

Intra- and interspecific abundance of birds affects detection of novel food sources by Great Tits *Parus major*

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Abstract. Unpredictable resources in seasonal environments may favour innovative individuals that efficiently explore and exploit such resources. We tested the hypothesis that potential intraspecific abundance is a more powerful predictor of detection of a novel food source than interspecific abundance and predation risk. The hypothesis was tested using latency of Great Tits *Parus major* to find bird-feeders in relation to the abundance of Great Tit and other birds, as well as cats recorded close to novel feeders in urban and rural habitats. Data were collected during winter 2013/2014 in eight cities and nearby rural areas across Poland. Generalized linear models, multimodel inference and hierarchical partitioning showed that the probability that Great Tits used a novel birdfeeder was positively correlated both with the number of Great Tits and all other tits combined in the vicinity of feeders. Latency in feeder usage was negatively related to the number of conspecifics, and it was less strongly negatively related to the number of other tits and the abundance of all other species. The effect of the number of other tits interacted with the environment; the number of tits positively correlated with latency in rural areas, while this relationship was negative in urban areas. Latency until arrival at a feeder was shorter for males than for females. The effect of cats at feeders on bird behaviour was statistically non-significant. Thus, latency until arrival at novel birdfeeders was predicted by local population size and abundance of other bird species, but not mammalian predators, and this relationship may be altered by the environment.

Key words: competition, feeders, public information, risk-taking behaviour, social facilitation

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INTRODUCTION

Fluctuating and scarce food in seasonal environments put a premium on individuals that most rapidly locate an unexploited resource. For example, the first individual arriving at a clumped food source is often the winner in terms of time and food quality and quantity (Wallace & Temple 1987, Villén-Pérez et al. 2013, Tryjanowski et al. 2015a). However, previous studies have rarely paid attention to the effects of the density of local foragers on foraging decisions. Locally, increased group size and abundance are prime predictors of the strength of both intra- and interspecific competition, which eventually affects e.g. the number of aggressive interactions between individuals and foraging interference (Wiens 1992, Skórka & Wójcik 2005, Skórka et al. 2006). Competition for food is generally intense in seasonal environ-

ments (Alatalo 1982, Newton 1998) because food requirements exceed resource abundance forcing less competitive individuals to disperse or migrate. Moreover, competition among species affects foraging behaviour with individuals belonging to competitively inferior species and sex and age classes being displaced to less favourable habitats, positions or microhabitats (Alatalo 1982, de Laet 1984).

Exploitation of food resources may also vary among environments. Urban environments may provide more novel but superabundant food than rural environments (Orros & Fellowes 2015, Tryjanowski et al. 2015b, Støstad et al. 2017). Thus, individuals of different species exploiting novel resources in urban environment will be winners. Moreover, higher temperature and its reduced variability make urban environments favourable winter habitats with important consequences for

the survival and the abundance of individuals (Bednekoff & Krebs 1995, Robb et al. 2008, Tryjanowski et al. 2015a). Thus in rural habitats, especially located in more pristine habitats, birds very rarely can find and/or explore novel food sources provided by humans in bird-feeders (Wesołowski 1995).

Resource use also depends on a sex. Males of many species take greater risks than females (Daly & Wilson 1983, Low 2000, Daly et al. 2001). If competition for limiting resources is more intense in one sex than the other, individuals belonging to the more competitive sex (i.e. males) of such species should take greater risks than individuals of the less competitive sex resulting in male-biased mortality mainly from reproductive age onwards (Daly & Wilson 1983, Low 2000, Daly et al. 2001). Such sex-specific differences are common in birds and mammals, and they can be directly predicted from the intensity of competition for limiting resources in the two sexes (Clutton-Brock & Isvaran 2007). Similar patterns apply to interspecific variation in risk taking behaviour among birds (Møller et al. 2011, Tryjanowski et al. 2015a).

Of course, foraging and use of novel food resources equate with risk-taking behaviour since individuals undertaking a decision to forage expose themselves to predators at the expense of reduced vigilance (Turney & Godin 2014). Secondly, eating food makes birds heavier and thus easier to capture by predators (Lima 1986). Thus, discovery and use of novel food resources may interact between potential decisions of competitors and activity of predators. Among the most common predators affecting bird populations are domestic cats *Felis catus*, with a global negative impact on wild birds (Loss et al. 2013), although also Eurasian Sparrowhawk *Accipiter nisus* is often present close to birdfeeders (De Laet 1985, Suhonen 1993). However, it is poorly known how the presence of predators influences risky behaviour in the context of intra- and interspecific competition.

