. M. and A. H. G. Fraser (1984). Risk of predation and the feeding behavior of juvenile coho salmon (*Oncorhynchus kisutch*). *Behavioral Ecology and Sociobiology* **16**(1): 65-71.

Dolman, P. M. (1995). The intensity of interference varies with resource density: evidence from a field study with snow buntings, *Plectrophenax nivalis*. *Oecologia* **102**(4): 511-514.

Ekman, J. (1987). Exposure and time use in willow tit flocks: the cost of subordination. *Animal Behaviour* **35**: 445-452.

Ekman, J. and B. Rosander (1987). Starvation risk and flock size of the social forager: when there is a flocking cost. *Theoretical Population Biology* **31**(1): 167-177.

Ekman, J. B. and C. E. H. Askenmo (1984). Social rank and habitat use in willow tit groups. *Animal Behaviour* **32**(May): 508-514.

Engqvist, L. (2005). The mistreatment of covariate interaction terms in linear model analyses of behavioural and evolutionary ecology studies. *Animal Behaviour* **70**(4): 967-971.

Enoksson, B. (1988). Age- and sex-related differences in dominance and foraging behavior of nuthatches *Sitta europaea*. *Animal Behaviour* **36**(1): 231-238.

Farine, D. R., L. M. Aplin, C. J. Garroway, R. P. Mann and B. C. Sheldon (2014). Collective decision making and social interaction rules in mixed-species flocks of songbirds. *Animal Behaviour* **95**: 173-182.

Farine, D. R., J. A. Firth, L. M. Aplin, R. A. Crates, A. Culina, C. J. Garroway, C. A. Hinde, L. R. Kidd, N. D. Milligan, I. Psorakis, R. Radersma, B. L. Verhelst, B. Voelkl and B. C. Sheldon (2015). The role of social and ecological processes in structuring animal populations: a case study from automated tracking of wild birds. *Royal Society Open Science* **2**(4): 150057.

Gibb, J. A. (1954). Feeding ecology of tits, with notes on treecreeper and goldcrest. *Ibis* **96**(4): 513-543.

Gilliam, J. F. and D. F. Fraser (1987). Habitat selection under predation hazard: test of a model with foraging minnows. *Ecology* **68**(6): 1856-1862.

Gosler, A. (1993). The great tit. London, Hamlyn.

Goss-Custard, J. D. (1980). Competition for food and interference among waders. *Ardea* **68**(1-4): 31-52.

Heath, J. P., H. G. Gilchrist and R. C. Ydenberg (2010). Interactions between rate processes with different timescales explain counterintuitive foraging patterns of arctic wintering eiders. *Proceedings of the Royal Society B: Biological Sciences* **277**(1697): 3179-3186.

Hegner, R. E. (1985). Dominance and anti-predator behavior in blue tits (*Parus caeruleus*). *Animal Behaviour* **33**(3): 762-768.

Houston, A. I. and J. M. McNamara (2014). Foraging currencies, metabolism and behavioural routines. *Journal of Animal Ecology* **83**(1): 30-40.

Huitema, B. E. (1980). The analysis of covariance and alternatives. New York, Wiley.

Jansson, C., J. Ekman and A. von Brömssen (1981). Winter mortality and food supply in tits Parus spp. *Oikos* **37**(3): 313-322.

Johnson, P. O. and J. Neyman (1936). Tests of certain linear hypotheses and their application to some educational problems. *Statistical Research Memoirs* **1**: 57-93.

Kenward, M. G. and J. H. Roger (1997). Small sample inference for fixed effects from restricted maximum likelihood. *Biometrics* **53**(3): 983-997.

Kotler, B. P., J. S. Brown, S. R. X. Dall, S. Gresser, D. Ganey and A. Bouskila (2002). Foraging games between gerbils and their predators: temporal dynamics of resource depletion and apprehension in gerbils. *Evolutionary Ecology Research* **4**(4): 495-518.

Kotrschal, K., J. Hemetsberger and J. Dittami (1993). Food exploitation by a winter flock of greylag geese: behavioral dynamics, competition and social status. *Behavioral Ecology and Sociobiology* **33**(5): 289-295.

Krams, I. (2000). Length of feeding day and body weight of great tits in a single- and a two-predator environment. *Behavioral Ecology and Sociobiology* **48**(2): 147-153.

Krause, J. D. and G. D. Ruxton (2002). Living in groups. Oxford, Oxford University Press.

Lack, D. (1966). Population studies of birds. Oxford, Clarendon Press.

Lima, S. L. (1985). Maximizing feeding efficiency and minimizing time exposed to predators: a trade-off in the black-capped chickadee. *Oecologia* **66**(1): 60-67.

Lima, S. L. (1988). Initiation and termination of daily feeding in dark-eyed juncos: influences of predation risk and energy reserves. *Oikos* **53**(1): 3-11.

Lima, S. L. and L. M. Dill (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* **68**(4): 619-640.

McCleery, R. H., R. A. Pettifor, P. Armbruster, K. Meyer, B. C. Sheldon and C. M. Perrins (2004). Components of variance underlying fitness in a natural population of the great tit *Parus major*. *American Naturalist* **164**(3): E62-E72.

McNamara, J. M. and A. I. Houston (1990). State-dependent ideal free distributions. *Evolutionary Ecology* **4**(4): 298-311.

Metcalfe, N. B. (1986). Intraspecific variation in competitive ability and food intake in salmonids: consequences for energy budgets and growth rates. *Journal of Fish Biology* **28**(5): 525-531.

Minderman, J., J. Lind and W. Cresswell (2006). Behaviourally mediated indirect effects: interference competition increases predation mortality in foraging redshanks. *Journal of Animal Ecology* **75**(3): 713-723.

Perrins, C. M. (1979). British Tits. London, Collins.

Pulliam, H. R. (1973). On the advantages of flocking. *Journal of Theoretical Biology* **38**(2): 419-422.

Quinn, J. L., E. F. Cole, J. Bates, R. W. Payne and W. Cresswell (2012). Personality predicts individual responsiveness to the risks of starvation and predation. *Proceedings of the Royal Society B: Biological Sciences* **279**(1735): 1919-1926.

R Development Core Team (2015). R: A language and environment for statistical computing. Vienna, R Foundation for Statistical Computing.

Rutten, A. L., K. Oosterbeek, S. Verhulst, N. J. Dingemanse and B. J. Ens (2010). Experimental evidence for interference competition in oystercatchers, Haematopus ostralegus. II. Free-living birds. *Behavioral Ecology* **21**(6): 1261-1270.

Sansom, A., W. Cresswell, J. Minderman and J. Lind (2008). Vigilance benefits and competition costs in groups: do individual redshanks gain an overall foraging benefit? *Animal Behaviour* **75**(6): 1869-1875.

Sasvári, L. (1992). Great tits benefit from feeding in mixed-species flocks: a field experiment. *Animal Behaviour* **43**(2): 289-296.

Savill, P. S., C. M. Perrins, K. J. Kirby and N. Fisher (2010). Wytham Woods: Oxford's ecological laboratory. Oxford, Oxford University Press.

Schmid-Hempel, P., A. Kacelnik and A. I. Houston (1985). Honeybees maximize efficiency by not filling their crop. *Behavioral Ecology and Sociobiology* **17**(1): 61-66.

Schoener, T. W. (1974). Resource partitioning in ecological communities. *Science* **185**(4145): 27-39.

Slotow, R. and S. I. Rothstein (1995). Influence of social status, distance from cover, and group size on feeding and vigilance in white-crowned sparrows. *Auk* **112**(4): 1024-1031.

Smith, R. D., G. D. Ruxton and W. Cresswell (2001). Dominance and feeding interference in small groups of blackbirds. *Behavioral Ecology* **12**(4): 475-481.

Stephens, D. W., J. S. Brown and R. C. Ydenberg (2007). Foraging: behavior and ecology. Chicago, University of Chicago Press.

Sutherland, W. J. (1996). From individual behaviour to population ecology. Oxford, Oxford University Press.

Svensson, L. (1992). Identification guide to European passerines. Thetford, British Trust for Ornithology.

Sweeney, B. W. and R. L. Vannote (1982). Population synchrony in mayflies: a predator satiation hypothesis. *Evolution* **36**(4): 810-821.

Vervaecke, H., H. De Vries and L. Van Elsacker (1999). An experimental evaluation of the consistency of competitive ability and agonistic dominance in different social contexts in captive bonobos. *Behaviour* **136**: 423-442.

Vines, G. (1980). Spatial consequences of aggressive behaviour in flocks of oystercatchers, *Haematopus ostralegus* L. *Animal Behaviour* **28**(Nov): 1175-1183.

Ziv, Y., Z. Abramsky, B. P. Kotler and A. Subach (1993). Interference competition and temporal and habitat partitioning in two gerbil species. *Oikos* **66**(2): 237-246.

APPENDIX

Supplementary Figures

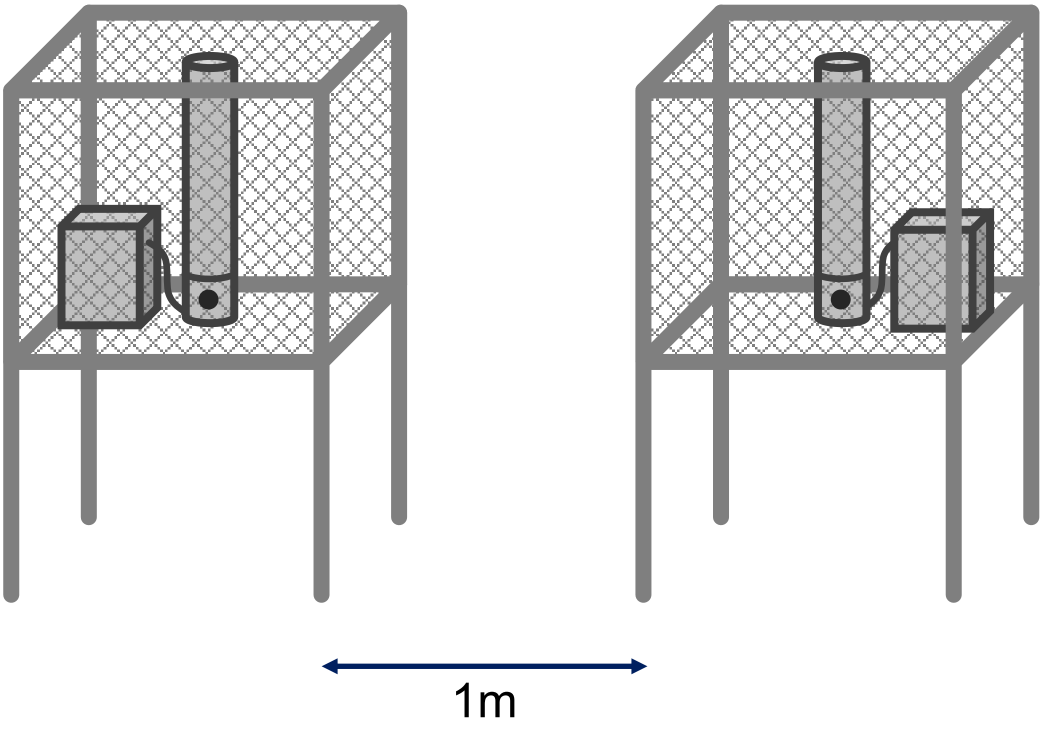


Fig. S1. Illustration of an experimental feeding station.

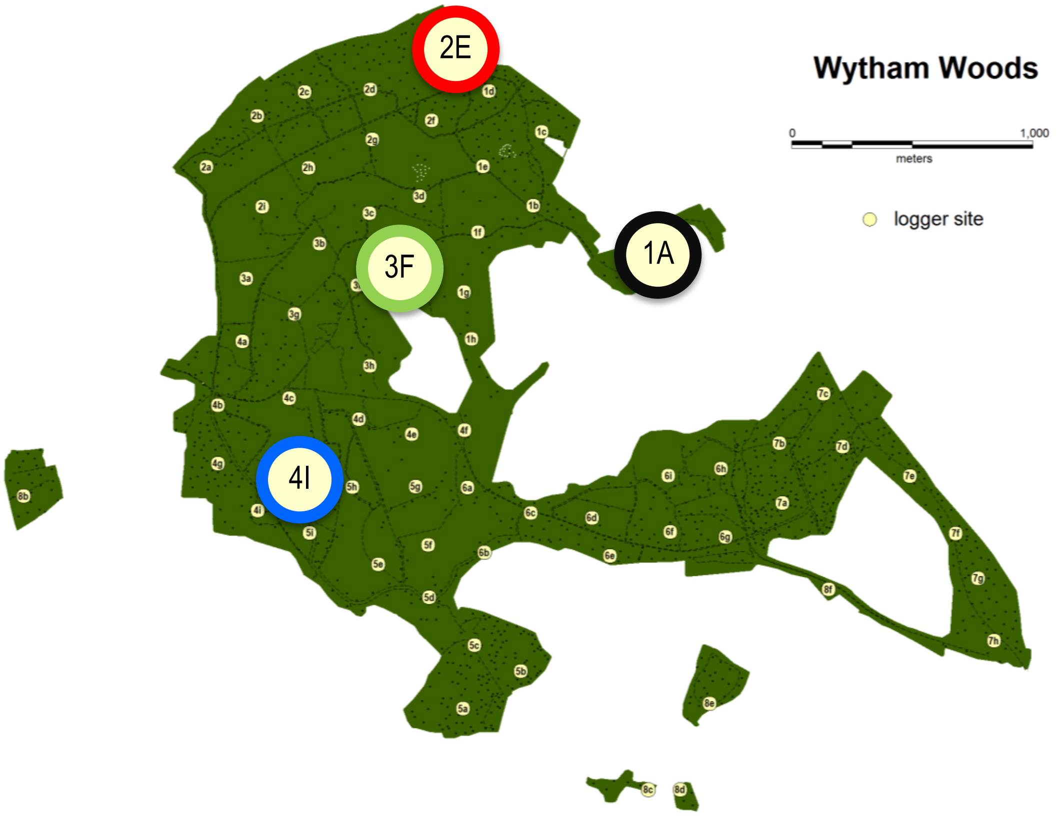


Fig. S2. Locations of experimental sites.

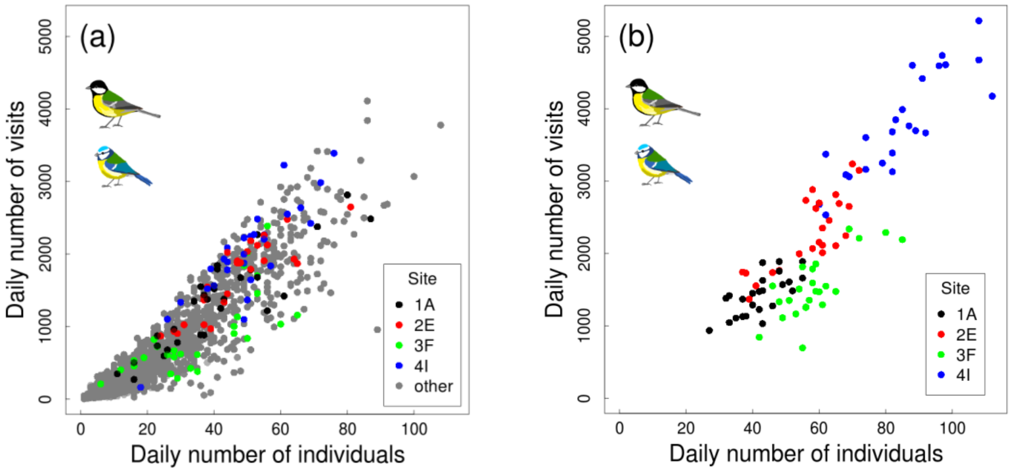


Fig. S3. Feeder traffic (the daily number of visits by great tits and blue tits) by the daily number of individuals in (a) the observational dataset, including experimental sites under non-experimental conditions, and (b) the experimental dataset. (One point per site per date.)

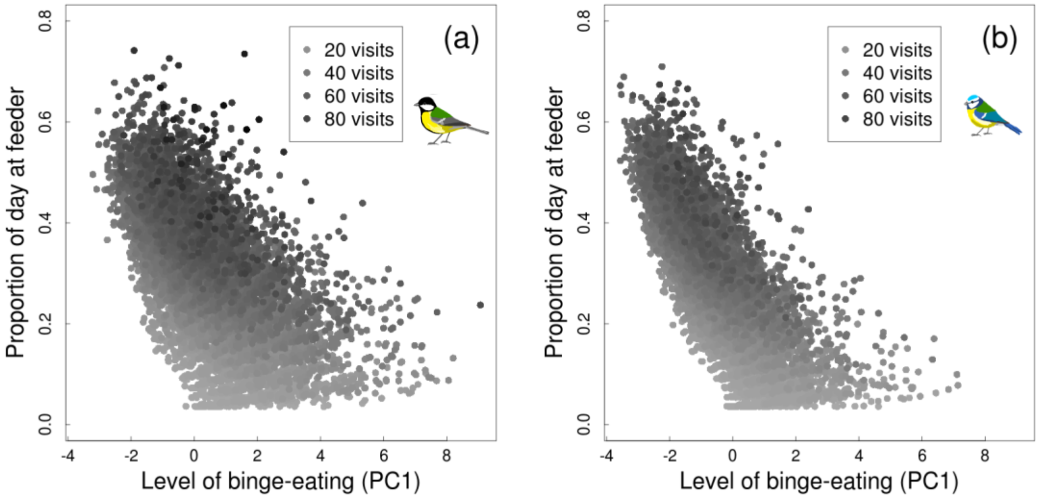


Fig. S4. Proportion of daytime spent at feeder by the level of binge-eating (PC1) in (a) great tits and (b) blue tits across 65 feeding stations. Shading of points represents the daily number of feeder visits. (One point per individual per date.)

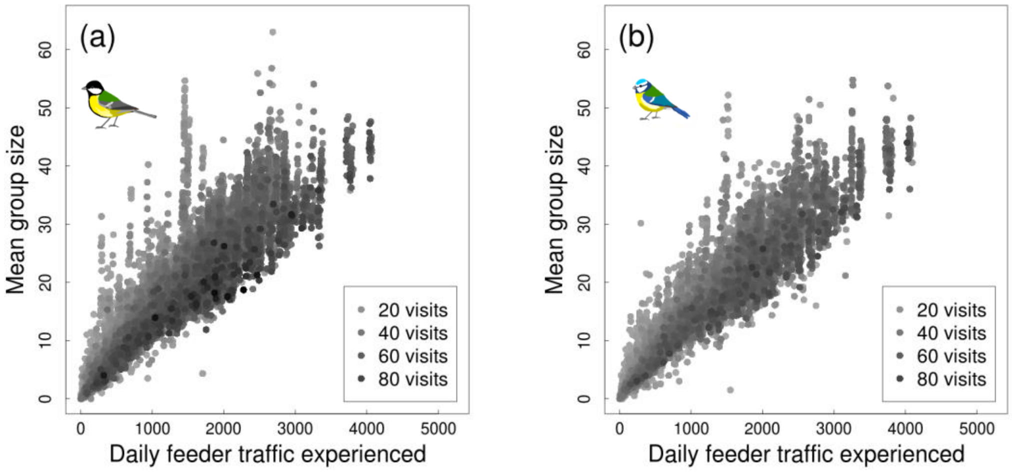


Fig. S5. Mean group size by the daily feeder traffic experienced in (a) great tits and (b) blue tits across 65 feeding stations. Shading of points represents the daily number of feeder visits. (One point per individual per date.)

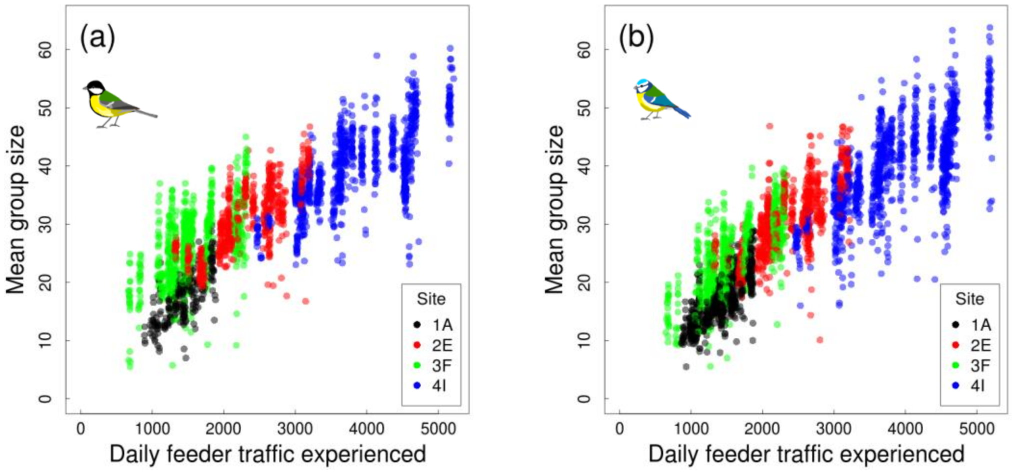


Fig. S6. Mean group size by the daily feeder traffic experienced in (a) great tits and (b) blue tits across 4 experimental feeding stations. (One point per individual per date.)

Supplementary Tables

Table S1. Linear mixed models on factors affecting the level of **binge-eating (PC1)** when either one or two feeders were open at a feeding site in (a) great tits and (b) blue tits. Number of observations: (a) n=2387 and (b) n=3034.

(a)

Fixed effect	Coefficient	SE	t	*P*
treatment (2 feeders)	0.14	0.11	1.19	0.237
scaled daily visits	-0.51	0.03	-14.97	<0.001
age (juvenile)	-0.61	0.17	-3.65	<0.001
scaled average feeder traffic	-0.11	0.10	-1.11	0.269
scaled deviation feeder traffic	-0.40	0.09	-4.61	<0.001
treatment * average feeder traffic	0.12	0.05	2.64	0.009

Johnson-Neyman region of significance for interaction: daily feeder traffic > 3343.