Many species of birds only rarely or never visit birdfeeders, while others are some of the most common birds in cities, and presence of birdfeeders is a very important factor in shaping their numbers (Chamberlain et al. 2005, Robb et al. 2008, Galbraith et al. 2017). One of the most common bird species at feeders in Europe is the Great Tit *Parus major*, which is a model species for research on life history and population ecology (Perrins 1979). This species plays an important role in personality research, particularly for the trait “exploratory tendency”, which describes

movement and behaviour in novel environments (e.g. Dingemanse et al. 2002, Drent et al. 2003, Aplin et al. 2013, Brauze & Zieliński 2016). Thus, it is an excellent species for studying differences in individual decisions, competitive behaviour among individuals, and sexes (Preisner et al. 2017).

Here, we investigated the behaviour of Great Tits, heterospecific birds and a mammal predator at novel feeders in an attempt to quantify patterns of use of novel food resources during winter, when food resources are particularly scarce for many bird species in temperate and arctic climate zones. The first objective of this study was to quantify the effect of the number of Great Tits, the number of individuals of all species of tits and the number of all bird species on (1) the probability that a novel food location is used by birds, and (2) if used, latency until start of foraging at birdfeeders, and, finally, (3) how potential social interactions may modify the use of bird feeders by foraging tits. We considered these predictions in the context of predation risk by domestic cats. If intraspecific competition is important for gaining access to food, we should expect latency until arrival at a novel feeder to decrease with increasing numbers of Great Tits. If interspecific competition is important, we should expect that latency until arrival will decrease with increasing numbers of birds other than Great Tits. The difference in slope between the effects of conspecifics and heterospecifics, as well as partitioning of the variance in these effects, should reflect the difference in relative effects of intraspecific and interspecific competition. Moreover, presence of predators should expand latency independent of social context since all competing individuals belonging to different species are potential prey. The second objective was to compare latency between urban and rural environments. We predicted that in urban environments quick decision-making by competing individuals should be favoured compared to those in rural environments leading to shorter latency. Furthermore, we tested for an interaction between abundance of different species and environment (urban vs. rural) to investigate if strength of potential intra- or interspecific competition differed between environments. The third objective was to test for sex differences in latency, predicting that the sex with greater variance in survival and reproductive prospects (i.e. males) would take less time before arriving at a feeder. We compared the behaviour of birds at feeders with null expectations based on bird census data from the same locations as where

the feeders were located. We are unaware of any studies of birds at feeders taking the composition of the local bird community into account. For example, that was not the case in the extensive study by Chamberlain et al. (2005), who instead compared presence of birds at feeders with abundance during the breeding season many months later. Likewise, there was no such information reported in the review of effects of feeders by Robb et al. (2008). In the present study of feeder use, data on the composition of the community should be taken into account because current behaviour cannot otherwise be interpreted or put into perspective (Farine et al. 2015).

We tested the above-mentioned predictions by using novel feeders positioned in pairs in urban and rural habitats in eight cities in Poland.

METHODS

Data were collected during December 2013–February 2014 in eight cities and nearby rural areas across Poland (Tryjanowski et al. 2015a). In total 138 experimental trials (80 and 58 in rural and urban areas, respectively) were carried out (1–4 hrs after sunrise) to reduce daily variation (Farine & Lang 2013) under favourable weather conditions (no snow nor rain, no strong wind). The feeders were provided mainly in small gardens close to buildings, both in urban in rural habitats, and the site for an experiment was chosen randomly, as a trade-off between a beneficial site for observing foraging birds and access to the property. In each experiment (only one per site to avoid pseudo-replication) birdfeeders contained at the bottom four different kinds of food (containing carbohydrates and lipids): animal fat, sunflower seeds, millet seeds and dry fruits of rowanberry, and among them the first two food categories were chosen by the Great Tit. Birdfeeders of a single model for all trials were used across the entire country, each having the shape of a small house with a roof placed on top of a 1.20 m pole that was dug into the ground (grass/soil) — see details and pictures in Tryjanowski et al. (2016).

Before starting observations of activity at a birdfeeder, we quantified the composition of the local wintering bird community recorded at three points at distances of 100 m from the feeder, located at virtual triangle tips with the birdfeeder in the middle. All birds seen or heard, except highly flying individuals, were recorded using the point count method with 5-minute observations at each

point (Blondel et al. 1970, Vorisek et al. 2010). Birds were counted by well trained observers with long-term practice on research on winter bird assemblages, and data from point counts were summed and used to describe the winter bird community around each of the locations of the feeders.