Random term	Variance	SD	n
individual ID	1.13	1.07	184
individual ID with random feeder traffic slope	0.28	0.53	184
date	0.07	0.26	24
residual	0.94	0.97	

(b)

Fixed effect	Coefficient	SE	t	*P*
treatment (2 feeders)	0.16	0.09	1.72	0.087
scaled daily visits	-0.65	0.02	-28.53	<0.001
age (juvenile)	-0.27	0.13	-2.09	0.037
scaled average feeder traffic	0.04	0.07	0.52	0.604
scaled deviation feeder traffic	-0.25	0.06	-4.13	<0.001

Random term	Variance	SD	n
individual ID	0.94	0.97	267
individual ID with random feeder traffic slope	0.16	0.40	267
date	0.04	0.21	24
residual	0.66	0.81	

Table S2. Linear mixed models on factors affecting the **daily number of feeder visits** by individuals when either one or two feeders were open at a feeding site in (a) great tits and (b) blue tits. Number of observations: (a) n=2387 and (b) n=3034.

(a)

Fixed effect	Coefficient	SE	t	*P*
treatment (2 feeders)	0.25	0.97	0.26	0.793
scaled day length	-1.86	0.56	-3.34	0.001
age (juvenile)	-3.62	1.84	-1.97	0.050
scaled average feeder traffic	9.12	1.00	9.09	<0.001
scaled deviation feeder traffic	8.38	0.95	8.82	<0.001

Random term	Variance	SD	n
individual ID	131.59	11.47	184
individual ID with random feeder traffic slope	31.44	5.61	184
date	4.44	2.11	24
residual	110.84	10.53	

(b)

Fixed effect	Coefficient	SE	t	*P*
treatment (2 feeders)	1.89	1.03	1.84	0.067
age (juvenile)	-3.89	1.65	-2.35	0.020
scaled average feeder traffic	2.90	0.94	3.09	0.002
scaled deviation feeder traffic	7.99	0.83	9.62	<0.001
treatment * average feeder traffic	1.70	0.49	3.50	0.001

Johnson-Neyman region of significance for interaction: daily feeder traffic > 2474.

Random term	Variance	SD	n
individual ID	151.47	12.31	267
individual ID with random feeder traffic slope	26.30	5.13	267
date	5.13	2.26	24
residual	141.37	11.89	

Table S3. Linear mixed models on factors affecting the **proportion of daytime spent at feeders** when either one or two feeders were open at a feeding site in (a) great tits and (b) blue tits. Number of observations: (a) n=2081 and (b) n=1376.

(a)

Fixed effect	Coefficient	SE	t	*P*
treatment (2 feeders)	-0.51	0.58	-0.88	0.384
scaled day length	-1.47	0.30	-4.87	<0.001
scaled daily visits	9.17	0.11	85.03	<0.001
scaled binge-eating (PC1)	-3.25	0.09	-34.27	<0.001
scaled average feeder traffic	-0.82	0.28	-2.89	0.006
scaled deviation feeder traffic	-1.48	0.30	-4.96	<0.001
treatment * avg feeder traffic	-0.55	0.14	-4.08	<0.001

Johnson-Neyman region of significance for interaction: daily feeder traffic > 3880.

Random term	Variance	SD	n
individual ID	9.62	3.10	184
individual ID with random feeder traffic slope	3.88	1.97	184
date	1.92	1.39	24
residual	8.38	2.89	

(b)

Fixed effect	Coefficient	SE	t	*P*
treatment (2 feeders)	-0.43	0.45	-0.94	0.349
scaled day length	-2.38	0.24	-9.96	<0.001
scaled daily visits	8.36	0.10	86.28	<0.001
scaled binge-eating (PC1)	-4.48	0.10	-45.29	<0.001
age (juvenile)	1.15	0.41	2.81	0.007
scaled average feeder traffic	-0.43	0.23	-1.86	0.069
scaled deviation feeder traffic	0.27	0.25	1.07	0.288
treatment * avg feeder traffic	-0.45	0.13	-3.51	0.001

Johnson-Neyman region of significance for interaction: daily feeder traffic > 3760.

Random term	Variance	SD	n
individual ID	9.21	3.03	267
individual ID with random feeder traffic slope	2.49	1.58	267
date	1.14	1.07	24
residual	9.71	3.12	

Table S4. Linear mixed models on factors affecting the average **group size** that individuals foraged in when either one or two feeders were open at a feeding site in (a) great tits and (b) blue tits. Number of observations: (a) n=2387 and (b) n=3034.

(a)

Fixed effect	Coefficient	SE	t	*P*
treatment (2 feeders)	-0.85	0.97	-0.88	0.388
scaled average feeder traffic	9.35	0.28	32.88	<0.001
scaled deviation feeder traffic	9.54	0.29	32.72	<0.001
treatment * average feeder traffic	-1.45	0.17	-8.64	<0.001

Johnson-Neyman region of significance for interaction: daily feeder traffic > 3266.

Random term	Variance	SD	n
individual ID	8.99	3.00	184
individual ID with random feeder traffic slope	0.83	0.91	184
date	5.47	2.34	24
residual	12.97	3.60	

(b)

Fixed effect	Coefficient	SE	t	*P*
treatment (2 feeders)	-0.49	0.70	-0.70	0.491
scaled average feeder traffic	10.18	0.23	43.57	<0.001
scaled deviation feeder traffic	10.02	0.27	37.04	<0.001
treatment * average feeder traffic	-1.11	0.15	-7.66	<0.001

Johnson-Neyman region of significance for interaction: daily feeder traffic > 3360.

Random term	Variance	SD	n
individual ID	8.97	2.99	267
individual ID with random feeder traffic slope	2.58	1.61	267
date	2.81	1.67	24
residual	12.59	3.55	

Table S5. Linear mixed models on factors affecting the level of **binge-eating (PC1)** across 65 feeding sites in (a) great tits and (b) blue tits. Number of observations: (a) n=10,722 and (b) n=7833.

(a)

Fixed effect	Coefficient	SE	t	*P*
scaled daily visits	-0.43	0.02	-27.77	<0.001
age (juvenile)	-0.19	0.04	-4.78	<0.001
sex (male)	0.16	0.05	3.09	0.002
scaled average feeder traffic	0.09	0.04	2.01	0.046
scaled deviation feeder traffic	-0.26	0.03	-9.43	<0.001
age * average feeder traffic	-0.18	0.04	-4.35	<0.001
sex * average feeder traffic	0.10	0.04	2.13	0.035

Johnson-Neyman regions of significance for interaction with age: feeder traffic < 146 or > 777.
Johnson-Neyman region of significance for interaction with sex: feeder traffic > 770.

Random term	Variance	SD	n
individual ID	0.71	0.84	1296
individual ID with random feeder traffic slope	0.09	0.30	1296
site	0.23	0.48	65
date	0.07	0.26	30
residual	1.08	1.04	

(b)

Fixed effect	Coefficient	SE	t	*P*
scaled daily visits	-0.72	0.01	-51.02	<0.001
age (juvenile)	-0.09	0.04	-2.25	0.026
scaled average feeder traffic	-0.11	0.03	-3.15	0.002
scaled deviation feeder traffic	-0.26	0.03	-9.32	<0.001
age * average feeder traffic	0.11	0.05	2.18	0.030

Johnson-Neyman region of significance for interaction with age: feeder traffic < 1270.

Random term	Variance	SD	n
individual ID	0.52	0.72	916
individual ID with random feeder traffic slope	0.07	0.27	916
site	0.18	0.42	64
date	0.06	0.24	30
residual	0.72	0.85	

Table S6. Linear mixed models on factors affecting the **daily number of feeder visits** by individuals across 65 feeding sites in (a) great tits and (b) blue tits. Number of observations: (a) n=10,722 and (b) n=7833.

(a)

Fixed effect	Coefficient	SE	t	*P*
age (juvenile)	2.56	0.43	5.90	<0.001
sex (male)	2.63	0.61	4.33	<0.001
scaled average feeder traffic	4.27	0.48	8.99	<0.001
scaled deviation feeder traffic	7.80	0.33	23.77	<0.001
sex * average feeder traffic	-1.12	0.50	-2.22	0.029

Johnson-Neyman region of significance for interaction with sex: feeder traffic < 1856.

Random term	Variance	SD	n
individual ID	93.64	9.68	1296
individual ID with random feeder traffic slope	25.87	5.09	1296
site	57.98	7.61	65
date	28.51	5.34	30
residual	129.93	11.40	

(b)

Fixed effect	Coefficient	SE	t	*P*
age (juvenile)	0.63	0.56	1.12	0.266
sex (male)	4.67	0.80	5.86	<0.001
scaled average feeder traffic	5.16	0.66	7.81	<0.001
scaled deviation feeder traffic	7.04	0.40	17.74	<0.001
age * average feeder traffic	2.32	0.67	3.46	0.001
sex * average feeder traffic	-1.57	0.68	-2.29	0.023

Johnson-Neyman regions of significance for interaction with age: feeder traffic < 492 or > 1340.
Johnson-Neyman region of significance for interaction with sex: feeder traffic < 2457.

Random term	Variance	SD	n
individual ID	104.88	10.24	916
individual ID with random feeder traffic slope	23.23	4.82	916
site	14.73	3.84	64
date	6.65	2.58	30
residual	131.25	11.46	

Table S7. Linear mixed models on factors affecting affecting the **proportion of daytime spent at feeders** across 65 feeding sites in (a) great tits and (b) blue tits. Number of observations: (a) n=10,722 and (b) n=7833.

(a)

Fixed effect	Coefficient	SE	t	*P*
scaled daily visits	9.34	0.05	179.27	<0.001
scaled binge-eating (PC1)	-4.22	0.05	-89.08	<0.001
age (juvenile)	0.49	0.12	3.95	<0.001
sex (male)	-1.47	0.16	-9.19	<0.001
scaled average feeder traffic	0.07	0.13	0.49	0.626
scaled deviation feeder traffic	0.10	0.09	1.10	0.277
sex * average feeder traffic	-0.51	0.14	-3.58	0.001

Johnson-Neyman region of significance for interaction with sex: feeder traffic > 229.

Random term	Variance	SD	n
individual ID	6.52	2.55	1296
individual ID with random feeder traffic slope	1.13	1.06	1296
site	2.44	1.56	65
date	3.44	1.85	30
residual	11.76	3.43	

(b)

Fixed effect	Coefficient	SE	t	*P*
scaled daily visits	9.28	0.06	152.20	<0.001
scaled binge-eating (PC1)	-4.81	0.06	-80.93	<0.001
age (juvenile)	0.93	0.15	6.27	<0.001
sex (male)	-0.88	0.19	-4.74	<0.001
scaled average feeder traffic	0.19	0.17	1.11	0.272
scaled deviation feeder traffic	0.13	0.11	1.18	0.242
sex * average feeder traffic	-0.55	0.17	-3.17	0.002

Johnson-Neyman region of significance for interaction with sex: feeder traffic > 689.

Random term	Variance	SD	n
individual ID	5.36	2.31	916
individual ID with random feeder traffic slope	1.27	1.13	916
site	0.90	0.95	64
date	1.76	1.33	30
residual	10.64	3.26	

Table S8. Linear mixed models on factors affecting the average **group size** that individuals foraged in across 65 feeding sites in (a) great tits and (b) blue tits. Number of observations: (a) n=10,722 and (b) n=7833.

(a)

Fixed effect	Coefficient	SE	t	*P*
scaled daily visits	-1.38	0.04	-33.00	<0.001
age (juvenile)	0.28	0.09	3.00	0.003
scaled average feeder traffic	10.38	0.09	110.30	<0.001
scaled deviation feeder traffic	10.53	0.09	116.79	<0.001

Random term	Variance	SD	n
individual ID	2.34	1.53	1296
individual ID with random feeder traffic slope	2.48	1.57	1296
site	6.55	2.56	65
date	1.50	1.22	30
residual	8.45	2.91	

(b)

Fixed effect	Coefficient	SE	t	*P*
scaled daily visits	-0.79	0.05	-17.36	<0.001
age (juvenile)	-0.29	0.12	-2.37	0.019
scaled average feeder traffic	9.97	0.11	87.38	<0.001
scaled deviation feeder traffic	10.17	0.11	90.61	<0.001
age * average feeder traffic	0.45	0.15	3.05	0.003

Johnson-Neyman regions of significance for interaction with age: feeder traffic < 1266 or > 3069.

Random term	Variance	SD	n
individual ID	1.96	1.40	916
individual ID with random feeder traffic slope	2.54	1.59	916
site	5.17	2.27	64
date	1.52	1.23	30
residual	8.40	2.90	

Table S9. Generalized linear mixed model on factors affecting the level of **binge-eating (PC1)** across 65 feeding sites in great tits and blue tits. Number of observations: n=18,555.

Fixed effect	Coefficient	SE	t	*P*
scaled daily visits	-0.56	0.01	-51.83	<0.001
species (great tit)	0.99	0.04	24.55	<0.001
scaled average feeder traffic	-0.12	0.03	-3.88	<0.001
scaled deviation feeder traffic	-0.26	0.02	-12.69	<0.001
species * average feeder traffic	0.19	0.03	5.74	<0.001

Random term	Variance	SD	n
individual ID	0.66	0.81	2212
individual ID with random feeder traffic slope	0.09	0.31	2212
site	0.19	0.44	65
date	0.06	0.25	30
residual	0.95	0.97	

Table S10. Generalized linear mixed model on factors affecting the **daily number of feeder visits** by individuals across 65 feeding sites in great tits and blue tits. Number of observations: n=18,555.

Fixed effect	Coefficient	SE	t	*P*
species (great tit)	10.01	0.50	20.07	<0.001
scaled average feeder traffic	2.47	0.39	6.35	<0.001
scaled deviation feeder traffic	7.38	0.26	28.83	<0.001
species * average feeder traffic	2.13	0.41	5.25	<0.001

Random term	Variance	SD	n
individual ID	103.81	10.19	2212
individual ID with random feeder traffic slope	23.65	4.86	2212
site	38.36	6.19	65
date	13.48	3.67	30
residual	134.41	11.59	

Table S11. Generalized linear mixed model on factors affecting affecting the **proportion of daytime spent at feeders** across 65 feeding sites in great tits and blue tits. Number of observations: n=18,555.

Fixed effect	Coefficient	SE	t	*P*
scaled daily visits	9.56	0.04	237.32	<0.001
scaled binge-eating (PC1)	-4.64	0.04	-120.48	<0.001
species (great tit)	1.10	0.13	8.31	<0.001
scaled average feeder traffic	0.24	0.11	2.26	0.028
scaled deviation feeder traffic	0.12	0.07	1.74	0.088
species * average feeder traffic	-0.59	0.11	-5.23	<0.001

Johnson-Neyman region of significance for interaction with species: feeder traffic < 2163.

Random term	Variance	SD	n
individual ID	6.93	2.63	2212
individual ID with random feeder traffic slope	1.47	1.21	2212
site	1.26	1.12	65
date	2.50	1.58	30
residual	11.60	3.41	

Table S12. Summary of individual great tits and blue tits in the experimental data set and the observational data set.

data set	category	individual great tits	individual blue tits	great tit observations (one per individual per date)	blue tit observations (one per individual per date)
4 experimental sites	adults	78	136	1143	1793
	juveniles	106	131	1244	1241
3 days per week (8 weeks)	**total**	**184**	**267**	**2387**	**3034**
65 observational sites	adult males	413	478	3909	4651
	adult females	394	297	3324	1919
	juvenile males	345	168	1819	849
5 weekends per winter	juvenile females	325	104	1670	414
(3 winters)	**total**	**1296**	**916**	**10722**	**7833**

Table S13. Experimental treatment schedule for four experimental feeding stations from December 2013 – February 2014. Each station had two feeders, termed F1 and F2.

	observational	experiment		
dates	weekend	Tues	Wed	Thurs
21 Dec - 22 Dec	F2			
24 Dec - 25 Dec - 26 Dec		both	F1	both
28 Dec - 29 Dec	F2			
31 Dec - 01 Jan - 02 Jan		F1	both	F1
04 Jan - 05 Jan	F1			
07 Jan - 08 Jan - 09 Jan		both	F1	both
11 Jan - 12 Jan	F1			
14 Jan - 15 Jan - 16 Jan		F1	both	F1
18 Jan - 19 Jan	F2			
21 Jan - 22 Jan - 23 Jan		both	F2*	both
25 Jan - 26 Jan	F1			
28 Jan - 29 Jan - 30 Jan		F2	both	F2
01 Feb - 02 Feb	F1			
04 Feb - 05 Feb - 06 Feb		both	F2	both
08 Feb - 09 Feb	F2			
11 Feb - 12 Feb - 13 Feb		F2	both	F2
15 Feb - 16 Feb	F2			
18 Feb - 19 Feb - 20 Feb		both	F2	both
22 Feb - 23 Feb	F1			

---

* Scheduling error: should have been both-F2-both, but both feeders opened all three days at site 2E; experimental data excluded for this week.

CHAPTER 5

Individual foraging strategies are assorted in wild social networks and pair bonds predict convergence of feeding behaviour

Individual foraging strategies are assorted in wild social networks and pair bonds predict convergence of feeding behaviour

Nicole D. Milligan, Lucy M. Aplin, Josh A. Firth, Damien R. Farine, Reinder Radersma, Ella F. Cole and Ben C. Sheldon

1. All animals must feed and, for those that do so in groups, foraging behaviour is likely to interact with social behaviour with consequences for social structure which can feed back to influence behaviour. Though challenging, the recording of individual behaviour simultaneously across a population whilst monitoring social structure offers a unique opportunity to gain a better understanding of the link between foraging behaviour in a social context and social structure itself.

2. Here we quantify winter foraging behaviour in a wild population of great tits using data collected during midwinter throughout Wytham Woods, Oxfordshire, over three consecutive years. We combine these data with yearly social networks, constructed using the co-occurrence of individuals at feeders, and calculate social network metrics to quantify how individual variation in social behaviour is related to foraging behaviour. We then examine how feeding patterns relate to the resultant social structure by assessing whether the networks show assortment by foraging behaviour. Finally, we examine whether breeding pairs have feeding patterns more similar to their partner than their non-partners.

3. Feeding patterns were associated with individual social network metrics for each winter: individuals that visited feeders in highly clustered foraging bouts had the weakest social associations, despite there being no difference in the number of their associates. Individuals were non-randomly distributed across each winter network by foraging behaviour; this positive assortment showed that individual feeding patterns and social structure were linked.

4. Finally, subsequent breeding partners exhibited feeding patterns more similar to each other than their non-partners, but only on days when they visited the same feeding site. This convergence in behaviour suggests that social relationships such as pair bonds are likely to influence group structure as well as individual foraging preferences, thus mediating the relationship between feeding behaviour and population structure.

INTRODUCTION

Social organisation is important in many animal populations, with consistent, non-random interactions often occurring between individuals within these populations (Croft *et al.* 2008). These social connections between individuals can be quantified as social networks, which are often complex and heterogeneous in structure, and in which the component individuals can have different strengths and numbers of association (Croft *et al.* 2008). More generally, such grouping patterns can provide individuals with numerous benefits, including increased foraging opportunities, protection from predators, and chance of finding a mate, all of which may outweigh the associated costs such as competition and the spread of disease (Krause & Ruxton 2002).

Resource distribution, a spatial aspect of the environment, will have some impact on grouping behaviour through its effect on the spatial distribution of animals (Johnson *et al.* 2002). This interplay between sociality and resource distribution can also extend to social network structure; this has perhaps been best demonstrated in New Caledonian crows (*Corvus moneduloides*), where social connectivity can be manipulated by the patchiness and predictability of their food resource (St Clair *et al.* 2015). This interaction between resource distribution and social organisation can also be influenced by individual differences in behaviour. For example in Eurasian shore crabs (*Carcinus maenas*), individual exploratory behaviour predicted connectedness in the social network, group stability and synchrony, but only when resources were clustered (Tanner & Jackson 2011). Theoretical work suggests that this link between resource distribution and grouping behaviour can be dynamic and two-way (Tania *et al.* 2012).

Even when all individuals within a population experience similar resource availability and distribution, individual differences in foraging behaviour may lead to variation in the timing and location of feeding among individuals. This will then affect which conspecifics an individual can interact with, their rates of encounter, and the subsequent interplay between individual foraging behaviour and social interactions will therefore influence the resultant social structure. Assortative mixing by behavioural traits in social networks, which entails heterogeneous patterns of association between different behavioural phenotypes, has been documented in several systems including sticklebacks (Pike *et al.* 2008), guppies (Croft *et al.* 2009) and great tits (Aplin *et al.* 2013; Farine 2014). More specific to foraging behaviour, it has been demonstrated that spatially overlapping bottlenose dolphins (genus *Tursiops*) with alternative foraging tactics became socially segregated and formed distinct communities (Daura-Jorge *et al.* 2012; Chilvers & Corkeron 2001; Ansmann *et al.* 2012) and were able to reintegrate with each other when one of the two tactics was restricted (Ansmann *et al.* 2012). In addition to influencing social organisation, individual differences in foraging behaviour are also likely to have important implications for the formation of breeding partnerships, if such pairs are formed within social groups (Oh & Badyaev 2010). Social relationships can then feed back to impact on the behaviour of individuals (Bates & Chappell 2002; Rands *et al.* 2006). For example, pair bonds in great tits can influence winter foraging behaviour, with individuals prioritising partner affiliation over food accessibility, which in turn can have consequences for social structure and individual foraging strategies (Firth *et al.* 2015).

The temporal scale at which behaviour is measured is important in drawing appropriate conclusions about behavioural patterns (Heath *et al.* 2010). It has been demonstrated in previous chapters that individual great tits exhibit marked variation in the timing of feeding within days. Since group dynamics in this species can be fluid at similarly fine temporal scales, a characteristic of highly fission-fusion systems, it is likely that individual fine-scale temporal foraging patterns will influence aggregations and vice-versa, and together will shape the resultant social structure.

For this study, we quantified the temporal clustering and daily number of feeder visits by individual great tits in midwinter over three years. Social network metrics were calculated from each winter network (with networks constructed from co-occurrences at feeding stations) to measure the social phenotype of these individuals. We then asked whether these measures of feeding and social behaviour were related, predicting that grazers (individuals that spread their daily feeder visits over many foraging bouts) should have stronger social connections than binge-eaters (individuals that cluster their visits tightly in few foraging bouts), since grazers spend a larger proportion of the day at feeders (as shown in chapter 4) and are therefore likely to encounter other individuals more frequently. To assess whether foraging types showed social assortment in the networks, i.e. whether dyadic social associations were non-randomly distributed in relation to foraging behaviour, network permutations were used to determine whether the observed patterns of associations differed from the expected patterns under the null hypothesis of spatially constrained random associations. Finally, assortment by feeding types has implications for pair formation. Therefore, we also assessed whether birds that paired up to breed in the subsequent spring were more similar in feeding type to each other than expected under the null hypothesis. If true, this would suggest that social preferences can feed back to influence feeding patterns.

METHODS

Study system

This study was undertaken as part of a larger project investigating the social ecology of a wild population of great tits in Wytham Woods (Aplin *et al.* 2015, Farine *et al.* 2015). Birds were trapped at nest boxes during the breeding season and, to include immigrants to the population, at mist nets at other times of year in Wytham. Each individual was fitted with both a unique metal leg ring from the British Trust for Ornithology (BTO) and a passive integrated transponder (PIT) tag from IB Technology; age and sex, determined by plumage (Svensson 1992), were recorded along with the ring and PIT-tag numbers. 65 feeding stations, each containing a black sunflower seed feeder, an automated data logger and two radio frequency identification (RFID) antennae at the feeder access points, were positioned in a grid approximately 250m apart. These were programmed to open access to seed pre-dawn and to close post-dusk every Saturday and Sunday from September* to February in 2011-2012, 2012-2013 and 2013-2014. Data loggers recorded the PIT-tag number, location and time whenever a tagged bird perched on an antenna to access seed at a feeding station; antennae scanned for PIT-tags three times per second and sunflower seeds were supplied *ad libitum* when feeders were open.

Great tits form aggregations in winter with fission-fusion group dynamics during the day (Ekman 1989) and roost solitarily at night (Kluijver 1950). Movements tend to be made within overlapping home ranges, with males exhibiting some territoriality during winter, but with a lot of variation due to age, temperature, and other seasonal factors (Perrins 1979). Adult males, having bred previously, are territorial from autumn onwards while first year birds tend to establish their territories later in winter (Kluijver 1951). Territoriality is much reduced during cold weather when foraging becomes a higher priority; when foraging in winter, great tits often join mixed-species flocks that pass within their home ranges which are typically larger than their breeding territories. As spring approaches, males defend their non-overlapping territories more intensively, while during spring, each breeding pair of great tits remains within their territory until the brood is independent in summer (Kluijver 1951).

Individual foraging strategies

We used two measures to quantify individual foraging strategies: the temporal clustering of feeder visits into foraging bouts and the daily number of feeder visits. To quantify visit clustering, we ran a principal component analysis (PCA) on six aspects of the daily timing of feeder visits. The first principal component (PC1) captures the extent to which individuals cluster their visits to feeders, with high values indicating binge-eaters and low values grazers. Daily visit rate was

---

* Except prior to December 2011, when feeding stations were programmed to open on Thursdays only.

measured as the number of visits recorded in one day by an individual. Raw data records were allocated to individual feeder visits and visits allocated to foraging bouts using the distribution of inter-record intervals. In order to reduce the effect of seasonality on feeding pattern measures, only records from the five weekends centred on the winter solstice of each winter were included in the PCA and daily visit counts. Individuals that moved between sites within a day or only visited feeders in one bout in a day were also excluded prior to quantifying feeding patterns. Full details and description of these measures are given in chapter 2.

Social network construction and network metrics

Three months of feeding station data, from the first weekend in December, were used to construct a social network for each winter. This allowed for the majority of immigrants to be included, since the largest wave of immigration to Wytham occurs during autumn (Matechou *et al.* 2015). The spatio-temporal data streams of PIT-tag detections across sites contained bursts of feeding activity separated by periods of inactivity. A Gaussian mixture model was applied to these data streams in order to identify gathering events (flocks) of great tits visiting each feeder (Psorakis *et al.* 2012; Psorakis *et al.* 2015). This method does not require the assumption of a fixed time window separating sequential flocks. Instead, it detects temporal regions of increased feeder activity and then allocates each visit to the most likely gathering event by using distributions of visit times, outputting a matrix of gathering events and the individuals they comprise.

A gambit of the group approach was used to convert the gathering events into a social network (Whitehead & Dufault 1999). In each winter network, nodes thus represent individual great tits and non-zero association strengths form the edges between nodes. Association strengths were calculated using a simple ratio index (SRI; Cairns & Schwager 1987). This index scales all edges between two individuals as between 0 (both individuals were never observed in the same gathering event) and 1 (both individuals were always observed in the same gathering events). Three network metrics were then calculated for each individual for each winter: weighted degree centrality, unweighted degree centrality and average association strength. Association strength or weighted degree centrality is calculated by summing an individual's edge strengths, unweighted degree centrality is a count of an individual's edges, and average association strength is calculated by dividing an individual's weighted degree by its number of edges. All network analyses were conducted using R 3.2.0 (R Core Team 2015), with the packages *asnipe* (Farine 2013), *assortnet* (Farine 2014), *igraph* (Csárdi & Nepusz 2006) and *sna* (Butts 2008). Finally, network metrics were tested against potential explanatory factors using linear models (LMs), as generalized linear mixed-effect models (GLMMs) failed to converge. Winter and age were included as factors, along with an individual's mean level of binge-eating (PC1), mean daily number of visits, mean daily number of visits squared, and the mean number of visits by other tagged birds at the same site (feeder traffic). For individual great tits observed in multiple winters, we used data from one winter selected at random.

Network assortativity

We used Newman's assortative mixing method (Newman 2002; Newman 2003), adapted for weighted networks (Farine 2014), to calculate social assortment by foraging behaviour. We calculated the assortativity coefficient and standard error using the *assortnet* package in R (Farine 2014). We used a function for continuous trait values (i.e. level of binge-eating or daily visits). Positive values indicate assortativity (e.g. binge-eaters would tend to associate with other binge-eaters), zero represents random assortment, and negative values indicate disassortativity (e.g. binge-eaters would tend to associate with grazers). Standard errors in *assortnet* are calculated using the jackknife technique.

Due to the non-independence of social network data, we further tested the significance of the observed association patterns with a randomization test using the R package *asnipe*. This test used a null model which randomized group membership within date and site, maintaining observation frequencies and group sizes, as well as the temporal and spatial distribution of individuals (Croft *et al.* 2011; Whitehead 2008). We generated 1000 random networks incrementally, permuting 100 pairs of individuals between gathering events and recalculating assortativity scores (for binge-eating, daily visits and weighted degree) at each step. The assortativity coefficient of the observed network was then compared to the frequency distribution of assortativity coefficients calculated for the random networks.

Pair bonds and foraging pattern similarity

Can partner's behaviour predict focal behaviour?

To examine whether individuals feed more like their partner on days when they visited the same feeder than on days visiting different feeders, we tested the predictive power of the partner's (i) binge-eating and (ii) daily visit rate on the focal bird's behaviour. First we fitted a GLMM with an individual's level of binge-eating (PC1) as the response variable and the partner's PC1 score, partner's site (same as or different from focal individual), number of daily visits, age, daily feeder traffic (total visits by other birds at that feeder; one term each for the mean and deviation from mean), and an interaction between the partner's PC1 score and the partner's site (same or different to focal bird) as fixed effects. Individual ID, date and site were included as random effects, with a random slope within individual for feeder traffic. A second GLMM was fitted with the daily number of feeder visits as a response variable with the partner's visits, partner's site (same or different), age, feeder traffic, and partner's visits * partner's site as fixed effects and including the same random effects as the first model. We define a breeding pair as a male and female identified at the same nest box during a breeding attempt in the subsequent spring; data were analysed separately for males and females.

When paired, are partners more similar to each other than non-partners?

Next, we tested whether an individual's feeding pattern was more like its partner's than its non-partners' on the days when observed pairs visited the same feeding station. For each site on each recording date that recorded at least two subsequent breeding pairs, we permuted all observed female partners IDs, conducting 1000 sets of these between-pair permutations. We excluded data for sites and dates on which fewer than two pairs were recorded, since partner permutations were not possible; data for pairs that were observed on different sites on the same date were also excluded for that date. Males and females were analysed separately. A

GLMM was fitted to the observed data and separately to the 1000 sets of permuted data, with the level of binge-eating (PC1) as the response variable. The partner's level of binge-eating was fitted as a fixed effect, along with the focal individual's daily number of visits, age, and daily feeder traffic (mean and deviation from mean). Individual, individual with random feeder traffic slope, site and date were included as random effects. The effect size of the observed partner's PC1 score was compared to the frequency distribution of effect sizes of permuted partners' PC1 scores. We fitted a similar GLMM for the daily number of visits and also compared the effect size of the partner's daily visits with that of the distribution of permuted partners' daily visits.

Since the date of partnership formation for each pair was not known, we fitted a further GLMM for each sex, with binomial error distribution and logit link function, to test how the likelihood of an individual being recorded exclusively at the same feeding station as its subsequent breeding partner in a day changed with time of year. Individual and site were included as random effects; winter (categorical), day of winter (relative to the winter solstice), age, and the daily number of visits were fitted as fixed effects. A positive relationship between the time of year and the likelihood of partners being recorded at the same site would suggest that the days on which subsequent partners are recorded at different sites pre-date pair-bond formation.

When not yet paired, are future partners more compatible than non-partners?

Finally, in order to determine if subsequent breeding partners had similar feeding habits prior to pair formation, we analysed the subset of data where pairs were recorded exclusively at different feeding stations in a day. We assumed that most dates when subsequent partners were observed at different feeding stations were pre-pair formation, and call these data 'pre-partnership'. To compare the difference in feeding patterns between subsequent partners and non-partners, we permuted each observed future partner with another 'pre-partner' that visited a different feeding station to the focal individual (and also different to that of its subsequent partner). We then generated a significance test by calculating the difference in PC1 value and number of daily visits between observed partners and permuted partners over 1000 sets of ‘pre-partnership’ permutations.

RESULTS

Social networks

Social associations

Over the three month network data collection period of each winter, 1053 (winter 1), 729 (winter 2) and 816 (winter 3) individuals were recorded across the 65 feeding stations. Using the Gaussian mixture model, 73,737 (winter 1), 68,057 (winter 2) and 70,447 (winter 3) gathering events involving these individuals were detected. Feeding patterns were quantified over five consecutive weekends in midwinter each year for 848 (winter 1), 589 (winter 2) and 538 (winter 3) individuals, a subset of the network individuals described above.

Feeding behaviour and network centrality measures

The temporal clustering of feeder visits showed a negative relationship with both the overall and average strength of individuals’ associations, but no relationship with the number of associates. Specifically, great tits that binged more had lower weighted degree centrality (Fig. 1a and Table S1; β=-0.12, SE=0.02, t=-5.05, df=1279, $P<0.001$), weaker average association strength (Fig 1c and Table S3; β=-0.13, SE=0.04, t=-3.72, df=1278, $P<0.001$), but there was no significant relationship with unweighted degree centrality (Fig. 1b and Table S2; β=-1.11, SE=0.73, t=-1.52, df=1278, P=0.129). That is, binge-eaters had weaker associations with the flock-mates they visited feeders with, and co-occurred with these associates less often, than grazers with their respective associates. In contrast, the daily feeder visit rate of individuals showed a positive relationship with the average strength of their associations, while the overall association strength and number of associates increased with individuals’ daily visit rates up to an intermediate number of visits, above which there was a negative relationship. Great tits that visited feeders more times per day thus had stronger average association strength (Fig. 2c and Table S3; effect of daily visits: β=0.22, SE=0.06, t=3.54, df=1278, P<0.001), while individuals that visited feeders an intermediate number of times per day (median=40 visits) had a relatively higher weighted degree centrality (Fig. 2a and Table S1; effect of daily visits squared: β=-0.09, SE=0.03, t=-3.12, df=1279, P=0.002) and higher unweighted degree centrality (Fig. 2b and Table S2; effect of daily visits squared: β=-3.14, SE=0.87, t=-3.60, df=1278, P<0.001) than those visiting few or many times per day.

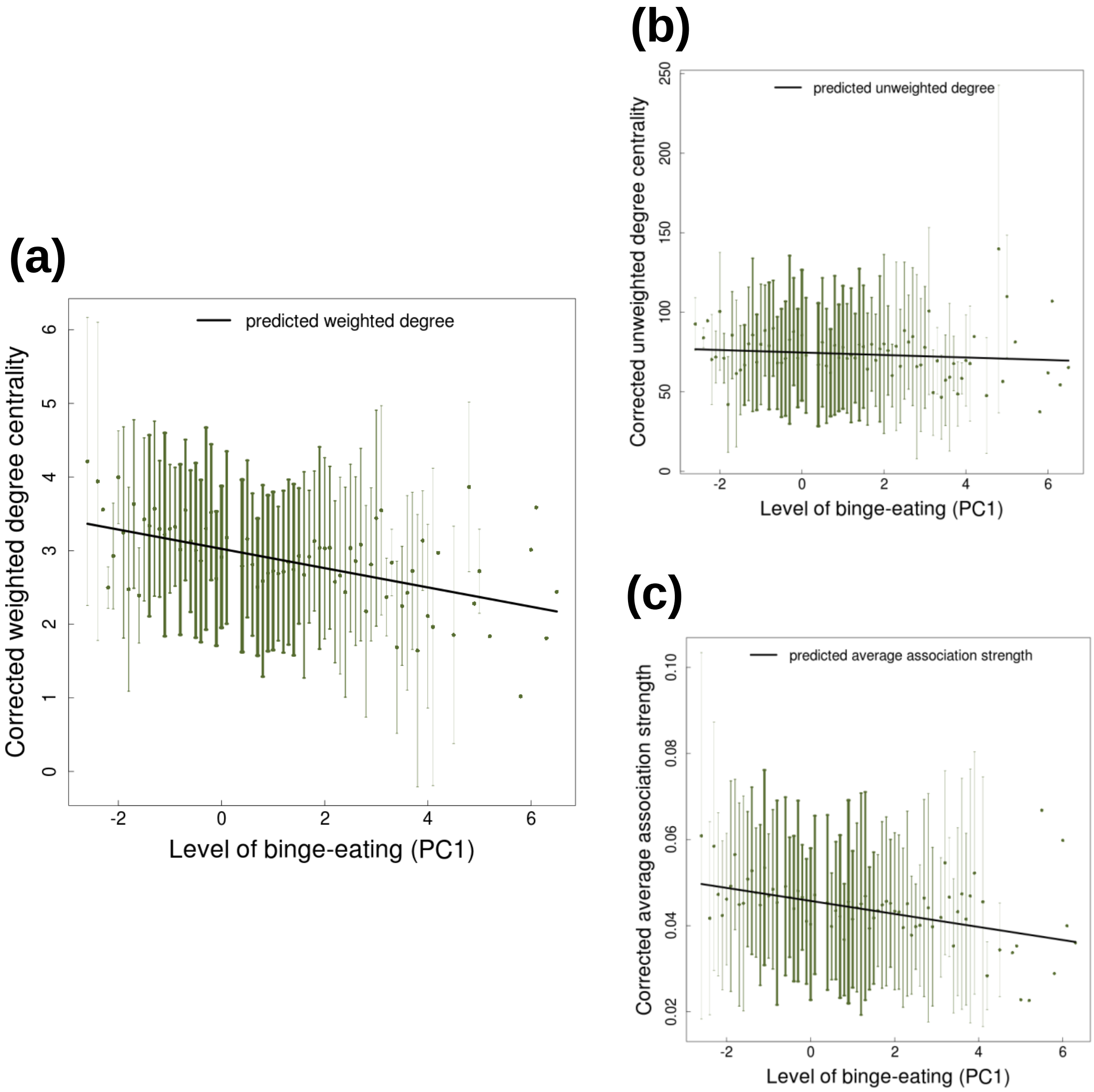


Fig. 1. Network metrics: (a) weighted degree, (b) number of associates and (c) average strength of association with each associate, corrected for age, average daily visits and feeder traffic, of individual great tits in a winter feeder social network with the level of binge-eating (PC1). Points show corrected means ± SD with error bar widths indicating the amount of data. Data were binned by 0.1 PC1 score; n=1287. Lines show the model prediction of the relationship between binge-eating (PC1) and each network metric.

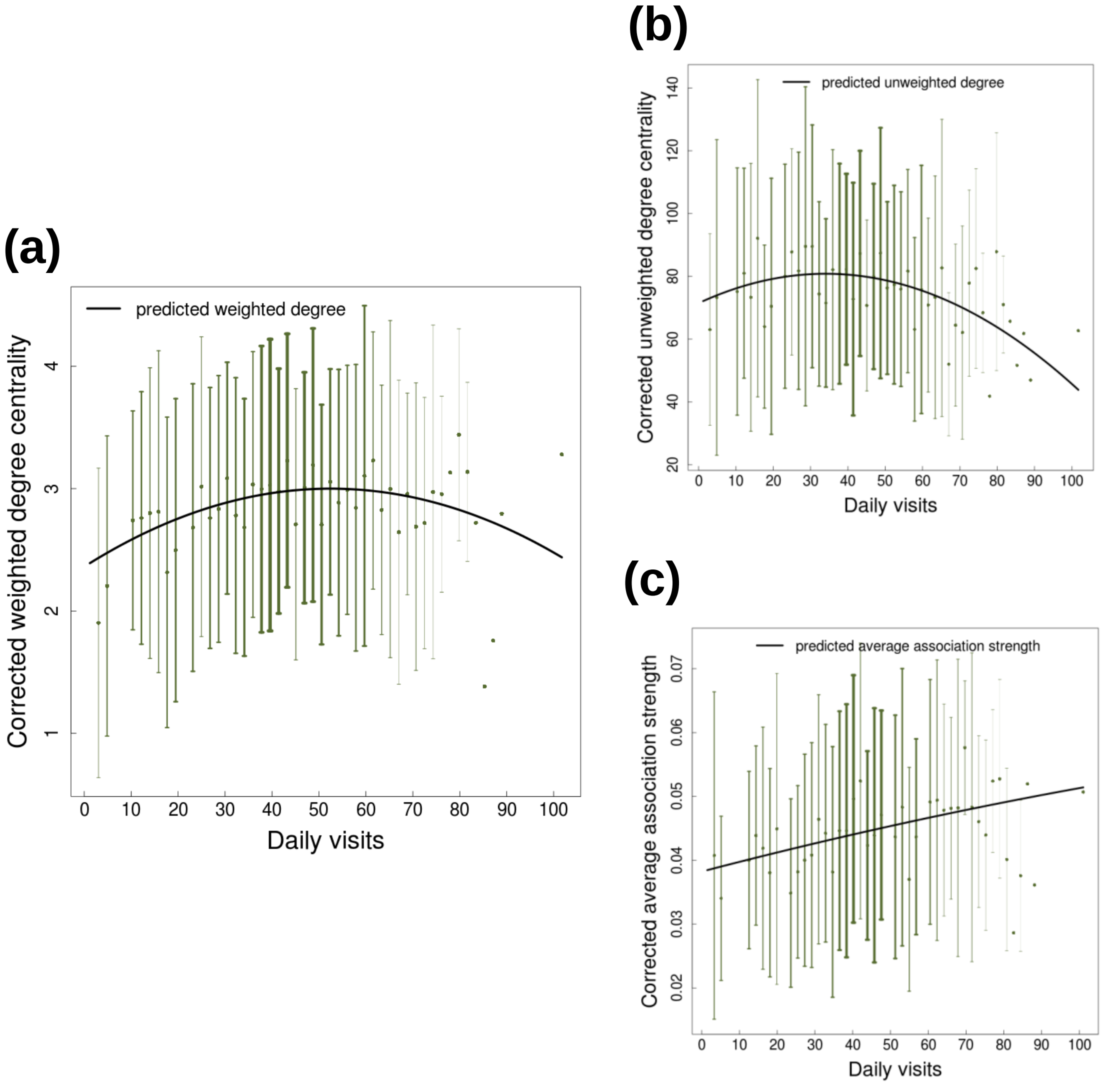


Fig. 2. Network metrics: (a) weighted degree, (b) number of associates and (c) average strength of association with each associate, corrected for age, average daily visits and feeder traffic, of individual great tits in a winter feeder social network with the daily number of feeder visits. Points show corrected means ± SD with error bar widths indicating the amount of data. Data were binned by 2 visits; n=1287. Lines show the model prediction of the relationship between daily visits and each network metric.

Social structure and assortment by foraging pattern

Newman's assortment measure was computed for each type of feeding pattern (individual mean level of binge-eating or daily feeder visit rate) and for weighted degree on each winter network (based on observed groups and on each of 1000 sets of permutations of group membership) for each winter. Great tits showed significant positive assortment by both daily feeder visit clustering (Fig. 3a;

weighted assortativity coefficient ± SE and P from 1000 permuted networks: $r_{winter1}=0.142\pm0.002$, n=848, P=0.006; $r_{winter2}=0.164\pm0.002$, n=589, P<0.001, $r_{winter3}=0.195\pm0.004$, n=538, P=0.002) and daily feeder visit rate (Fig. 3b; $r_{winter1}=0.320\pm0.002$, n=848, P=0.01; $r_{winter2}=0.261\pm0.004$, P<0.001, n=589, $r_{winter3}=0.323\pm0.003$, n=538, P<0.001). Individuals were also positively assorted by weighted degree (Fig. S1; $r_{winter1}=0.521\pm0.001$, n=848, P=0.003; $r_{winter2}=0.698\pm0.001$, n=589, P=0.001, $r_{winter3}=0.558\pm0.002$, n=538, P<0.001); this degree assortment is a common feature of animal social networks (Croft *et al.* 2008).