When a new experimental birdfeeder was provided at a specific site (bird-feeder installation took maximum 15-min), it was observed for 120 minutes from a distance (e. g. from a parked car with good visibility). The observer noted when (to the nearest second) and which bird species first started to explore food in the feeder, and the latency (minutes since the start of the experiment) when this first bird was noted. Immediately when the first bird (any species, not necessarily the Great Tit) used the experimental birdfeeder, or if no birds arrived at the birdfeeders following an experimental trial during 120 min, the experiment was terminated, and the observer with the experimental feeder moved to another place, located at least 2 km from the previous one. Great Tits were sexed from the wider breast stripe and the more intense yellow breast colour of males with binoculars (Svensson 1984), although this was not possible for all individuals. Sample sites were chosen randomly by an observer, and treated as statistically independent observations because the values of spatial autocorrelation were low (Mantel test, $p > 0.05$, $n = 138$).

During the first 15-minutes of feeder observations we recorded the number of cats within a distance of 100 m. It is important to note, that the design of the feeder has been prepared so as to prevent entry by cats and other predatory mammals. This, of course, will not eliminate the effect of predators on birds using the feeder by sitting and entering the feeder area.

Statistical analysis

Our modelling approach consisted of four steps: (1) modelling the probability that birds use a novel feeder in a 120 minute period; (2) modelling latency in use of bird feeders by Great Tits with inclusion of other bird species that arrived first at the feeder; (3) latency in use of birdfeeders by Great Tits when this species was the first to arrive. All these tests included predation risk (presence of cats). Finally, (4) we tested the effect of sex on latency in use of novel birdfeeders by Great Tits.

Modelling the probability that birds use a novel feeder. As in 48 feeders out of 138 we did not record any birds during a 120-min period, we classified feeders as those where Great Tits were

observed (coded as 1) and those where no birds were detected (coded as 0). Then, we analysed the probability that a feeder was used by Great Tits during a 120-min period. Generalized linear models with binomial error variance and logit link function were used. The continuous explanatory variables were the number of Great Tits, the number of individuals of all tit species combined and the total number of individuals of all other bird species combined during bird counts. Categorical explanatory variables were the presence of cats (yes or no) and the environment (urban or rural). We intended to use data on cats as a continuous variable although the maximum number of cats recorded in a plot was 2 (at four feeders; cats were recorded at 33 feeders in total). Continuous variables representing the number of birds were $\log(x+1)$ -transformed in order to minimize effects of detached observations (Quinn & Keough 2002). We also included the following interaction terms: (1) number of Great Tits \times environment type; (2) abundance of all tit species \times environment type; (3) the total abundance of all bird species \times environment type; and (4) presence of cats \times environment type. We used multi-model inference based on the Akaike criterion (Burnham & Anderson 2002) to select models best describing the data. First, we built all model combinations and chose those with ΔAICc smaller than 2 as supporting the data. Model estimates were averaged across the selected range of ΔAICc . As explanatory variables were correlated, we also used hierarchical partitioning (Chevan & Sutherland 1991) to determine the independent contribution of the explanatory continuous variables and presence of cats to the probability of use of a birdfeeder during a 120-min period. Binomial distribution and log-likelihood were used as the goodness-of-fit measures in the analyses. Hierarchical partitioning computes the increase in fit for all models containing a given variable, compared to an equivalent model without that variable. The average improvement in fit across all possible models containing that predictor is then computed. This process results in the estimation of the independent contribution of each explanatory variable (%I), and the joint contribution (%J) resulting from correlation with other variables (MacNally 2002). Following Pont et al. (2005), a predictor with %I larger than $100/N$ (where N is the number of predictors) was considered to have high explanatory power. Therefore, predictors with %I higher than 25% were considered to be important. Moreover, we used randomization tests that yield z-scores to determine

statistical significance of the relative independent contributions based on an upper confidence limit of 0.95 (MacNally 2002).

Modelling latency in use of bird feeders by Great Tits. We used general linear models to investigate factors affecting latency (in minutes) of foraging Great Tits. We included three continuous exploratory variables (the same as in the above model) and three categorical variables (presence of cats, environment type and a variable “sequence” denoting if the Great Tit was the first species at the feeder (coded as 1) or not (coded as 0)). We also included the following interaction terms: (1) number of Great Tits \times environment type; (2) abundance of all tit species \times environment type; (3) the total abundance of all bird species \times environment type; and (4) presence of cats \times environment type. Multi-model inference based on the Akaike criterion and model averaging (Burnham & Anderson 2002) were used to select models best describing data in the same way as in the generalized linear model described above. Furthermore, analogously to the former analysis hierarchical partitioning was used (Chevan & Sutherland 1991). However, in this analysis the error distribution was Gaussian and the goodness of fit was R-square (MacNally 2000). In the above model one of the categorical variable was “sequence”: a notation if the Great Tit was a first species arriving at a feeder or not. Theoretically, this variable should account for the situation when other species were first foragers at the feeder and affected foraging decisions of Great Tits. However, the behaviour of Great Tits may vary depending on which species is the first at the feeder. For example, one species, like Great Spotted Woodpecker *Dendrocopos major* or Eurasian Nuthatch *Sitta europaea*, may socially attract Great Tits and reduce latency, while another may deter use of birdfeeders by Great Tits extending latency (Sasvári 1992, Mönkkönen et al. 1996).

However, our sample size did not allow for such species-level analysis. Therefore, to get a better understanding of the factors affecting latency in use of birdfeeders by Great Tits, we performed a similar analysis on the subset of data with only Great Tits as first foragers at novel feeders, although the Great Tit was definitely the species most often starting foraging (here: 59 out of 90 cases, see also Tryjanowski et al. 2015a). The model structure was the same as in the former general linear model (excluding the variable „sequence”).

Finally, we used t-test to compare the effect of sex of Great Tits on latency. We only determined sex of 28 individuals out of 90 and thus we could not build a more complex model.

In cases when results from model selection and averaging differed from hierarchical partitioning, the latter method was used as conclusive. Model selection and averaging was performed with the package MuMIn, and hierarchical partitioning was performed using the 'hier.part' package version 1.0-3 available in R statistical package version 3.1.1 (R Development Core Team 2004).

RESULTS

Use of feeders

In total, Great Tits were first birds at feeders in 59 cases. Other species that were first foragers at bird feeders were: Blue Tit *Cyanistes caeruleus* (15 cases), Marsh Tit *Poecile palustris* (5), Eurasian Jay

Garrulus glandarius (5), Greenfinch *Chloris chloris* (1), Robin *Erithacus rubecula* (1), House Sparrow *Passer domesticus* (1), Eurasian Magpie *Pica pica* (1), Eurasian Nuthatch *Sitta europaea* (1) and Common Blackbird *Turdus merula* (1). The mean number of foraging Great Tits at feeders (where this species was recorded during 120 min period of observations) was 5.6 ± 0.3 (min = 1, max = 16). The mean number of all birds and species foraging at bird feeders were 28.7 ± 2.0 SE (min = 0, max = 124) and 6.5 ± 0.3 SE (min = 0, max = 35), respectively.

The three best models explained the probability that a novel birdfeeder was used by Great Tits during a 120 min period (Table 1). They included an effect of number of Great Tits, number of all tits combined and habitat. Model averaging suggested that the single-most important statistically significant effect was the number of tits that positively affected the probability (Table 2, Fig. 1). However, hierarchical partitioning revealed that

Table 1. Best generalized linear models describing use of feeders (whether a feeder was used by Great Tit or not during a 120 min period) and latency between placing food in feeder and observation of first Great Tits. Latency was analyzed in two ways. The first analysis included cases when other species visiting feeders first. The second analysis included only cases when Great Tits were the first species at feeders. The log-likelihood (logLik), Akaike information criterion score (Δ AICc), the difference between the given model and the most parsimonious model (Δ AICc) and the Akaike weight (w) are listed. Explanation of variable codes: Environment — environment type (rural = 0 vs. urban = 1), Cats — presence of domestic cats, and Sequence — dichotomous variable describing whether Great Tit was first species at the feeder or not.