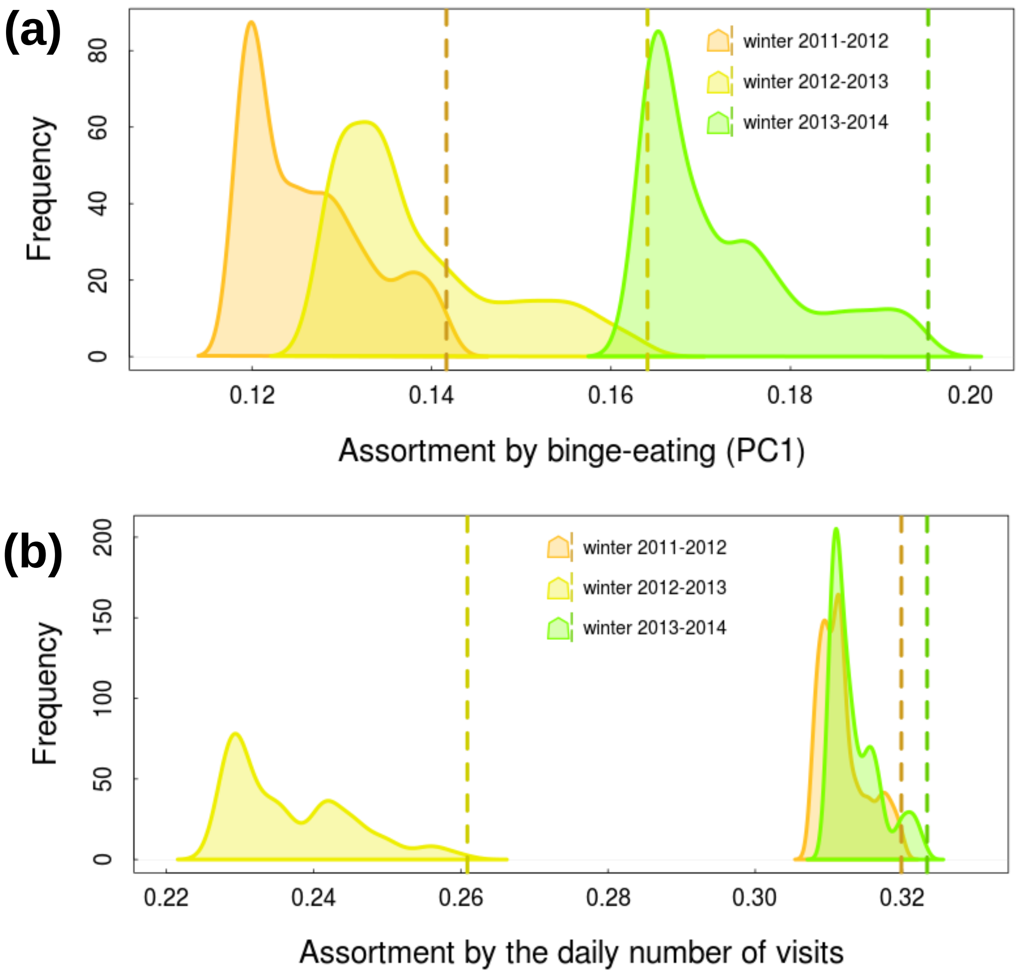
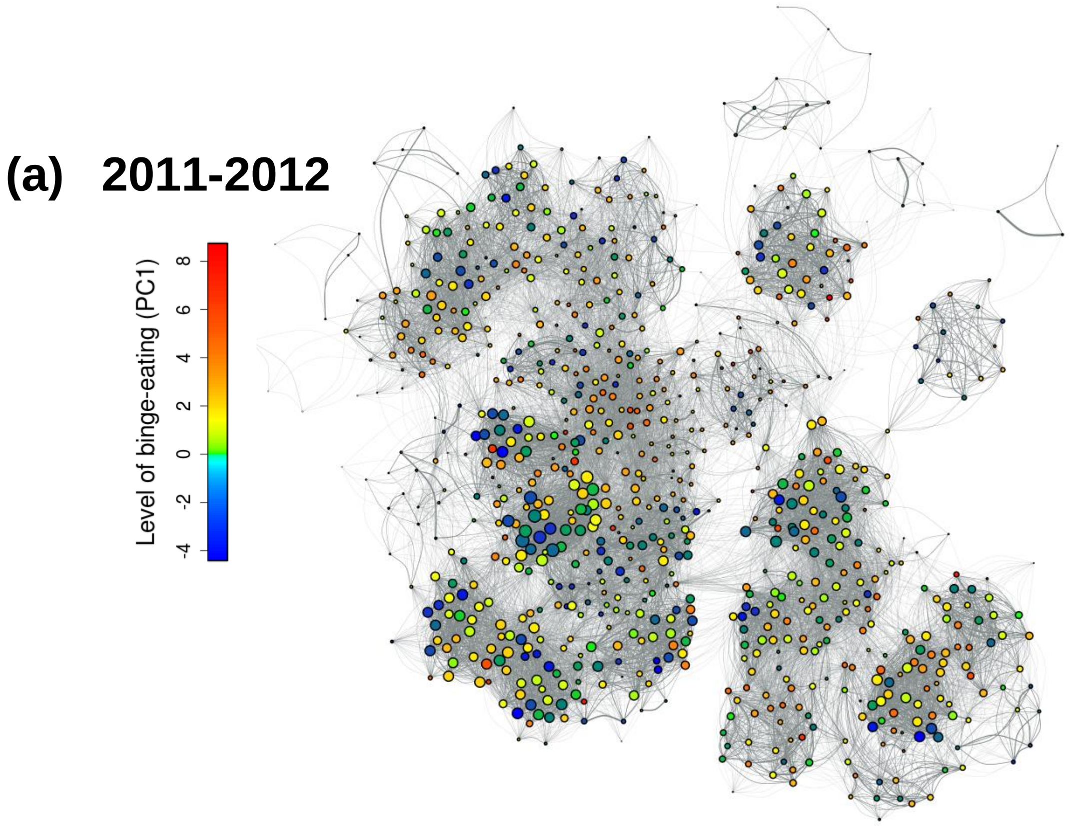
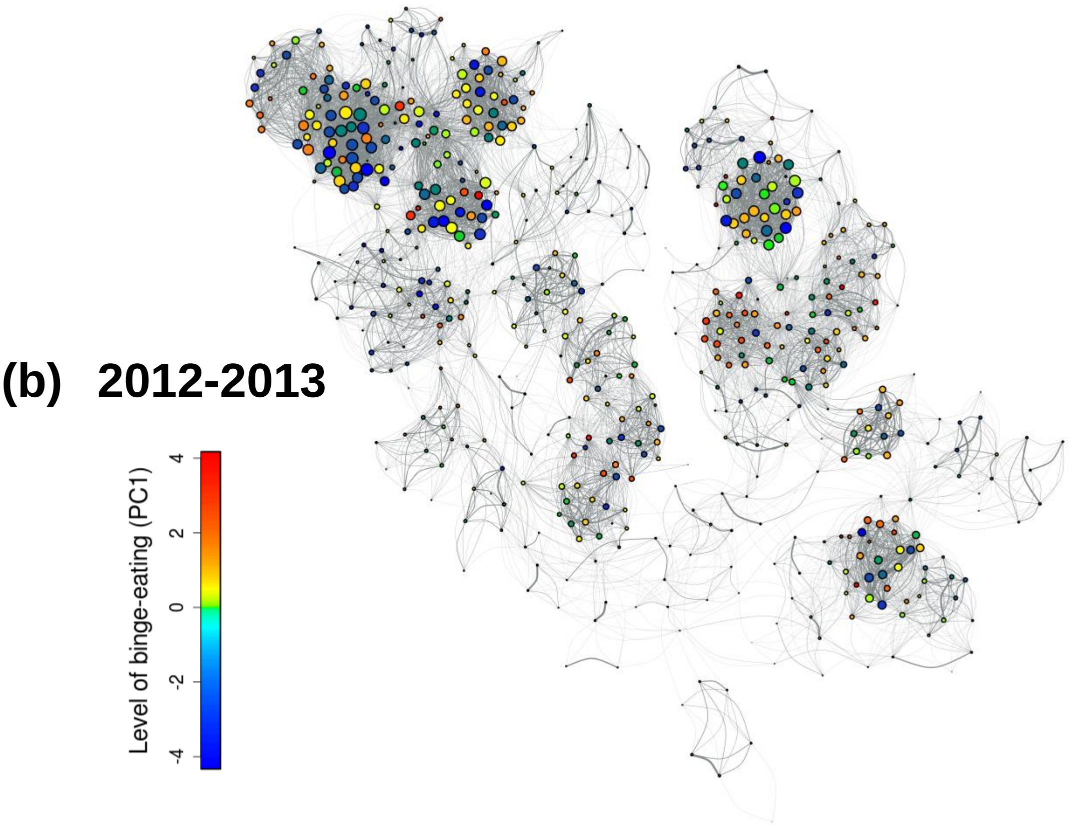


Fig. 3. Social assortment patterns of great tits within flocking events: assortment of individuals by (a) mean level of binge-eating and by (b) mean number of daily feeder visits in each winter ($n_{winter1}$=848; $n_{winter2}$=589, $n_{winter3}$=538). Dashed lines show assortment scores of the observed data; distributions show assortment scores of 1000 permutations of individual ID between flocking events.

When the social assortment was examined more closely, different dyadic combinations were observed to have different impacts on the overall pattern. Fig. 4 illustrates the observed social network of great tits for each winter. The boxplots in Fig. S2 show the association strengths between binge-eaters (top 33% mean PC1 scores), between grazers (bottom 33% mean PC1 scores), and between binge-eaters and grazers for each winter. Grazer-grazer dyads had stronger associations than binger-binger dyads (Welch’s two-sample t-test; winter 1: $t_{(495)}=9.49$, $P<0.001$, winter 2: $t_{(330)}=6.48$, $P<0.001$, winter 3: $t_{(292)}=8.23$, $P<0.001$) which had stronger associations than grazer-binger dyads (winter 1: $t_{(562)}=5.35$, $P<0.001$, winter 2: $t_{(384)}=3.31$, $P=0.001$, winter 3: $t_{(336)}=3.78$, $P<0.001$). Thus, grazer-grazer associations were also stronger than grazer-binger dyads (winter 1: $t_{(477)}=13.86$, $P<0.001$, winter 2: $t_{(303)}=9.14$, $P<0.001$, winter 3: $t_{(251)}=11.29$, $P<0.001$).


(a) 2011-2012
Level of binge-eating (PC1)
8
6
4
2
0
-2
-4


(b) 2012-2013
Level of binge-eating (PC1)
4
2
0
-2
-4

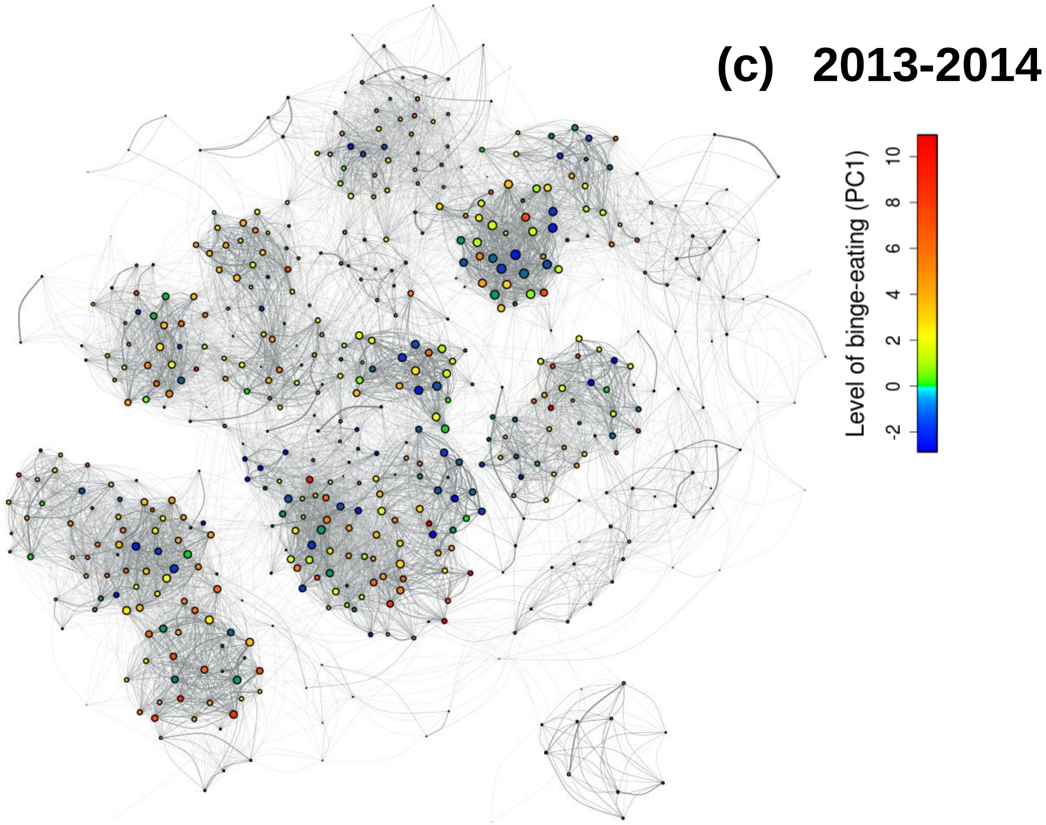


Fig. 4. Observed social network of great tits in winter (a) 2011-2012, (b) 2012-2013 and (c) 2013-2014. Each node represents one individual and lines connecting nodes indicate the associations between individuals, with size of node representing an individual's weighted degree centrality ($n_{winter1}$=848; $n_{winter2}$=589, $n_{winter3}$=538). Node colour represents the mean temporal clustering (PC1) of feeder visits during mid-winter, ranging from binge-eaters in red to grazers in blue.

Pair bonds

Feeding similarity to partner across sites

Within pairs of great tits that bred together in the subsequent spring, individuals exhibited similar levels of binge-eating (PC1) and similar daily numbers of feeder visits to their partner, but only on the dates when they were recorded exclusively at the same feeding station (see Fig. 5 and Tables S4 and S5 for model estimates of binge-eating; see Fig. 6 and Tables S6 and S7 for model estimates of daily visits).

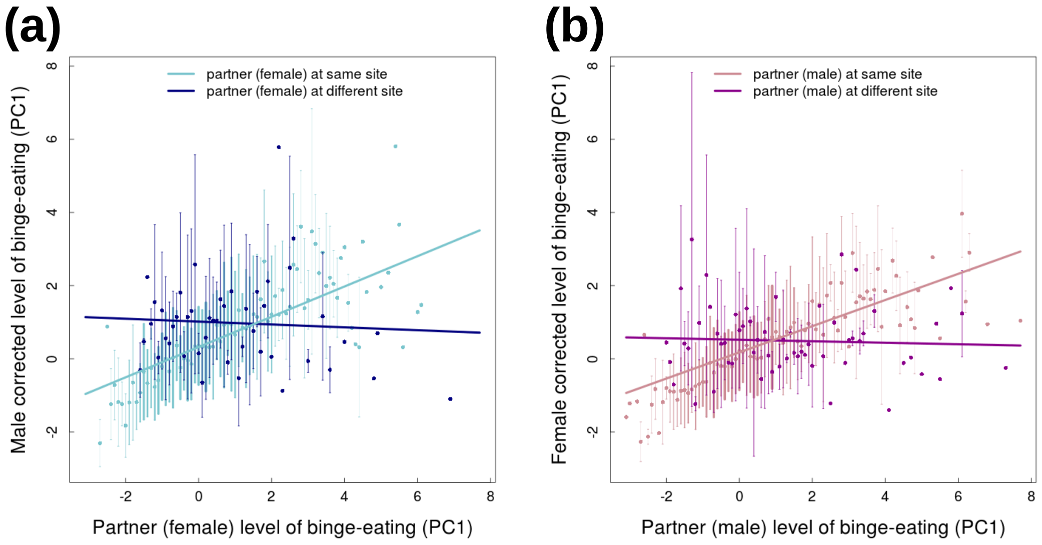


Fig. 5. Level of binge-eating of (a) 217 male and (b) 208 female great tits with their subsequent breeding partner's level of binge-eating, corrected for age, daily number of visits, and feeder traffic. Partners recorded at the same site and day (167 instances) are plotted separately from partners recorded at different sites on the same day (1116 instances). Points show corrected means ± SD with error bar widths indicating the amount of data; data were binned by 0.1 PC1. Lines show the model prediction of the relationship for same-site pairs and different-site pairs.

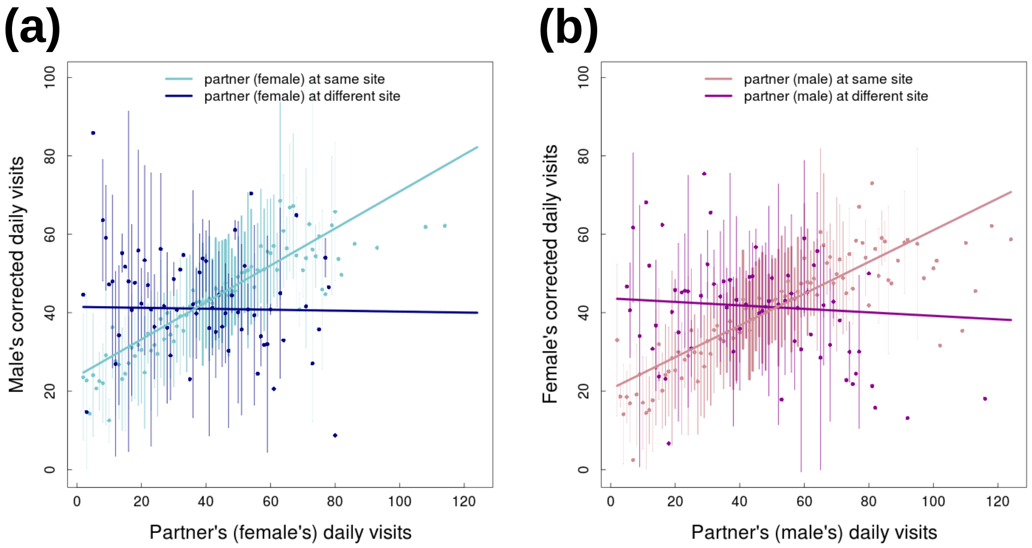


Fig. 6. Daily number of feeder visits of (a) 217 male and (b) 208 female great tits with their subsequent breeding partner's daily visits, corrected for age and feeder traffic. Partners recorded at the same site and day (167 instances) are plotted separately from partners recorded at different sites on the same day (1116 instances). Points show corrected means ± SD with error bar widths indicating the amount of data; data were binned by 1.5 visits. Lines show the model prediction of the relationship for same-site pairs and different-site pairs.

Between-pair permutations

Individuals of subsequent breeding pairs binged more similarly to their partner than to other subsequently paired members of the opposite sex at the same site on the same date (Fig. 7; β_{males}=0.43, P<0.001 from 1000 sets of partner permutation, n=192; $\beta_{females}$=0.37, P<0.001 from 1000 permutations, n=187; model estimates for observed pairs are given in Tables S8 and S9). The daily frequency of their feeder visits was also more like their partner than non-partners, as defined above (Fig. 8; β_{males}=0.51, P<0.001 from 1000 sets of partner permutation, n=192; $\beta_{females}$=0.42, P<0.001 from 1000 permutations, n=187; model estimates for observed pairs are given in Tables S10 and S11).

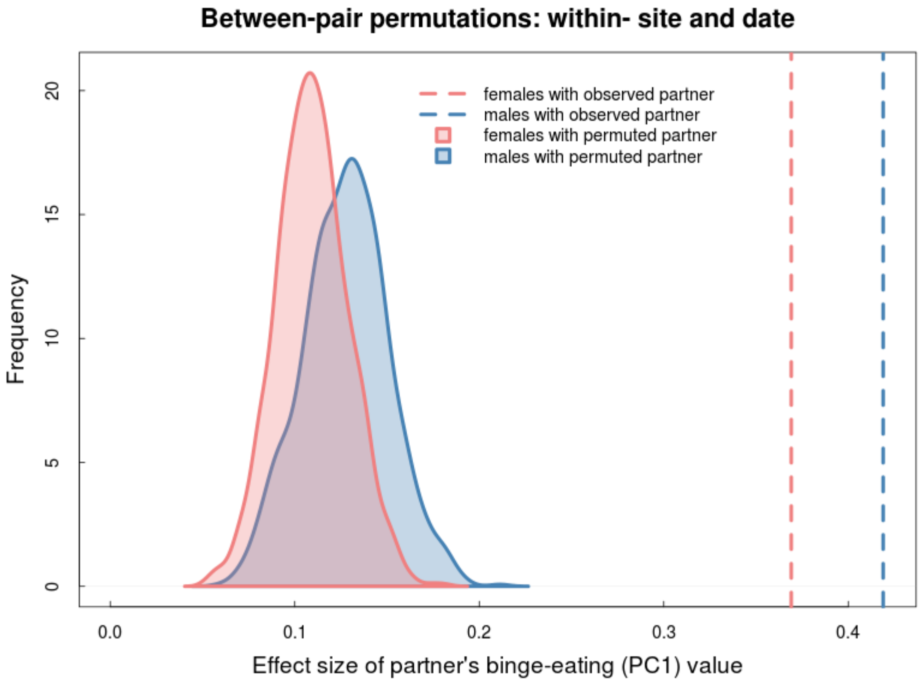


Fig. 7. Effect of subsequent breeding partner’s level of binge-eating (PC1) on focal individual’s binge-eating. Effects of observed partner are shown by dotted lines; effects of 1000 sets of permuted partners shown in density plots. n_{male}=192; n_{female}=187.

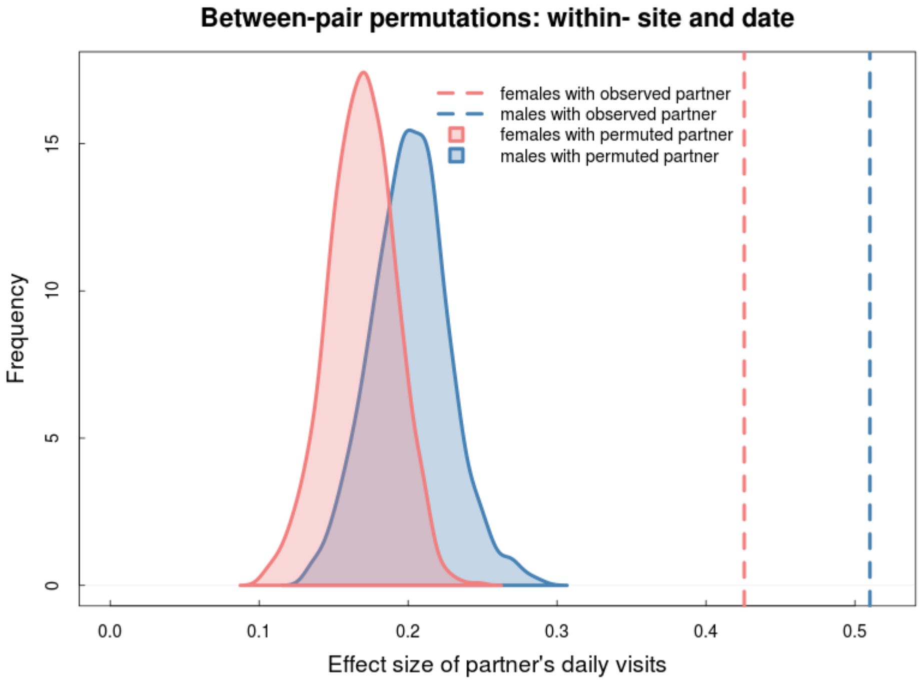


Fig. 8. Effect of subsequent breeding partner’s daily number of feeder visits on focal individual’s daily visits. Effects of observed partner are shown by dotted lines; effects of 1000 sets of permuted partners shown in density plots. n_{male}=192; n_{female}=187.

'Pre-partnership' permutations

Great tits were more likely to be recorded at the same site as their subsequent breeding partner later in winter (males: day of winter β=0.40, SE=0.18, z=2.26, P=0.024; females: day of winter β=0.41, SE=0.20, z=2.04, P=0.041; see Tables S12 and S13 for model estimates). Therefore, assuming that pairs feed together once a partnership is formed (Psorakis *et al.* 2012; Firth *et al.* 2015), we use the term 'pre-partnership' for records of individuals that had a subsequent breeding partner on dates when they were recorded at a different feeding station to their partner. On dates when visiting different sites, subsequent breeding partners were no more similar, in either binge-eating or daily visits, to their partner than their non-partner. This was determined by permuting 'pre-partners'; the identity of each focal bird's permuted partner was selected at random from the subset of 'pre-partners' of the opposite sex that visited a different site from the focal bird on that date. Fig. S3 illustrates the difference in binge-eating between focal birds and observed partners and between focal birds and 1000 sets of permuted partners and Fig. S4 the daily visit difference between focal birds and observed partners and between focal birds and 1000 sets of permuted partners; model estimates given in tables S14-S17. Thus there is no evidence of pre-partnership compatibility of foraging behaviour, i.e. no assortative pairing.

Male great tits binged less when recorded at the same site as their partner than when at different sites (Fig. S5; Welch's two-sample t-test: $t_{(108)}$=2.36, P=0.020), but there was no significant difference in female binge-eating with the presence or absence of partner (Fig. S5; $t_{(150)}$=1.46, P=0.147). In contrast, male great tits visited feeders more often than females on days when recorded at the same site as their subsequent breeding partner (Fig. S6; $t_{(376)}$=2.14, P=0.033) but not when visiting at a different site to their partner (Fig. S6; $t_{(145)}$=1.43, P=0.156).

DISCUSSION

By quantifying individual foraging behaviour while also monitoring social associations, we demonstrate that individual variation in daily foraging routines is linked to social network phenotype and social structure in a wild population of great tits. Since social structure and interaction patterns influence encounter rates, this suggests that individual foraging strategies might have implications for emergent social properties such as the spread of information and disease as well as for mate choice (Lusseau & Newman 2004; Aplin *et al.* 2012; Adelman *et al.* 2015; Oh & Badyaev 2010). In addition, we show that pairs of great tits that subsequently bred together exhibit feeding patterns more similar to their partners than to their non-partners, but only on days when they visit the same feeding stations. This suggests that social relationships such as pair bonds can, in turn, feed back to influence foraging behaviour. However, we did not find evidence that mate choice was based on similarity of foraging strategy prior to pair formation.

Network metrics

Binge-eaters (with high PC1 values: individuals with highly clustered feeder visits within a day) had weaker associations in the social network constructed for each winter than grazers (with low PC1 values: individuals with highly spread out feeder visits across a day). This result is intuitive since binge-eaters, having longer inter-bout intervals and spending a smaller proportion of the day (chapter 4) at feeding stations, have less opportunity to interact with other individuals at feeders than grazers. However, there was no relationship between the mean level of binge-eating and unweighted degree over a winter: binge-eaters did not have fewer associates than grazers, only weaker associations. A previous study on the same system which showed that exploration behaviour (a measure of personality) affected both average association strength and number of associates; fast explorers had weak associations with more individuals while slow explorers associated more strongly with fewer individuals (Aplin *et al.* 2013). A similar result was also found for the number and strength of associations between captive sticklebacks with a measure of boldness (Pike *et al.* 2008). It seems possible that this is because of the localised nature of the individual differences observed in this study – over the course of a day, individuals may encounter most other possible foraging companions regardless of their foraging strategy, but only grazers would have repeated, sustained, interactions.

The daily feeder visit rate of individual great tits could also predict some of the variation in social phenotype: the more feeder visits an individual made in a day, the stronger its association strength and the more associates it had in the winter social network. Since daily feeder visit rates represent the extent to which individuals rely on artificial food, and the social network was constructed with records of co-occurrence at feeding stations, it follows that ‘feeder specialists’ will spend more time at and interact more at feeders than ‘natural-food specialists’. As shown in Chapter 2, individuals with subsequent breeding territories that were further from feeders visited feeders less often than individuals with nearby territories. Thus, distance to territory also explains some of the variation in feeder use. Based on calculations given in Chapter 3, approximately 60 sunflower seeds would provide a typical great tit with its daily midwinter energy requirement. The few great tits that visits feeders more often than 60 times per day appear to be making excess trips to feeders which do not add to their count of associates (Fig. 2).

Assortative mixing

Great tits were positively assorted on each winter social network by their level of binge-eating (PC1) – see networks in Fig. 4, coloured by mean PC1 value. They also exhibited assortative mixing by daily visit rate and weighted degree. While relatively strong for this system (e.g. Aplin *et al.* 2013), the assortment by feeding pattern within each Wytham winter network was not strong enough to induce separate binge-eating and grazing communities, as in dolphin studies which reported social segregation by foraging type (Daura-Jorge *et al.* 2012; Ansmann *et al.* 2012). However in this study, great tits were more strongly assorted by degree than by either feeding pattern and such degree assortment made up a large (although not absolute) component of the observed social structure. Social networks are often degree-assorted, tending to have core(s) of high-degree nodes and a less dense periphery of low-degree nodes; this can be driven by the presence of tightly-knit subgroups of different size, with high-degree individuals in large subgroups and low-degree individuals in small subgroups (Newman 2010). In this study, there was considerable variation in the number of individuals visiting each of the 65 feeding stations and individuals tended to exclusively visit a single feeder or neighbouring feeders within a winter. Spatially-driven subgroups of different size are thus apparent in the social network for each winter, with high-degree individuals (large nodes in Fig. 4) in a few large clusters. However, further tests are required to tease out network assortativity to investigate whether (i) there is some assortment by feeding pattern in addition to the assortment by degree, or (ii) the assortativity described in this chapter is simply driven by the significant relationship between foraging behaviour and degree, or (iii) whether the assortment in foraging behaviour drives the assortment by degree. Regardless, it remains the case that those with more similar feeding habits are more likely to interact, and this could have consequences for how they engage with competition, how information flows through a population, assortative mating, and social learning dynamics.

Grazers spend more time at feeding stations each day than binge-eaters and can co-occur with other individuals more than binge-eaters that visit less often in highly clustered foraging bouts. Thus binge-eaters, spending less time visiting feeders, have more potential to be choosy about when and with whom they visit feeders. They could avoid other binge-eaters to reduce the effects of competition during their foraging bouts, or they could feed together in binge-eating ‘parties’ which might then temporarily exclude grazers. It has been shown in previous chapters that binge-eaters tend to be more dominant (males and adults over females and juveniles), supporting the latter possibility. Additionally, binge-eaters associate more strongly with other binge-eaters than with grazers (Fig. S2).

There are likely multiple mechanisms of assortative mixing which could be passive (for example through the proportion of time spent at sites of aggregation, i.e. feeders, or diet preference; Kleinhappel *et al.* 2014) or active (such as avoidance of aggressive proactive individuals by reactive individuals; Aplin *et al.* 2013). Further work will be required to elucidate the mechanisms of assortment and its effect on the emergent social structure. A previous study on the Wytham great tit population has demonstrated positive assortment by age and immigration status (Farine *et al.* 2015). Immigrant juveniles were more likely to be observed in large groups than immigrant adults. Disassortative mixing is a less common phenomenon in social networks than assortative mixing, but an obvious example is the disassortment by sex, which has also been shown in this study system, with male-female dyads associating more strongly than same-sex dyads (Aplin *et al.* 2013). This is likely driven by pair bonds, which are formed and/or maintained throughout the winter in great tits (Hinde 1952). Similarly, experiments have shown directly that social assortment can be imposed by manipulating which great tits can feed together, and this assortment carries over to other contexts (Firth & Sheldon 2015).

Breeding partnerships

Here, we have shown that a partner's feeding patterns can predict those of a focal bird, but only on dates when recorded at the same feeder. These results are suggestive of some form of convergence in foraging behaviour within pairs. However, it is also possible that this observed convergence could simply be due to a combination of site-related differences and within-partner site-typical behaviour (given a pair is usually at the same site). We therefore conducted between-pair permutations within-site, showing that the observed partner's feeding behaviour predicted their partner's behaviour more than that of non-partners. Next, we asked whether individual foraging behaviour prior to partnership formation had any constraint on partner choice through behavioural compatibility.

Great tits form pair bonds during winter and while the date of partnership formation is not known, we have assumed that dates on which subsequent breeding pairs are observed exclusively at different sites are 'pre-partnership'. So do pair bonds form between individuals with initially smaller differences in behaviour between each other than between themselves and other potential partners? We used a permutation of potential partners to show that 'pre-partnership' great tits did not exhibit feeding patterns any more like their subsequent breeding partner than other 'pre-pair' members of the opposite sex. The results presented here suggest that once pair bonds are formed, partners with initially alternative foraging strategies can shift their behaviour to converge on a more similar strategy. This also supports previous work in Firth *et al.* (2015), where an experimental manipulation demonstrated that pair bonds affected foraging behaviour. Finally, we showed that males visiting the same feeder as their subsequent partner binged less than 'pre-partnership' males while there was no difference in females (Fig. S5). Male great tits tend to binge-eat more than females (as shown in previous chapters); this is likely related to dominance status. Therefore, it is possible that females are unable to increase their level of binge-eating, leaving their partners to reduce their binge-eating to a closer level to the females in order to mirror their foraging behaviour.

Consistency and plasticity

While there is evidence of consistent individual differences in foraging patterns (Chapter 2) and social network metrics (Aplin *et al.* 2015) both within- and between-years, this study also demonstrates that individuals can exhibit flexibility in feeding patterns to accommodate a partner's behavioural strategy. Firth *et al.* (2015) also demonstrate that individual great tits can alter their foraging behaviour to maintain a pair bond when food accessibility is restricted for one pair member; a consequence of this was that individuals' wider social associations to other flock-mates were also shaped by their pair bonds. Extending these results, it would be interesting to ask in a future study whether partnership formation also affects social phenotypes. This would involve constructing networks based on subsets of the winter feeder visits, say per weekend, and comparing network metrics of partners before and after a pair bond was established. An estimate of the time of partnership formation would also be required. This could be roughly approximated by identifying the date on which the subsequent pair first co-occurred at a feeding station (Culina 2014), or the first date of co-occurrence after the last date visiting different sites. A more accurate estimate could potentially be achieved by analysing the distribution of inter-partner visit intervals, since paired birds should visit at similar times with shorter intervals (Firth *et al.* 2015).

In great tits, social units change over time; in their first winter, individuals often join large juvenile flocks which can be composed of multiple species (Perrins 1979). The spatial aspects of an individual's behaviour will also change with dispersal, pair formation and territoriality. In combination with the highly fission-fusion group dynamics, these behaviours will all influence social structure. However while there has been a surge in observational studies of animal social networks, there is still a paucity of repeated network sampling, and of experimental manipulations of factors influencing social associations (but see Aplin *et al.* 2015; Firth & Sheldon 2015). Two recent studies have shown that the manipulation of available foraging modes or accessibility of food affects association patterns and the emergent social structure (Ansmann *et al.* 2012; Firth & Sheldon 2015). They also demonstrated that when the imposed disturbance was removed, manipulated social phenotypes were plastic and the social structure resilient to change. It remains to be investigated whether the interplay between foraging behaviour and social phenotypes could be manipulated in a similar manner.

Limitations and extensions

Here we relate foraging behaviour at feeders with social associations at feeders. It would be preferable to have the two measures recorded in independent contexts, as in studies relating personality (assayed during short term captivity) and social networks based on feeder associations (e.g. Aplin *et al.* 2013). Alternatively, social networks could be constructed with data collected in a context other than foraging. For example in great tits, social networks have been constructed at the brood level based on interactions between siblings in nest boxes (Royle *et al.* 2012) or associations during nest-box prospection (Verhelst, unpublished data; Firth & Sheldon 2015). In other systems, examples include grooming/aggression networks (primates: Flack *et al.* 2006; Carter *et al.* 2015), roosting networks (bats: Rhodes *et al.* 2006), proximity/contact networks (lizards: Godfrey *et al.* 2014; crows: Rutz *et al.* 2012; manakins: Ryder *et al.* 2012). Direct observations are valuable for their accuracy in quantifying interactions, rather than inferring social associations as described in this chapter, but difficult to record in the quantities possible with automated data collection. Despite the limitations of inferring social interactions at feeders, a previous study on great tits has shown that associations in the social networks based on feeder data can carry over into other contexts, including the associations between individuals when inspecting potential nesting locations (Firth & Sheldon 2015). This suggests that the automated data collection may still be meaningful. It has also been shown to have functional significance; For instance, Aplin *et al.* (2012) showed that socially well connected tits were more likely to acquire the social information to locate novel foraging patches. We suggest that the links explored in this chapter between feeding patterns, social interactions and social structure could have consequences for multiple processes, including the use of social information in foraging, and the response to competition. For example, previous work on sticklebacks showed that the social environment, in combination with competition avoidance, affected when individuals decided to move to a newly available food patch (Laskowski & Bell 2013).

In order to investigate the evolutionary consequences of social associations and network structure, measures of fitness need to be quantified in future studies. Additionally, environmental changes could impact individual behaviours and social interactions between individuals and ultimately the resultant group structure (Wittemyer *et al.* 2005; de Silva *et al.* 2011) so it would be useful to monitor environmental conditions and incorporate these variables in future analyses of individual behaviour and repeatedly-sampled social networks.

General conclusions & implications.

In this study we have explored the question of why non-random associations and social structures occur with respect to individual foraging behaviour. Spatial variation in resource availability and conspecific density, in combination with temporal behavioural variation and food preferences (in this case natural or artificial food), will impact on rates of contact and thus social associations and network structure. Social preferences, such as pair bonds, can also feed back to influence patterns of individual behaviour, social associations and foraging strategies (Firth *et al.* 2015).

Alternative foraging tactics explain some of the variation in social phenotypes and multiple processes, working at different scales, influence the emergent social network structure. Great tits show repeatability in feeding patterns and social metrics, but are also capable of adjusting these in response to social partnerships. The interrelations between foraging, associations and social structure will all affect rates of encounter, with implications for the spread of information or disease, inbreeding avoidance, and sexual selection.

ACKNOWLEDGEMENTS

We thank the social network group for help with collecting winter logger data, catching and tagging birds during the winter, and all the Wytham tit fieldworkers for assistance in catching and tagging birds during the spring. This work was funded by a European Research Council (ERC) grant to B.C.S (AdG 250164).

REFERENCES

Adelman, J. S., S. C. Moyers, D. R. Farine and D. M. Hawley (2015). Feeder use predicts both acquisition and transmission of a contagious pathogen in a North American songbird. *Proceedings of the Royal Society B: Biological Sciences* **282**(1815): 20151429.

Ansmann, I. C., G. J. Parra, B. L. Chilvers and J. M. Lanyon (2012). Dolphins restructure social system after reduction of commercial fisheries. *Animal Behaviour* **84**(3): 575-581.

Aplin, L. M., D. R. Farine, J. Morand-Ferron, E. F. Cole, A. Cockburn and B. C. Sheldon (2013). Individual personalities predict social behaviour in wild networks of great tits (*Parus major*). *Ecology Letters* **16**(11): 1365-1372.

Aplin, L. M., D. R. Farine, J. Morand-Ferron and B. C. Sheldon (2012). Social networks predict patch discovery in a wild population of songbirds. *Proceedings of the Royal Society B: Biological Sciences* **279**(1745): 4199-4205.

Aplin, L. M., J. A. Firth, D. R. Farine, B. Voelkl, R. A. Crates, A. Culina, C. J. Garroway, C. A. Hinde, L. R. Kidd, I. Psorakis, N. D. Milligan, R. Radersma, B. L. Verhelst and B. C. Sheldon (2015). Consistent individual differences in the social phenotypes of wild great tits, *Parus major*. *Animal Behaviour* **108**: 117-127.

Bates, L. and J. Chappell (2002). Inhibition of optimal behavior by social transmission in the guppy depends on shoaling. *Behavioral Ecology* **13**(6): 827-831.

Butts, C. T. (2008). Social network analysis with sna. *Journal of Statistical Software* **24**(6): 1-51.

Cairns, S. J. and S. J. Schwager (1987). A comparison of association indexes. *Animal Behaviour* **35**(5): 1454-1469.

Carter, A. J., A. E. G. Lee, H. H. Marshall, M. T. Ticó and G. Cowlishaw (2015). Phenotypic assortment in wild primate networks: implications for the dissemination of information. *Royal Society Open Science* **2**(5): 140444.

Chilvers, B. L. and P. J. Corkeron (2001). Trawling and bottlenose dolphins' social structure. *Proceedings of the Royal Society B: Biological Sciences* **268**(1479): 1901-1905.

Croft, D. P., R. James and J. D. Krause (2008). Exploring animal social networks. Princeton, Princeton University Press.

Croft, D. P., J. Krause, S. K. Darden, I. W. Ramnarine, J. J. Faria and R. James (2009). Behavioural trait assortment in a social network: patterns and implications. *Behavioral Ecology and Sociobiology* **63**(10): 1495-1503.

Croft, D. P., J. R. Madden, D. W. Franks and R. James (2011). Hypothesis testing in animal social networks. *Trends in Ecology & Evolution* **26**(10): 502-507.

Csárdi, G. and T. Nepusz (2006). The igraph software package for complex network research. *InterJournal, Complex Systems* **1695**(5): 1-9.

Culina, A. (2014). With or without you – pair fidelity and divorce in monogamous birds. *DPhil thesis, University of Oxford*. Oxford, UK.

Daura-Jorge, F. G., M. Cantor, S. N. Ingram, D. Lusseau and P. C. Simões-Lopes (2012). The structure of a bottlenose dolphin society is coupled to a unique foraging cooperation with artisanal fishermen. *Biology Letters* **8**(5): 702-705.

de Silva, S., A. D. Ranjeewa and S. Kryazhimskiy (2011). The dynamics of social networks among female Asian elephants. *BMC Ecology* **11**: 17.

Ekman, J. (1989). Ecology of non-breeding social systems of *Parus*. *Wilson Bulletin* **101**(2): 263-288.

Farine, D. R. (2013). Animal social network inference and permutations for ecologists in R using *asnipe*. *Methods in Ecology and Evolution* **4**(12): 1187-1194.

Farine, D. R. (2014). Measuring phenotypic assortment in animal social networks: weighted associations are more robust than binary edges. *Animal Behaviour* **89**: 141-153.

Farine, D. R., J. A. Firth, L. M. Aplin, R. A. Crates, A. Culina, C. J. Garroway, C. A. Hinde, L. R. Kidd, N. D. Milligan, I. Psorakis, R. Radersma, B. L. Verhelst, B. Voelkl and B. C. Sheldon (2015). The role of social and ecological processes in structuring animal populations: a case study from automated tracking of wild birds. *Royal Society Open Science* **2**(4): 150057.

Firth, J. A. and B. C. Sheldon (2015). Experimental manipulation of avian social structure reveals segregation is carried over across contexts. *Proceedings of the Royal Society B: Biological Sciences* **282**(1802): 20142350.

Firth, J. A., B. Voelkl, D. R. Farine and B. C. Sheldon (2015). Experimental evidence that social relationships determine individual foraging behavior. *Current Biology* **In press**.

Flack, J. C., M. Girvan, F. B. M. de Waal and D. C. Krakauer (2006). Policing stabilizes construction of social niches in primates. *Nature* **439**(7075): 426-429.

Godfrey, S. S., T. H. Ansari, M. G. Gardner, D. R. Farine and C. M. Bull (2014). A contact-based social network of lizards is defined by low genetic relatedness among strongly connected individuals. *Animal Behaviour* **97**: 35-43.

Heath, J. P., H. G. Gilchrist and R. C. Ydenberg (2010). Interactions between rate processes with different timescales explain counterintuitive foraging patterns of arctic wintering eiders. *Proceedings of the Royal Society B: Biological Sciences* **277**(1697): 3179-3186.

Hinde, R. A. (1952). The behaviour of the great tit (*Parus major*) and some other related species. *Behaviour (Supplement)* **2**: 1-201.

Johnson, D. D. P., R. Kays, P. G. Blackwell and D. W. Macdonald (2002). Does the resource dispersion hypothesis explain group living? *Trends in Ecology & Evolution* **17**(12): 563-570.

Kleinhappel, T. K., O. H. P. Burman, E. A. John, A. Wilkinson and T. W. Pike (2014). Diet-mediated social networks in shoaling fish. *Behavioral Ecology* **25**(2): 374-377.

Kluijver, H. N. (1950). Daily routines of the great tit, *Parus m. major* L. *Ardea* **38**(3-4): 99-135.

Kluijver, H. N. (1951). The population ecology of the great tit, *Parus m. major* L. *Ardea* **39**(1): 1-135.

Krause, J. D. and G. D. Ruxton (2002). Living in groups. Oxford, Oxford University Press.

Laskowski, K. L. and A. M. Bell (2013). Competition avoidance drives individual differences in response to a changing food resource in sticklebacks. *Ecology Letters* **16**(6): 746-753.

Lusseau, D. and M. E. J. Newman (2004). Identifying the role that animals play in their social networks. *Proceedings of the Royal Society B: Biological Sciences* **271**: S477-S481.

Matechou, E., S. C. Cheng, L. R. Kidd and C. J. Garroway (2015). Reproductive consequences of the timing of seasonal movements in a nonmigratory wild bird population. *Ecology* **96**(6): 1641-1649.

Newman, M. E. J. (2002). Assortative mixing in networks. *Physical Review Letters* **89**(20): 208701.

Newman, M. E. J. (2003). Mixing patterns in networks. *Physical Review E* **67**(2): 026126.

Newman, M. E. J. (2010). Networks: an introduction. Oxford, Oxford University Press.

Oh, K. P. and A. V. Badyaev (2010). Structure of social networks in a passerine bird: consequences for sexual selection and the evolution of mating strategies. *American Naturalist* **176**(3): E80-E89.

Perrins, C. M. (1979). British Tits. London, Collins.

Pike, T. W., M. Samanta, J. Lindstrom and N. J. Royle (2008). Behavioural phenotype affects social interactions in an animal network. *Proceedings of the Royal Society B: Biological Sciences* **275**(1650): 2515-2520.

Psorakis, I., S. J. Roberts, I. Rezek and B. C. Sheldon (2012). Inferring social network structure in ecological systems from spatio-temporal data streams. *Journal of the Royal Society Interface* **9**(76): 3055-3066.

Psorakis, I., B. Voelkl, C. J. Garroway, R. Radersma, L. M. Aplin, R. A. Crates, A. Culina, D. R. Farine, J. A. Firth, C. A. Hinde, L. R. Kidd, N. D. Milligan, S. J. Roberts, B. Verhelst and B. C. Sheldon (2015). Inferring social structure from temporal data. *Behavioral Ecology and Sociobiology* **69**(5): 857-866.

R Development Core Team (2015). R: A language and environment for statistical computing. Vienna, R Foundation for Statistical Computing.

Rands, S. A., R. A. Pettifor, J. M. Rowcliffe and G. Cowlishaw (2006). Social foraging and dominance relationships: the effects of socially mediated interference. *Behavioral Ecology and Sociobiology* **60**(4): 572-581.

Rhodes, M., G. W. Wardell-Johnson, M. P. Rhodes and B. Raymond (2006). Applying network analysis to the conservation of habitat trees in urban environments: a case study from Brisbane, Australia. *Conservation Biology* **20**(3): 861-870.

Royle, N. J., T. W. Pike, P. Heeb, H. Richner and M. Kolliker (2012). Offspring social network structure predicts fitness in families. *Proceedings of the Royal Society B: Biological Sciences* **279**(1749): 4914-4922.

Rutz, C., Z. T. Burns, R. James, S. M. H. Ismar, J. Burt, B. Otis, J. Bowen and J. J. H. St Clair (2012). Automated mapping of social networks in wild birds. *Current Biology* **22**(17): R669-R671.

Ryder, T. B., B. M. Horton, M. van den Tillaart, J. D. Morales and I. T. Moore (2012). Proximity data-loggers increase the quantity and quality of social network data. *Biology Letters* **8**(6): 917-920.

Silk, M. J., A. L. Jackson, D. P. Croft, K. Colhoun and S. Bearhop (2015). The consequences of unidentifiable individuals for the analysis of an animal social network. *Animal Behaviour* **104**: 1-11.

St Clair, J. J. H., Z. T. Burns, E. M. Bettaney, M. B. Morrissey, B. Otis, T. B. Ryder, R. C. Fleischer, R. James and C. Rutz (2015). Experimental resource pulses influence social-network dynamics and the potential for information flow in tool-using crows. *Nature Communications* **6**: 7197.

Svensson, L. (1992). Identification guide to European passerines. Thetford, British Trust for Ornithology.

Tania, N., B. Vanderlei, J. P. Heath and L. Edelstein-Keshet (2012). Role of social interactions in dynamic patterns of resource patches and forager aggregation. *Proceedings of the National Academy of Sciences* **109**(28): 11228-11233.

Tanner, C. J. and A. L. Jackson (2012). Social structure emerges via the interaction between local ecology and individual behaviour. *Journal of Animal Ecology* **81**(1): 260-267.

Whitehead, H. (2008). Analyzing animal societies: quantitative methods for vertebrate social analysis. Chicago, University of Chicago Press.

Whitehead, H. and S. Dufault (1999). Techniques for Analyzing Vertebrate Social Structure Using Identified Individuals: Review and Recommendations. Advances in the Study of Behavior. P. J. B. Slater, J. S. Rosenblatt, C. T. Snowden and T. J. Roper, Academic Press. **28:** 33-74.

Wittemyer, G., I. Douglas-Hamilton and W. M. Getz (2005). The socioecology of elephants: analysis of the processes creating multitiered social structures. *Animal Behaviour* **69**(6): 1357-1371.

APPENDIX

Supplementary Figures

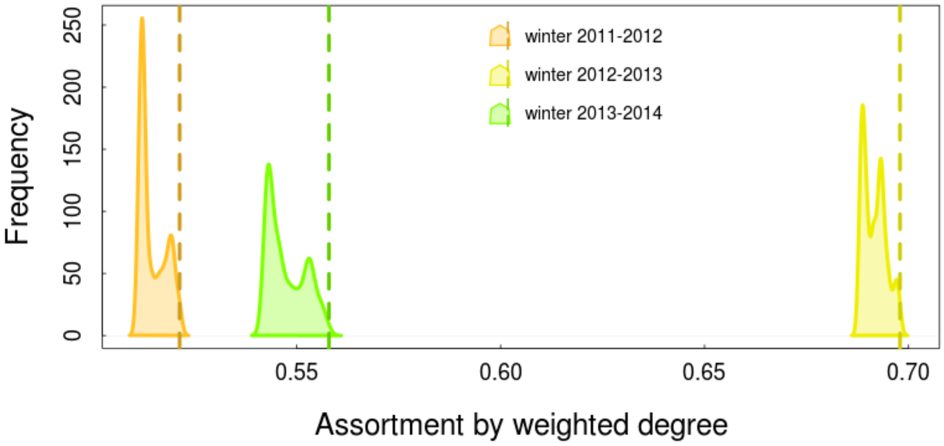


Fig. S1. Mixing patterns of great tits within flocking events: assortment of individuals by weighted degree (overall association strength) in each winter ($n_{winter1}$=848; $n_{winter2}$=589, $n_{winter3}$=538). Dashed lines show assortment scores of the observed data; distributions show assortment scores of 1000 permutations of individual ID between flocking events.

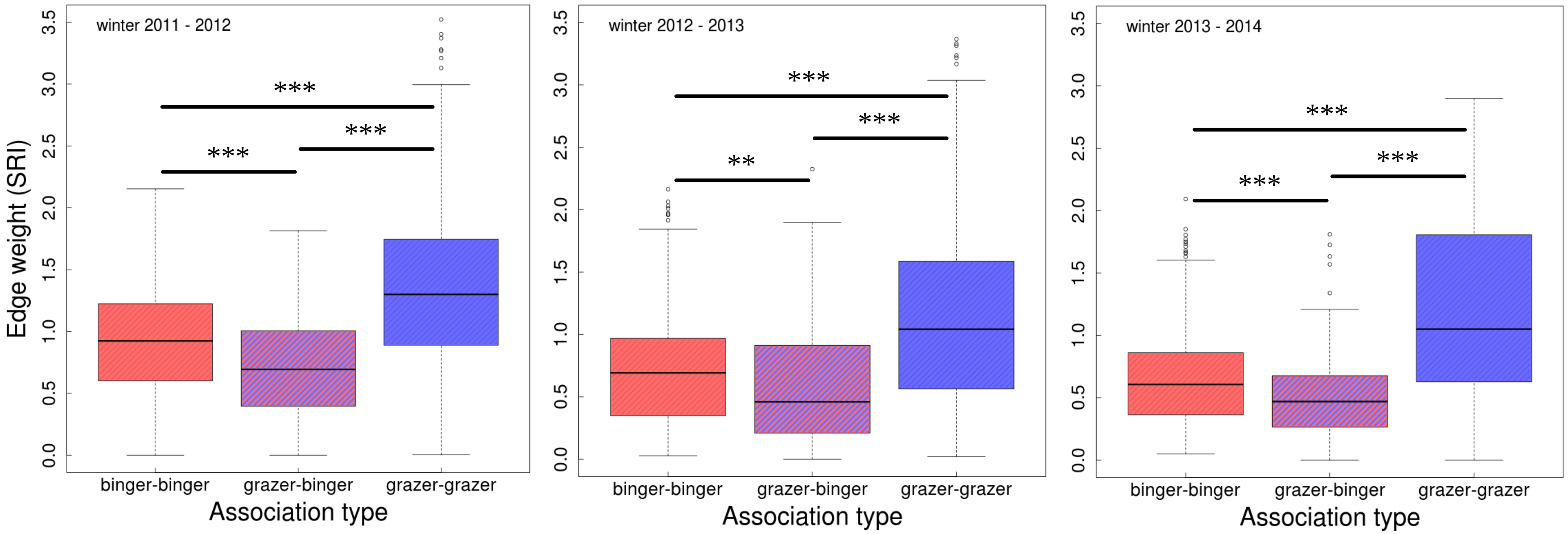


Fig. S2. Association strengths (i) between binge-eating dyads, (ii) between binge-eater – grazer dyads, and (iii) between grazing dyads, for each winter. Binge-eaters comprise the top 33% of PC1 scores and grazers comprise the bottom 33% of PC1 scores in each winter ($n_{winter1}$=566, $n_{winter2}$=394, $n_{winter3}$=360). Boxes indicate interquartile range (IQR) with mid-line for median; whiskers show the range with outliers (outside 1.5 × IQR) as points.

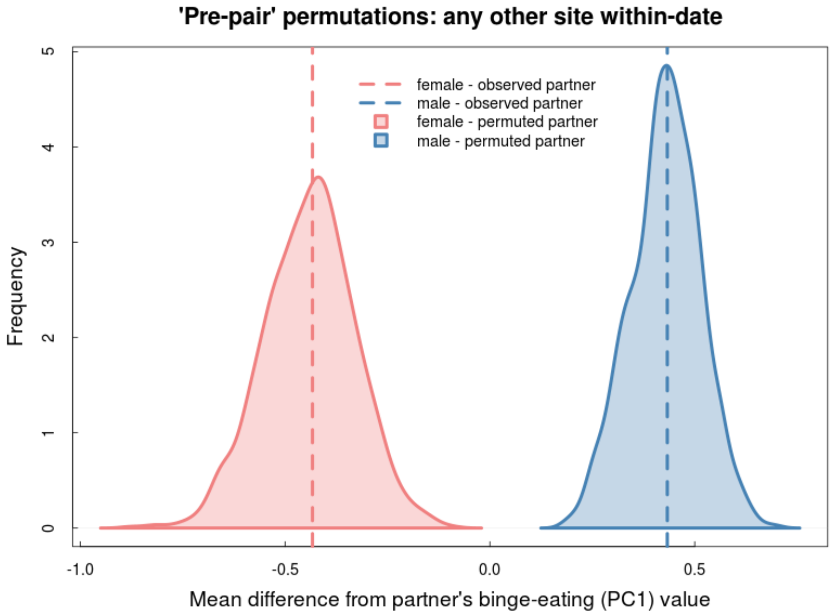


Fig. S3. Mean difference between subsequent breeding partner’s level of binge-eating and focal individual’s binge-eating (partner’s PC1 subtracted from focal’s PC1) on dates when the pair visited different feeding stations; 74 male and 74 female focal birds plotted separately. Difference from observed partner indicated by dotted line; difference from 1000 sets of permuted partners shown in density plot. Observed partners were swapped at random with individuals of the opposite sex that visited any site except the focal’s and that also visited a different site to their subsequently observed partner.

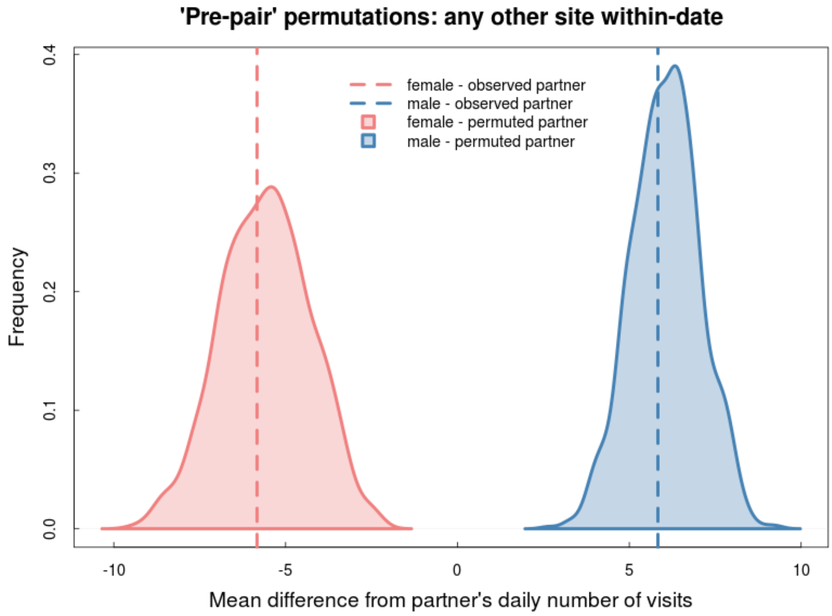


Fig. S4. Mean difference between subsequent breeding partner’s daily number of feeder visits and focal individual’s daily visits (partner’s visits subtracted from focal’s visits) on dates when the pair visited different feeding stations; 74 male and 74 female focal birds plotted separately. Difference from observed partner indicated by dotted line; difference from 1000 sets of permuted partners shown in density plot. Observed partners were swapped at random with individuals of the opposite sex that visited any site except the focal’s and that also visited a different site to their subsequently observed partner.

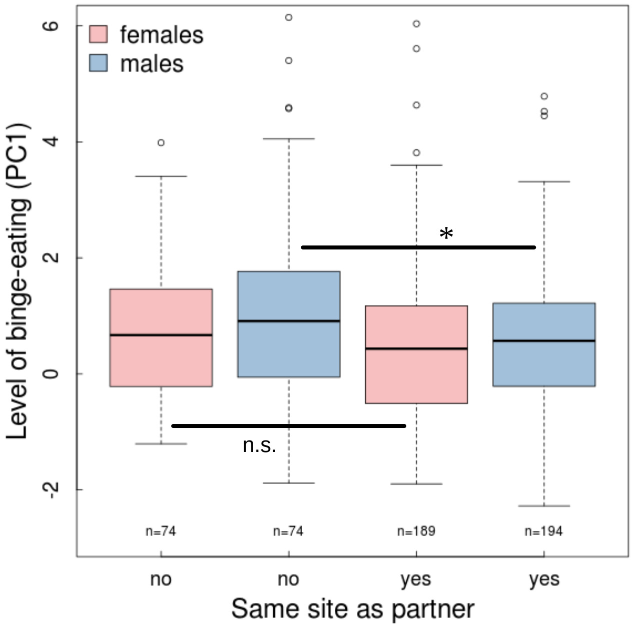


Fig. S5. Mean level of binge-eating (PC1) when visiting a different site or the same site as a subsequent breeding partner. Male and female means plotted separately. Mid-lines and boxes show median and IQR respectively; whiskers indicate the range with outliers (outside 1.5 × IQR) as points.

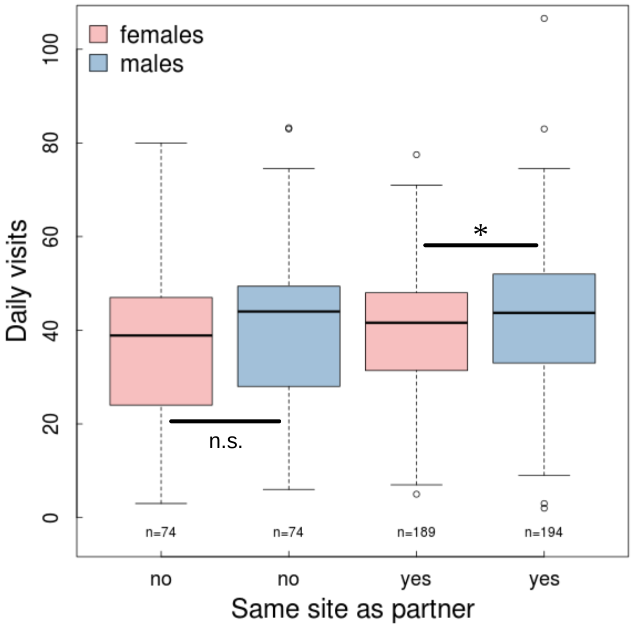


Fig. S6. Mean daily feeder visits when recorded at a different site or the same site as a subsequent breeding partner. Male and female means plotted separately. Mid-lines and boxes show median and IQR respectively; whiskers indicate the range with outliers (outside 1.5 × IQR) as points.

Supplementary Tables

Table S1. Linear model on factors affecting the **weighted degree** (overall association strength) of 1287 individual great tits in winter feeder social networks. One network was constructed for each winter.

Variable	Coefficient	SE	t	*P*
winter (2)	-0.66	0.08	-8.19	<0.001
winter (3)	-0.43	0.08	-5.28	<0.001
binge-eating PC1	-0.12	0.02	-5.05	<0.001
scaled daily visits	0.12	0.04	3.03	0.003
scaled daily visits ^2	-0.09	0.03	-3.12	0.002
scaled feeder traffic	0.60	0.04	16.13	<0.001

Table S2. Linear model on factors affecting the **unweighted degree** (number of associates) of 1287 individual great tits in winter feeder social networks. One network was constructed for each winter.

Variable	Coefficient	SE	t	*P*
winter (2)	-35.42	2.60	-13.65	<0.001
winter (3)	-19.92	2.57	-7.74	<0.001
binge-eating PC1	-1.11	0.73	-1.52	0.129
scaled daily visits	-1.45	1.23	-1.18	0.239
scaled daily visits ^2	-3.14	0.87	-3.60	<0.001
age (juvenile)	18.35	2.18	8.42	<0.001
scaled feeder traffic	5.26	1.17	4.49	<0.001

Table S3. Linear model on factors affecting the **average association strength** (scaled by 100) of 1287 individual great tits in winter feeder social networks. One network was constructed for each winter.

Variable	Coefficient	SE	t	*P*
winter (2)	1.11	0.13	8.46	<0.001
winter (3)	0.11	0.13	0.84	0.399
binge-eating PC1	-0.13	0.04	-3.72	<0.001
scaled daily visits	0.22	0.06	3.54	<0.001
scaled daily visits ^2	0.04	0.04	0.95	0.342
age (juvenile)	-0.75	0.11	-6.83	<0.001
scaled feeder traffic	0.48	0.06	8.17	<0.001

Table S4. Linear mixed model on factors affecting the level of **binge-eating (PC1)** of male great tits on dates when they and their subsequent breeding partner visited one feeding station each. There were 1116 instances of same-site pairs and 167 of different-site pairs.

Variable	Coefficient	SE	t	*P*
partner's level of binge-eating PC1	-0.04	0.06	-0.61	0.543
partner at same site (yes)	-0.65	0.13	-5.18	<0.001
scaled daily visits	-0.24	0.04	-5.63	<0.001
age (juvenile)	-0.19	0.12	-1.54	0.125
mean scaled feeder traffic	0.16	0.08	1.88	0.061
deviation scaled feeder traffic	-0.26	0.07	-3.58	<0.001
partner's PC1 * partner at same site (yes)	0.45	0.07	6.51	<0.001

Random term	Variance	SD	n
individual ID	0.78	0.88	217
individual ID with random feeder traffic slope	0.15	0.38	217
site	0.08	0.28	59
date	0.05	0.22	30
residual	0.88	0.94	

Table S5. Linear mixed model on factors affecting the level of **binge-eating (PC1)** of female great tits on dates when they and their subsequent breeding partner visited one feeding station each. There were 1116 instances of same-site pairs and 167 of different-site pairs.

Variable	Coefficient	SE	t	*P*
partner's level of binge-eating PC1	-0.02	0.05	-0.42	0.675
partner at same site (yes)	-0.30	0.12	-2.46	0.014
scaled daily visits	-0.30	0.04	-7.16	<0.001
age (juvenile)	-0.12	0.11	-1.08	0.281
mean scaled feeder traffic	0.03	0.07	0.47	0.637
deviation scaled feeder traffic	-0.15	0.07	-2.28	0.023
partner's PC1 * partner at same site (yes)	0.38	0.05	7.19	<0.001

Random term	Variance	SD	n
individual ID	0.53	0.73	208
individual ID with random feeder traffic slope	0.08	0.29	208
site	0.09	0.29	60
date	0.02	0.15	30
residual	0.78	0.89	

Table S6. Linear mixed model on factors affecting the daily **number of feeder visits** of male great tits on dates when they and their subsequent breeding partner visited one feeding station each. There were 1116 instances of same-site pairs and 167 of different-site pairs.

Variable	Coefficient	SE	t	*P*
partner's daily visits	-0.01	0.06	-0.20	0.840
partner at same site (yes)	-16.37	2.78	-5.89	<0.001
age (juvenile)	6.01	1.31	4.59	<0.001
mean scaled feeder traffic	4.22	0.87	4.83	<0.001
deviation scaled feeder traffic	4.27	0.80	5.33	<0.001
partner's daily visits * partner at same site (yes)	0.48	0.07	7.37	<0.001

Random term	Variance	SD	n
individual ID	96.23	9.81	217
individual ID with random feeder traffic slope	27.15	5.21	217
site	4.83	2.20	59
date	5.31	2.30	30
residual	96.25	9.81	

Table S7. Linear mixed model on factors affecting the daily **number of feeder visits** of female great tits on dates when they and their subsequent breeding partner visited one feeding station each. There were 1116 instances of same-site pairs and 167 of different-site pairs.

Variable	Coefficient	SE	t	*P*
partner's daily visits	-0.04	0.05	-0.83	0.409
partner at same site (yes)	-16.89	2.70	-6.26	<0.001
age (juvenile)	3.31	1.22	2.72	0.007
mean scaled feeder traffic	4.16	0.82	5.11	<0.001
deviation scaled feeder traffic	5.37	0.77	7.00	<0.001
partner's daily visits * partner at same site (yes)	0.45	0.06	7.65	<0.001

Random term	Variance	SD	n
individual ID	55.58	7.46	208
individual ID with random feeder traffic slope	21.50	4.64	208
site	20.45	4.52	60
date	12.10	3.48	30
residual	85.02	9.22	

Table S8. Linear mixed model on factors affecting the level of **binge-eating (PC1)** of male great tits on dates when they and their subsequent breeding partner visited only the **same feeding station**.

Variable	Coefficient	SE	t	*P*
partner's level of binge-eating PC1	0.43	0.03	15.10	<0.001
scaled daily visits	-0.20	0.04	-4.60	<0.001
age (juvenile)	-0.12	0.13	-0.90	0.368
mean scaled feeder traffic	0.13	0.07	1.71	0.087
deviation scaled feeder traffic	-0.27	0.07	-3.62	<0.001

Random term	Variance	SD	n
individual ID	0.76	0.87	192
individual ID with random feeder traffic slope	0.16	0.4	192
site	0.08	0.28	57
date	0.04	0.19	30
residual	0.78	0.88	

Table S9. Linear mixed model on factors affecting the level of **binge-eating (PC1)** of female great tits on dates when they and their subsequent breeding partner visited only the **same feeding station**.

Variable	Coefficient	SE	t	*P*
partner's level of binge-eating PC1	0.37	0.02	15.02	<0.001
scaled daily visits	-0.25	0.04	-6.22	<0.001
age (juvenile)	-0.14	0.12	-1.15	0.252
mean scaled feeder traffic	0.06	0.06	0.87	0.384
deviation scaled feeder traffic	-0.12	0.06	-2.02	0.044

Random term	Variance	SD	n
individual ID	0.56	0.75	187
individual ID with random feeder traffic slope	0.02	0.14	187
site	0.03	0.16	57
date	0.01	0.1	30
residual	0.75	0.87	

Table S10. Linear mixed model on factors affecting the daily **number of feeder visits** of male great tits on dates when they and their subsequent breeding partner visited only the **same feeding station**.

Variable	Coefficient	SE	t	*P*
partner's daily visits	0.51	0.03	17.90	<0.001
age (juvenile)	7.26	1.36	5.34	<0.001
mean scaled feeder traffic	2.50	0.82	3.06	0.002
deviation scaled feeder traffic	3.34	0.78	4.30	<0.001

Random term	Variance	SD	n
individual ID	77.11	8.78	192
individual ID with random feeder traffic slope	13.28	3.64	192
site	13.60	3.69	57
date	5.26	2.29	30
residual	89.54	9.46	

Table S11. Linear mixed model on factors affecting the daily **number of feeder visits** of female great tits on dates when they and their subsequent breeding partner visited only the **same feeding station**.

Variable	Coefficient	SE	t	*P*
partner's daily visits	0.42	0.02	17.80	<0.001
age (juvenile)	3.44	1.32	2.61	0.009
mean scaled feeder traffic	4.21	0.74	5.70	<0.001
deviation scaled feeder traffic	4.14	0.74	5.62	<0.001

Random term	Variance	SD	n
individual ID	54.35	7.37	187
individual ID with random feeder traffic slope	13.11	3.62	187
site	14.19	3.77	57
date	7.07	2.66	30
residual	78.51	8.86	

Table S12. Generalized linear mixed model, with binomial error distribution and logit link function, on factors affecting whether male great tits are **recorded exclusively at the same feeding station as their subsequent breeding partner** on a recording day. There were 1116 instances of both pair members being recorded at the same feeding station and 167 of pair members at different feeding stations within a day.

Variable	Coefficient	SE	z	*P*
day of winter	0.40	0.18	2.26	0.024
winter (2)	0.55	0.78	0.71	0.476
winter (3)	2.64	1.00	2.64	0.008
age (juvenile)	0.68	1.04	0.65	0.513
scaled daily visits	0.75	0.26	2.85	0.004

Random term	Variance	SD	n
individual ID	169.90	13	217
site	10.65	3.26	59

Table S13. Generalized linear mixed model, with binomial error distribution and logit link function, on factors affecting whether female great tits are **recorded exclusively at the same feeding station as their subsequent breeding partner** on a recording day. There were 1116 instances of both pair members being recorded at the same feeding station and 167 of pair members at different feeding stations within a day.

Variable	Coefficient	SE	z	*P*
day of winter	0.41	0.20	2.04	0.041
winter (2)	-0.08	0.71	-0.12	0.907
winter (3)	3.59	0.97	3.69	<0.001
age (juvenile)	-4.18	1.19	-3.50	<0.001
scaled daily visits	0.94	0.28	3.30	0.001

Random term	Variance	SD	n
individual ID	133.60	11.6	208
site	14.53	3.81	60

Table S14. Linear mixed model on factors affecting the level of **binge-eating (PC1)** of male great tits on dates when they and their subsequent breeding partner visited **different feeding stations**.

Variable	Coefficient	SE	t	*P*
partner's level of binge-eating PC1	-0.10	0.09	-1.15	0.253
scaled daily visits	-0.53	0.16	-3.32	0.001
age (juvenile)	-0.62	0.36	-1.72	0.087
mean scaled feeder traffic	0.01	0.19	0.07	0.940
deviation scaled feeder traffic	-0.07	0.25	-0.28	0.777

Random term	Variance	SD	n
individual ID	1.24	1.11	74
individual ID with random feeder traffic slope	0.11	0.33	74
site	0.21	0.45	41
date	0.19	0.44	30
residual	1.29	1.14	

Table S15. Linear mixed model on factors affecting the level of **binge-eating (PC1)** of female great tits on dates when they and their subsequent breeding partner visited **different feeding stations**.

Variable	Coefficient	SE	t	*P*
partner's level of binge-eating PC1	-0.02	0.06	-0.41	0.686
scaled daily visits	-0.49	0.11	-4.39	<0.001
age (juvenile)	0.00	0.24	0.00	0.999
mean scaled feeder traffic	-0.03	0.15	-0.23	0.820
deviation scaled feeder traffic	-0.61	0.35	-1.73	0.085

Random term	Variance	SD	n
individual ID	0.30	0.54	74
individual ID with random feeder traffic slope	1.95	1.39	74
site	0.39	0.62	41
date	0.00	0.05	30
residual	0.89	0.95	

Table S16. Linear mixed model on factors affecting the daily **number of feeder visits** of male great tits on dates when they and their subsequent breeding partner visited **different feeding stations**.

Variable	Coefficient	SE	t	*P*
partner's daily visits	-0.01	0.07	-0.19	0.850
age (juvenile)	3.88	3.57	1.09	0.278
mean scaled feeder traffic	8.55	1.77	4.82	<0.001
deviation scaled feeder traffic	6.29	2.48	2.54	0.012

Random term	Variance	SD	n
individual ID	134.55	11.60	74
individual ID with random feeder traffic slope	30.42	5.52	74
site	26.33	5.13	41
date	<0.01	<0.01	30
residual	115.08	10.73	

Table S17. Linear mixed model on factors affecting the daily **number of feeder visits** of female great tits on dates when they and their subsequent breeding partner visited **different feeding stations**.

Variable	Coefficient	SE	t	*P*
partner's daily visits	0.04	0.07	0.66	0.509
age (juvenile)	0.91	3.43	0.27	0.790
mean scaled feeder traffic	2.70	1.90	1.42	0.157
deviation scaled feeder traffic	9.40	2.44	3.85	<0.001

Random term	Variance	SD	n
individual ID	115.91	10.77	74
individual ID with random feeder traffic slope	26.48	5.15	74
site	36.81	6.07	41
date	22.05	4.70	30
residual	86.87	9.32	

CHAPTER 6

General Discussion

General Discussion

This thesis presents an investigation of the causes and consequences of individual variation in foraging patterns, ranging in temporal scale from single feeding events to seasonal shifts in behaviour. Here I describe the goals of this study and give a summary of the key findings. I then place the work in the context of the field of foraging and, more broadly, behavioural ecology, discussing the implications of the results. I also consider some limitations of the methods used and suggest future directions for research that might further our understanding of individual variation in behaviour.

Aims and motivation

The main goal of this thesis was to examine the significance of individual variation in the daily foraging routines of wild great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*). The temporal scales at which behaviour is considered are important when quantifying behavioural patterns, especially when optimal strategies are being investigated (Heath *et al.* 2010; Fortin *et al.* 2002). In some cases, short-term reductions in efficiencies can lead to longer term benefits; for example, reducing speed during locomotion can improve long-term endurance (Kramer & McLaughlin 2001). Previous studies on foraging rates have often focused on hourly rates of food intake (e.g. Bonter *et al.* 2013; Cope 2003; Alanärä *et al.* 2001; Zhang *et al.* 1992), and therefore little is known of how individuals time their feeding at a finer timescale, and significant patterns of variation may have been overlooked. This is likely to be particularly true for small birds and mammals that, due to their high metabolisms, must obtain large numbers of food items each day (Houston & McNamara 1993; Perrins 1979; Kronfeld-Schor & Dayan 2008; Yunger *et al.* 2002). These animals may therefore exert fine control over the precise timing of feeding within a day in an attempt to reduce the risks of starvation and predation. The first aim of my thesis was to quantify fine-scale temporal patterns in individual foraging routines in a wild tit population.

While, in the past, it has been difficult to simultaneously monitor the behaviour of large numbers of individuals in the wild, the relatively recent application of passive integrated transponder (PIT) tags on passerines has made it possible to automatically record the time and individual identity of birds visiting feeders fitted with radio-frequency identification (RFID) antennae (Bonter & Bridge 2011). I applied a method, analogous to that used in the analysis of meal patterns in livestock (Howie *et al.* 2009), to define separate bouts of foraging behaviour made by individually PIT-tagged birds at feeders in a 385-hectare contiguous woodland. Alternative foraging strategies have been demonstrated in how individual tits trade-off the risks of starvation and predation (Quinn *et al.* 2012). I hypothesized that individuals would also exhibit alternative foraging strategies that differed in the extent to which they clustered foraging into bouts.

Behavioural variation can be decomposed into between- and within-individual components (Dingemanse & Dochtermann 2013). This is an important analytical approach since individual differences can be caused by (i) individuals behaving consistently themselves but differently in comparison to others, (ii) individuals on average behaving similarly to each other but themselves flexibly over time, or (iii) a combination of both inter- and intra-individual variation. That is, variance components can be used to test whether individuals differ in average behaviour and also whether they differ in behavioural flexibility. Using this approach, I set out to quantify an axis of individual variation in fine-scale temporal foraging patterns (i.e. the degree of clustering of feeder visits into foraging bouts). I then investigated whether individuals were repeatable in their foraging behaviour, and asked which factors, both intrinsic and environmental, affected an individual’s daily foraging patterns. Furthermore, I explored how flexible individual foraging strategies were and how they shifted with changes in competition level and seasonal conditions. Differential responses to competition would suggest variation in susceptibility to interference, with potential consequences for survival patterns and group composition (Sutherland 1996).

In addition to links with competitive ability, individual foraging behaviour is also likely to be related to social interactions in group-foraging species. Thus, individual differences in foraging pattern may have consequences for social organisation. Moreover, when individuals aggregate at food sources, variation in the timing of feeding will influence encounter rates with other individuals which in turn could have implications for the spread of disease, information sharing, or mate choice (Lusseau & Newman 2004; Aplin *et al.* 2012; Adelman *et al.* 2015; Oh & Badyaev 2010). Variation in encounter rates may also create non-randomness in the interactions with other individuals and hence structure in social networks with respect to behavioural phenotype. Social network theory provides a framework for characterizing social structure across scales from the individual level up to population level (Krause *et al.* 2007), and can capture some of the complexity of social interaction patterns not possible with standard measures of sociality such as group size (Wey *et al.* 2008). While there have been several recent studies on the social ecology of tits that apply social network approaches, inferring social associations from the co-occurrence of individuals at feeders (Aplin *et al.* 2013; Aplin *et al.* 2015; Farine *et al.* 2012; Farine *et al.* 2015), few have examined the direct relationship between individual foraging behaviour and social associations (but see Firth *et al.* 2015). This leaves a gap in our knowledge of foraging in a social context. In order to gain a more comprehensive understanding of the causes and consequences of social foraging dynamics, the final goal of this thesis was to investigate the relevance of variation in individual foraging patterns for social phenotype, pair bonds, and social structure.

Summary of principal findings

In the first part of this thesis, I used a principal component analysis (PCA) to collapse a number of variables into a novel measure, establishing an axis of variation in fine-scale temporal foraging patterns which captured the extent to which individuals clustered their visits to feeders within a day, with ‘binge-eaters’ at the high end of the spectrum and ‘grazers’ at the low end. The first principal component (PC1, hereafter referred to as binge-eating) explained 38% of the variation in the daily timing of feeding and was therefore used as an individual measure of daily foraging routine throughout the thesis. Individuals also varied in their usage of the supplemental feeders which I quantified as their daily number of feeder visits. As demonstrated in **Chapter 2**, individuals showed significant repeatability in both behavioural measures, both within- and between-years (*r* ranging between 0.42 and 0.60). These estimates fit within the range of repeatabilities reported for a personality trait in great tits (0.27-0.66; Dingemanse *et al.* 2002; Quinn *et al.* 2009). An analysis of binge-eating in relation to intrinsic factors revealed dominance-related differences between individuals, with dominant classes of individual tending to binge-eat more than subordinates. The distance between the feeder and an individual's subsequent breeding territory also played a role, moderating the effects of age and sex, so that dominants only binged more than subordinates when their territories were not close to their feeder. Moreover, an increase in distance between feeder and territory decreased the daily visit rate.

In **Chapter 2** I also examined the effects of competition on daily foraging routines. Competition (feeder traffic) was defined as the daily number of visits by other individuals of either species at the same feeder as the focal individual. Differences between individuals in the overall average competition level experienced did not affect the level of binge-eating. However, individuals did exhibit flexibility in binge-eating; with day-to-day changes in competition, birds binged less on relatively busy days and more on quiet days. Finally, the personality trait 'exploration behaviour in a novel environment', a measure of the proactive-reactive axis and previously linked to competitive ability (Cole & Quinn 2012), did not explain any variation in binge-eating or daily visit rates. Therefore, binge-eating, although a consistent behavioural characteristic of individuals influenced by species, age, sex, and distance to territory, varied with changes in competition level over time.

In **Chapter 3**, I demonstrated how individual foraging patterns shifted with seasonal changes in day length and temperature. By examining daily foraging routines with respect to seasonal changes from autumn to spring, I showed that individuals visited feeders more often during cold days, and arrived at feeders earlier relative to sunrise with decreasing day length. The measure of binge-eating (PC1) that I developed in Chapter 2 was also related to seasonal shifts, with individuals binge-eating more on shorter days. Furthermore, I showed that species, age and sex affected the degree of seasonal shifting of foraging patterns: (i) great tits increased binge-eating more than blue tits as day length decreased, (ii) with decreasing temperature, juvenile great tits increased their daily visit rates more than adult great tits, whereas in blue tits, adults increased their feeder visits more than juveniles, and (iii) males binged more than females, but this difference decreased over the non-breeding season. However, while these factors significantly influenced the shift in behaviour, their effects were relatively minor in comparison to the general seasonal shift of foraging patterns.

In **Chapter 4**, I extended the analysis in Chapter 2 to explicitly test the effect of varying competition levels on foraging patterns. A combination of an experimental manipulation of access to food and natural variation in competitor density was used to examine the relationship between variable competition and individual foraging patterns. Experimentally increasing the level of interference at feeders reduced the level of binge-eating (in great tits but not blue tits), reduced the daily number of visits (in blue tits but not great tits), and increased the proportion of daytime spent at feeders (in both species). With the larger, non-experimental, dataset I further tested for species, age, and sex interactions with background competition levels. This revealed evidence in all three behavioural measures that subordinates (blue tit, juvenile or female) were more negatively affected by an increase in competition, relative to the dominant classes (great tit, adult or male) of individual. Binge-eating and the proportion of day spent at feeders were negatively correlated; it thus seems likely that binge-eating, with the associated reduction in time spent at feeders, is a more efficient foraging strategy than grazing. In particular, juveniles, having corrected for daily visit rate, spent a consistently larger proportion of the day at feeders than adults, independent of competition level; this result is an example of an overall difference in foraging efficiency. Thus, this chapter demonstrated variation in both absolute foraging efficiency and the susceptibility to interference competition, which both contribute to the competitive ability of an individual (Sutherland 1996).

In **Chapter 5**, I used a social network approach to assess how individual great tits' foraging patterns were related to their social interactions at feeders. My results showed that foraging behaviour predicted the strength of conspecific associations, but not the overall number of associates. Great tits that binged generally had weaker social connections than grazers, with the strongest social associations found in grazer-grazer dyads. However, binge-eaters associated more strongly with other binge-eaters than with grazers. This positive assortment (i.e. grazers interacting more with grazers and binge-eaters more with binge-eaters) led to a non-random distribution of individuals over the social network, with consequences for social structure. In the second part of this chapter, I explored the relationship between individual foraging behaviour (level of binge-eating and daily visit rate) and pair bonds. Permutation tests revealed that great tits had feeding strategies more similar to their partner (observed at the same nest box during the following spring) than other birds of the opposite sex visiting the same feeder. However, on days when pair members were observed at different sites, which I hypothesized to be largely pre-partnership, great tits exhibited foraging patterns no more like their subsequent breeding partner than other pre-partnership individuals of the opposite sex, suggesting behavioural convergence rather than assortative mating.

Perspectives

Individual variation in foraging patterns

My novel measure of fine-scale temporal foraging patterns (level of binge-eating) was an improvement on the coarser (often hourly or other set timeframe) measures of foraging behaviour in previous studies, which had suggested steady feeding rates across a day (Bonter *et al.* 2013; Van der Veen 2000; see Chapter 2). Moreover, these studies did not investigate individual variation in temporal foraging patterns. When I did so, I found the level of binge-eating to be repeatable both within and between years, which motivated further investigation of the causes of these consistent individual differences. Variation was observed both between- and within-individuals. Differences between individuals were related to dominance class and moderated by distance to territory, with individuals that clustered their foraging visits the most also tending to be dominant birds that held territories at a greater distance from feeders.

In this study I used species, age and sex class as indicators of dominance rank. It would be possible to produce more detailed individual-level dominance hierarchies by monitoring the outcomes of aggressive encounters between individuals within flocks (Krams 2000; Dingemanse & De Goede 2004; Cole & Quinn 2012). This technique could help to further elucidate the dominance-related patterns in foraging behaviour in future studies. There is also scope for more research on winter territories. In this thesis I suggest that commuting between territories and feeding stations plays a role in shaping individual daily foraging patterns. While there has been much study of these territories during the breeding season, it is not clear how this information relates to their use during winter (Wilkin *et al.* 2006; Gosler, 1993; Perrins 1979). Open questions to investigate in future studies include: How much time do tits spend on their winter territories each day? How often do they return to their territory? How fixed are winter territories? When do juveniles settle in their territories? All of these may contribute to the cost of commuting and thus influence individual foraging strategies.

Theoretical studies of optimal foraging behaviour that account for the risks of starvation and predation often predict a bimodal pattern of feeding across a day when the risk of predation is high enough to favour a depression of feeding rates between morning and evening peaks (McNamara *et al.* 1994; Bednekoff & Houston 1994). It is this reduction in feeding rates during the middle of the day that is assumed to lower the risk of predation in systems where foraging exposes individuals to predators. Therefore, in these models, the risk of starvation is traded-off against the risk of predation: a change in feeding rate will decrease one risk while increasing the other. Bonter *et al.* (2013), using a similar study system to mine, found relatively consistent hourly feeding rates throughout the day (comparable to the pattern of hourly rates reported in this thesis). They suggested that this lack of bimodality demonstrated that the risk of starvation outweighed the risk of predation. However the results in this thesis suggest another possibility –

that individuals can reduce their overall proportion of daytime spent at feeders by clustering their visits into bouts, effectively ‘binge-eating’. This strategy could thus reduce the risk of predation without depressing hourly feeding rates in the middle of the day. Thus, if the birds studied in Bonter *et al.* (2013) exhibited similar individual variation in foraging behaviour, I would argue that predation risk may still be a strong determinant of individual foraging routines. Ideally, these data would be matched with information about hunting behaviour in their main predator, which in this system is the sparrowhawk during winter (Perrins 1979). Yet while sparrowhawk activity rates tend to be higher in the morning than afternoon during winter, with some evidence of bimodal activity in first year birds (Newton 1986; see Fig. 1), little detail is known about predation events in this system (Perrins 1979). The tracking of wild sparrowhawks would be worthwhile, particularly if incorporated into this study system so that attack and success rates of hunts could be estimated.

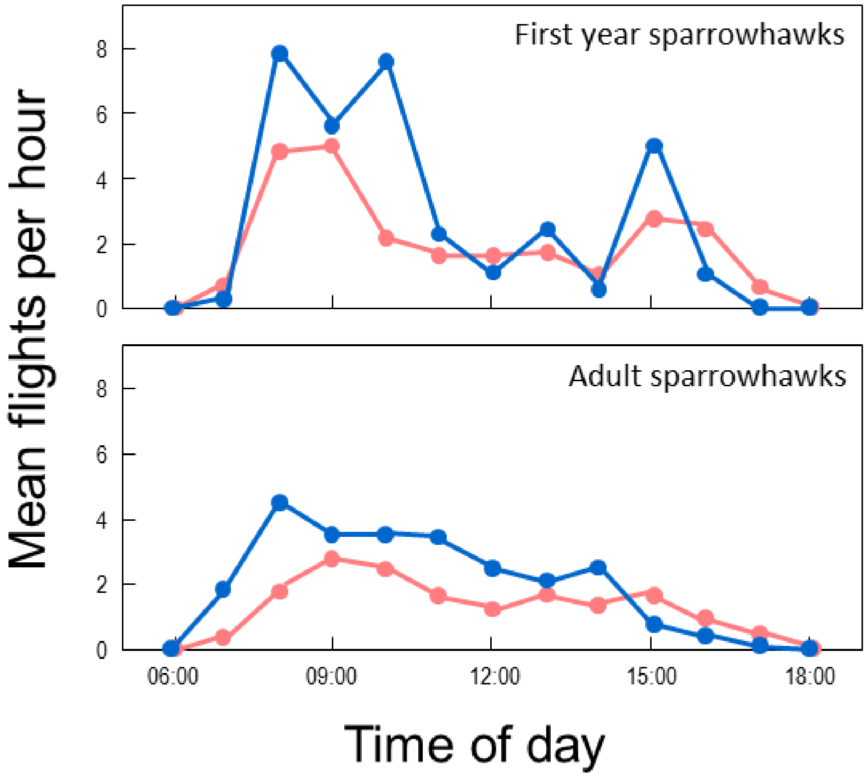


Fig. 1. Activity of radio-tagged sparrowhawks during winter, as indicated by mean frequency of flights, at different times of day. A flight is defined as a move > 50m, and up to 19 such moves were observed per hour. Inactive periods, which lasted up to 5 hours, were included in the calculations. ●: male; ●: female (adapted from Newton 1986).

As demonstrated in this thesis, individuals can differ consistently in their behavioural responses to different conditions. Furthermore, relatively recent studies have shown that these consistent individual differences can be correlated across contexts, often termed personality (Réale *et al.* 2007). There is now evidence that personality traits are linked to life-history traits; for instance, personality score can reflect a trade-off between productivity and survival (Biro & Stamps 2008, Quinn *et al.* 2012). The proactive-reactive personality axis is a commonly used measure, with proactive individuals expected to prioritize productivity over survival. Given that binge-eating appears to increases productivity, it could be predicted that this behavioural measure would be positively correlated with proactivity. In my dataset, however, I found no significant relationship between binge eating and ‘exploration behaviour of a novel environment’ - a commonly used proxy of proactivity. However, given that binge-eating is negatively related to variation in the proportion of time spent at feeders (i.e. binge-eaters spent less time at feeders than grazers), I argue that this difference in foraging time makes binge-eating a safer strategy than grazing as well as a more productive one. Therefore, binge-eating does not reflect a trade-off between productivity and safety, and this could explain the independence of personality and foraging strategy measures in this thesis. However, if it is indeed the case that binge-eating is both more productive and safer than grazing, this should be reflected in a corresponding difference in fitness outcomes. For example, it has been shown in gulls that alternative foraging strategies explain a significant amount of variation in survival, recruitment and reproductive success (Annett & Pierotti 1999). Future studies should investigate the potential relationship between foraging strategies and fitness in tits.

Flexibility of foraging routines

While the results in this thesis demonstrate considerable consistent differences between individuals, individuals also showed some plasticity in their level of binge-eating, varying their foraging behaviour with levels of local competition (feeder traffic). In addition to changes in the number of competitors, individuals were also exposed to a range of environmental conditions that varied seasonally. These exert strong pressures and constraints on foraging behaviour and all individuals shifted their foraging routines accordingly. Interestingly, there were generally good beechmast crops in the first and third winters of this study, while the crop was poor in the second winter. Tits are known to visit supplemental feeders more when natural food sources are scarce (Perrins 1979). Supporting this trend, I found that individuals typically made five more feeder visits per day in the year of the failed beechmast crop than in either of the good crop years. The level of binge-eating, however, did not differ between years.

In this study I have assumed that the majority of feeder visits by individuals result in the consumption of one seed. However, from observing birds at feeders it is apparent that birds sometimes have failed visits, when they do not obtain a seed. This is very likely related to dominance status, with subordinates being supplanted before they can collect a seed more often than dominants, so that the success rate will not be equal among all individuals. Personality has also been shown to have an effect on the success rate per visit, with bold individuals taking seeds quickly and successfully more than shy individuals which may hesitate more at feeders through vigilance (Cole & Quinn 2012). Future work could explore variation in success rates of different classes of bird (species, age, sex or personality type) under different conditions (seasonal, competitor density, distance to cover), which would give a more comprehensive view of foraging efficiency and response to changing environments.

Another potential strategy for coping with the negative effects of competition on foraging behaviour would be to move to another food patch. In this study, feeding stations were spaced 250m apart and 75% of individuals that visited feeders did not move between sites on a given date (those that did move within-day were excluded from analyses for that date). However, the study of movements between food patches would be particularly beneficial, especially if the distance between patches was reduced and/or depletion of resources incorporated into the protocol. For example, a recent study on the same population explored how personality influenced how individuals moved between patches that were spaced 50m apart and showed that proactive birds act as leaders to new patches while reactive birds follow (Aplin *et al.* 2014). While in this study I have investigated the effect of interference competition with continuous input of food, the depletion of resources over time is a ubiquitous process in nature (Sutherland 1996). Patch depletion, with the resultant decrease in foraging efficiency and with density-dependent exploitation, will add to the cost of interference competition and increase the likelihood of moving to a new patch.

Costs and benefits of group foraging

In tits, social dominance affects priority access to food, with dominant individuals able to supplant subordinates during foraging (Perrins 1979). The results presented in this study indicate that subordinate classes of bird (blue tits, juveniles and females) were more susceptible to the effects of competition than dominants (great tits, adults and males). This suggests that the cost of flocking increased more for subordinates with increasing group size than for dominants. While an increase in group size should benefit all members through reduced individual vigilance rates (Sutherland 1996), a different cost-benefit ratio between dominance ranks could result in group size having opposing effects on dominants and subordinates. That is, there is potential for subordinates to be negatively affected by increasing group size while dominants are positively affected. This was demonstrated in the comparison of great tits and blue tits in the proportion of day spent at feeders; this measure of foraging efficiency improved (i.e. decreased) in great tits but was hindered (i.e. increased) in blue tits. In this study, I did not obtain a direct measure of absolute foraging efficiency (foraging in the absence of competitors) but model predictions suggest that at zero feeder traffic, there were little or no differences between dominants and subordinates within species. Thus, susceptibility to interference appears to explain more variation in competitive ability than overall foraging efficiency in this study system. This is in contrast to the findings of a study on oystercatchers which showed that the absolute foraging efficiency of an individual is the main determinant of competitive ability (Caldow *et al.* 1999).

In group foragers, dominant individuals are able to monopolize the safest spatial positions within a group – these are typically within the centre (e.g. Barta *et al.* 1997). A potential test of this process in the tit study system could be to use a temporally central ‘position’ within a flocking event (either defined using a sliding-window approach or a Gaussian mixture model approach) as a proxy for a safe position. It has been demonstrated that subordinates tend to return to feeders first after the presence of a predator (De Laet 1985; Hegner 1985). Since I have shown that subordinates tend to spend more time at feeders than dominants, it is also possible that they might be the last to leave as the flock moves away from a feeder, leaving the dominants to visit feeders more centrally within a flocking event. This would add to our understanding of the variation among individuals in the costs and benefits of foraging in groups and how they cope with the pressure of competition. Furthermore, the introduction of selective feeders, where access to food is determined by the identity of the individual, would allow the manipulation of group size and composition as an avenue for further research.

Foraging behaviour in the context of social networks

In this thesis, I demonstrated links between individual foraging patterns and the social organisation that occurs at feeders among great tits. Foraging strategy predicted the strength of an individual’s social associations, with grazers having stronger social bonds. Individuals were also positively assorted in the social network by foraging strategy; that is, binge-eaters associated more with other binge-eaters and grazers more with grazers. However, since the level of binge-eating was related to degree centrality, and the social network was also (and more strongly) assorted by degree, it remains to be tested whether there is any assortment by foraging pattern in addition to the strong assortment by degree. The same issue holds for a similar study on the links between personality and social organisation (Aplin *et al.* 2013). Despite this uncertainty about the causes of network assortment, I have established links between foraging strategies and association patterns. This suggests that such individual-level differences in behaviour can have emergent properties at the social level, both in social behaviour and in population structure itself.

I further explored the similarity of foraging patterns (level of binge-eating) between pairs of great tits that bred together in the subsequent spring. These pairs did follow a foraging strategy more like their partner than their non-partners, but only on dates when they were recorded at the same feeding station. I assumed that most instances when pair members were observed at different sites happened before partnership formation, given that prior knowledge of this system suggests that pairs remain very closely associated after they have formed (Hinde 1952; Colquhoun 1942; Culina 2014). I then showed that pair members did not binge-eat more like their future partners than other potential partners. These results suggest that when great tits form pair bonds, their feeding patterns converge to become more similar. Furthermore, there was no evidence of foraging strategy compatibility limiting mate choice. The convergence of foraging strategies in partners indicates that social bonds can feed back to influence foraging behaviour (also see Firth *et al.* 2015). Yet the estimate of pre-partnership dates is quite crude in this study. An improvement would be to track the association rates of subsequent pairs over the winter and identify either the point in time at which association rates increase (pair formation) or to define a threshold value of association rates, above which a pair can be assumed to be partnered.

While it would be better to quantify social interactions in an independent context (i.e. not at feeders) for comparison with feeding patterns, a recent study has demonstrated that co-occurrences at feeders also predict social associations in non-feeding contexts (Firth & Sheldon 2015). In a similar vein, this study could be extended to investigate foraging strategies in a different context, such as provisioning behaviour during the breeding season. Even if winter foraging strategies do not relate to provisioning routines, there could be carry over effects of winter strategy for subsequent fitness. For example, if females that binge-eat more in late winter can maintain better body conditions going into the breeding season, they may have better reproductive success. This question remains to be investigated by future research.

Concluding remarks

Recent advances in tagging and automated tracking technology have allowed detailed and continuous monitoring of large numbers of individuals foraging in the wild. This further allows for a detailed examination of fine-scale patterns at different temporal scales. In this thesis I establish a novel measure of individual-level temporal patterns in the foraging behaviour of wild birds. The clustering of feeding behaviour within a day captured a large amount of previously unquantified individual variation, revealing alternative foraging strategies that differed at a fine temporal scale. I demonstrated that social dominance, territory location, environmental conditions, and interference competition all explain some of this variation, both between- and within-individuals.

By incorporating a social network approach, I further investigate the links between individual foraging strategies, patterns of social association, social structure and pair bonds. While this work suggests that foraging behaviour has implications for social organisation, it also shows that social bonds can feed back to influence behaviour.

REFERENCES

Adelman, J. S., S. C. Moyers, D. R. Farine and D. M. Hawley (2015). Feeder use predicts both acquisition and transmission of a contagious pathogen in a North American songbird. *Proceedings of the Royal Society B: Biological Sciences* **282**(1815): 20151429.

Alanärä, A., M. D. Burns and N. B. Metcalfe (2001). Intraspecific resource partitioning in brown trout: the temporal distribution of foraging is determined by social rank. *Journal of Animal Ecology* **70**(6): 980-986.

Annett, C. A. and R. Pierotti (1999). Long-term reproductive output in western gulls: consequences of alternate tactics in diet choice. *Ecology* **80**(1): 288-297.

Aplin, L. M., D. R. Farine, R. P. Mann and B. C. Sheldon (2014). Individual-level personality influences social foraging and collective behaviour in wild birds. *Proceedings of the Royal Society B: Biological Sciences* **281**(1789): 20141016.

Aplin, L. M., D. R. Farine, J. Morand-Ferron, E. F. Cole, A. Cockburn and B. C. Sheldon (2013). Individual personalities predict social behaviour in wild networks of great tits (*Parus major*). *Ecology Letters* **16**(11): 1365-1372.

Aplin, L. M., D. R. Farine, J. Morand-Ferron and B. C. Sheldon (2012). Social networks predict patch discovery in a wild population of songbirds. *Proceedings of the Royal Society B: Biological Sciences* **279**(1745): 4199-4205.

Aplin, L. M., J. A. Firth, D. R. Farine, B. Voelkl, R. A. Crates, A. Culina, C. J. Garroway, C. A. Hinde, L. R. Kidd, I. Psorakis, N. D. Milligan, R. Radersma, B. L. Verhelst and B. C. Sheldon (2015). Consistent individual differences in the social phenotypes of wild great tits, *Parus major*. *Animal Behaviour* **108**: 117-127.

Barta, Z., R. Flynn and L. A. Giraldeau (1997). Geometry for a selfish foraging group: a genetic algorithm approach. *Proceedings of the Royal Society B-Biological Sciences* **264**(1385): 1233-1238.

Bednekoff, P. A. and A. I. Houston (1994). Avian daily foraging patterns: effects of digestive constraints and variability. *Evolutionary Ecology* **8**(1): 36-52.

Biro, P. A. and J. A. Stamps (2008). Are animal personality traits linked to life-history productivity? *Trends in Ecology & Evolution* **23**(7): 361-368.

Bonter, D. N. and E. S. Bridge (2011). Applications of radio frequency identification (RFID) in ornithological research: a review. *Journal of Field Ornithology* **82**(1): 1-10.

Bonter, D. N., B. Zuckerberg, C. W. Sedgwick and W. M. Hochachka (2013). Daily foraging patterns in free-living birds: exploring the predation-starvation trade-off. *Proceedings of the Royal Society B: Biological Sciences* **280**(1760): 20123087.

Caldow, R. W. G., J. D. Goss-Custard, R. A. Stillman, S. E. A. L. D. Durell, R. Swinfen and T. Bregnballe (1999). Individual variation in the competitive ability of interference-prone foragers: the relative importance of foraging efficiency and susceptibility to interference. *Journal of Animal Ecology* **68**(5): 869-878.

Cole, E. F. and J. L. Quinn (2012). Personality and problem-solving performance explain competitive ability in the wild. *Proceedings of the Royal Society B: Biological Sciences* **279**(1731): 1168-1175.

Colquhoun, M. K. (1942). Notes on the social behaviour of blue tits. *British Birds* **35**: 234-240.

Cope, D. R. (2006). Variation in daily and seasonal foraging routines of non-breeding barnacle geese (*Branta leucopsis*): working harder does not overcome environmental constraints. *Journal of Zoology* **260**(1): 65-71.

Culina, A. (2014). With or without you – pair fidelity and divorce in monogamous birds. *DPhil thesis, University of Oxford*. Oxford, UK.

De Laet, J. F. (1985). Dominance and anti-predator behavior of great tits *Parus major*: a field study. *Ibis* **127**(3): 372-377.

Dingemanse, N. J., C. Both, P. J. Drent, K. Van Oers and A. J. Van Noordwijk (2002). Repeatability and heritability of exploratory behaviour in great tits from the wild. *Animal Behaviour* **64**(6): 929-938.

Dingemanse, N. J. and P. de Goede (2004). The relation between dominance and exploratory behavior is context-dependent in wild great tits. *Behavioral Ecology* **15**(6): 1023-1030.

Dingemanse, N. J. and N. A. Dochtermann (2013). Quantifying individual variation in behaviour: mixed-effect modelling approaches. *Journal of Animal Ecology* **82**(1): 39-54.

Farine, D. R., J. A. Firth, L. M. Aplin, R. A. Crates, A. Culina, C. J. Garroway, C. A. Hinde, L. R. Kidd, N. D. Milligan, I. Psorakis, R. Radersma, B. L. Verhelst, B. Voelkl and B. C. Sheldon (2015). The role of social and ecological processes in structuring animal populations: a case study from automated tracking of wild birds. *Royal Society Open Science* **2**(4): 150057.

Farine, D. R., C. J. Garroway and B. C. Sheldon (2012). Social network analysis of mixed-species flocks: exploring the structure and evolution of interspecific social behaviour. *Animal Behaviour* **84**(5): 1271-1277.

Firth, J. A., B. Voelkl, D. R. Farine and B. C. Sheldon (2015). Experimental evidence that social relationships determine individual foraging behavior. *Current Biology* **In press**.

Fortin, D., J. M. Fryxell and R. Pilote (2002). The temporal scale of foraging decisions in bison. *Ecology* **83**(4): 970-982.

Gosler, A. (1993). The great tit. London, Hamlyn.

Heath, J. P., H. G. Gilchrist and R. C. Ydenberg (2010). Interactions between rate processes with different timescales explain counterintuitive foraging patterns of arctic wintering eiders. *Proceedings of the Royal Society B: Biological Sciences* **277**(1697): 3179-3186.

Hegner, R. E. (1985). Dominance and anti-predator behavior in blue tits (*Parus caeruleus*). *Animal Behaviour* **33**(3): 762-768.

Hinde, R. A. (1952). The behaviour of the great tit (*Parus major*) and some other related species. *Behaviour (Supplement)* **2**: 1-201.

Houston, A. I. and J. M. McNamara (1993). A theoretical investigation of the fat reserves and mortality levels of small birds in winter. *Ornis Scandinavica* **24**(3): 205-219.

Howie, J. A., B. J. Tolkamp, S. Avendano and I. Kyriazakis (2009). A novel flexible method to split feeding behaviour into bouts. *Applied Animal Behaviour Science* **116**(2-4): 101-109.

Kramer, D. L. and R. L. McLaughlin (2001). The behavioral ecology of intermittent locomotion. *American Zoologist* **41**(2): 137-153.

Krams, I. (2000). Length of feeding day and body weight of great tits in a single- and a two-predator environment. *Behavioral Ecology and Sociobiology* **48**(2): 147-153.

Krause, J., D. P. Croft and R. James (2007). Social network theory in the behavioural sciences: potential applications. *Behavioral Ecology and Sociobiology* **62**(1): 15-27.

Kronfeld-Schor, N. and T. Dayan (2008). Activity patterns of rodents: the physiological ecology of biological rhythms. *Biological Rhythm Research* **39**(3): 193-211.

Lusseau, D. and M. E. J. Newman (2004). Identifying the role that animals play in their social networks. *Proceedings of the Royal Society B: Biological Sciences* **271**: S477-S481.

McNamara, J. M., A. I. Houston and S. L. Lima (1994). Foraging routines of small birds in winter: a theoretical investigation. *Journal of Avian Biology* **25**(4): 287-302.

Newton, I. (1986). The Sparrowhawk. Calton, Poyser.

Oh, K. P. and A. V. Badyaev (2010). Structure of social networks in a passerine bird: consequences for sexual selection and the evolution of mating strategies. *American Naturalist* **176**(3): E80-E89.

Perrins, C. M. (1979). British Tits. London, Collins.

Quinn, J. L., E. F. Cole, J. Bates, R. W. Payne and W. Cresswell (2012). Personality predicts individual responsiveness to the risks of starvation and predation. *Proceedings of the Royal Society B: Biological Sciences* **279**(1735): 1919-1926.

Quinn, J. L., S. C. Patrick, S. Bouwhuis, T. A. Wilkin and B. C. Sheldon (2009). Heterogeneous selection on a heritable temperament trait in a variable environment. *Journal of Animal Ecology* **78**(6): 1203-1215.

Réale, D., D. Garant, M. M. Humphries, P. Bergeron, V. Careau and P. O. Montiglio (2010). Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**(1560): 4051-4063.

Réale, D., S. M. Reader, D. Sol, P. T. McDougall and N. J. Dingemanse (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews* **82**(2): 291-318.

Sutherland, W. J. (1996). From individual behaviour to population ecology. Oxford, Oxford University Press.

Van der Veen, I. T. (2000). Daily routines and predator encounters in yellowhammers *Emberiza citrinella* in the field during winter. *Ibis* **142**(3): 413-420.

Wey, T., D. T. Blumstein, W. Shen and F. Jordán (2008). Social network analysis of animal behaviour: a promising tool for the study of sociality. *Animal Behaviour* **75**(2): 333-344.

Wilkin, T. A., D. Garant, A. G. Gosler and B. C. Sheldon (2006). Density effects on life-history traits in a wild population of the great tit *Parus major*: analyses of long-term data with GIS techniques. *Journal of Animal Ecology* **75**(2): 604-615.

Yunger, J. A., P. L. Meserve and J. R. Gutierrez (2002). Small-mammal foraging behavior: mechanisms for coexistence and implication for population dynamics. *Ecological Monographs* **72**(4): 561-577.

Zhang, Z. Q., J. P. Sanderson and J. P. Nyrop (1992). Foraging time and spatial patterns of predation in experimental populations: a comparative study of three mite predator-prey systems (Acari: Phytoseiidae, Tetranychidae). *Oecologia* **90**(2): 185-196.