Model	logLik	AICc	Δ AICc	w
<i>Use of feeders</i>				
No. tits	-77.13	158.34	0.00	0.57
No. Great Tits + No. tits	-77.03	160.24	1.90	0.22
No. tits + Environment	-77.04	160.26	1.92	0.22
<i>Latency (full data set)</i>				
No. birds + No. Great Tits	-63.93	136.33	0.00	0.12
No. birds + No. Great Tits + Environment	-62.93	136.57	0.24	0.1
No. birds + No. Great Tits + No. tits + Environment + No. Great Tit \times Environment + No. tits \times Environment	-59.71	137.2	0.87	0.08
No. birds + No. tits	-64.38	137.23	0.90	0.08
No. birds + No. tits + Sequence	-63.27	137.25	0.91	0.07
No. birds + No. Great Tits + Sequence	-63.29	137.3	0.97	0.07
No. birds + No. tits + Environment	-63.29	137.3	0.97	0.07
No. birds + No. Great Tits + Cats + Environment	-62.15	137.32	0.99	0.07
No. birds + No. Great Tits + Cats	-63.41	137.54	1.20	0.06
No. birds + No. tits + Sequence + Environment	-62.37	137.76	1.43	0.06
No. birds + No. Great Tits + No. tits	-63.54	137.79	1.46	0.06
No. birds + No. Great Tits + No. tits + Environment	-62.41	137.83	1.50	0.06
No. birds + No. Great Tits + Sequence + Environment	-62.45	137.92	1.59	0.05
No. birds + No. Great Tits + No. tits + Cats + Environment + No. Great Tits \times Environment + No. tits \times Environment	-58.98	138.21	1.88	0.05
<i>Latency (Great Tits at feeders as first species)</i>				
No. birds + No. Great Tits + Environment	-40.62	92.37	0.00	0.34
No. birds + No. Great Tits	-42.14	93.02	0.65	0.25
No. birds + No. Great Tits + Cats + Environment	-40.17	93.95	1.58	0.15
No. birds + No. tits + Environment	-41.58	94.29	1.93	0.13
No. Great Tits + Environment	-42.79	94.32	1.95	0.13

Table 2. Estimates of function slopes of variables present in the most parsimonious generalized linear models describing the use of feeders and latency between placing food in feeder and observation of first Great Tits. Adjusted standard errors (SE) are presented. Tests of significance of variables are given in the final two columns. For further explanations, see Table 1. * — rural environment set as a reference category equalling zero

Effect	estimate	SE	z	P
<i>Use of feeders</i>				
Intercept	-1.252	0.469	2.672	0.008
No. tits	2.861	0.888	3.223	0.001
No. Great Tits	0.591	1.391	0.425	0.671
Environment*	-0.165	0.398	0.413	0.679
<i>Latency (full data set)</i>				
Intercept	2.325	0.277	8.310	<0.001
No. birds	-0.487	0.181	2.653	0.008
No. Great Tits	-0.585	0.325	1.779	0.075
Environment	-0.253	0.259	0.969	0.333
No. tits	-0.561	0.308	1.801	0.072
No. Great Tits × Environment	-2.381	1.215	1.932	0.053
No. tits × Environment	2.649	1.181	2.210	0.027
Sequence	-0.137	0.114	1.188	0.235
Cats	0.147	0.131	1.103	0.270
<i>Latency (Great Tits at feeders as first species)</i>				
Intercept	2.263	0.347	6.529	<0.001
No. birds	-0.533	0.251	2.122	0.034
No. Great Tits	-0.755	0.327	2.312	0.021
Environment	-0.236	0.139	1.693	0.090
Cats	0.148	0.167	0.891	0.373
No. tits	-0.565	0.273	2.066	0.039

beside the number of all tits also the number of Great Tits had a statistically significant contribution to probability of feeder use (Fig. 2).

Latency

For full data set analysed, the mean latency time was 24.8 ± 2.6 SE minutes (min = 1, max = 112 minutes, n = 90). There were fourteen equally good models explaining latency (Table 1). They included all main effects and interactions between (a) number of Great Tits and environment type and (b) number of all tits and environment type (Table 1). Examination of function slopes and standard errors revealed statistically significant negative effects of number of birds on latency and the interaction between number of tits and environment type (Table 2). The interaction indicated that the increasing number of all tits decreased latency in urban environments, while it increased in rural environments (Fig. 3). Hierarchical partitioning indicated that both number of Great Tits, number of all tits combined and number of individual birds had statistically significant individual contributions to the decrease in latency (Fig. 2).

However, if we only used the data subset with Great Tits as the first species at feeders, the mean latency time for this subset was 21.5 ± 3.2

SE minutes (min = 1, max = 107 minutes, n = 59). The five best models explained variation in latency (Table 1). These models included all main effects but no interaction terms (Table 1). Examination of standard errors indicated that the number of Great Tits, the number of all tits and

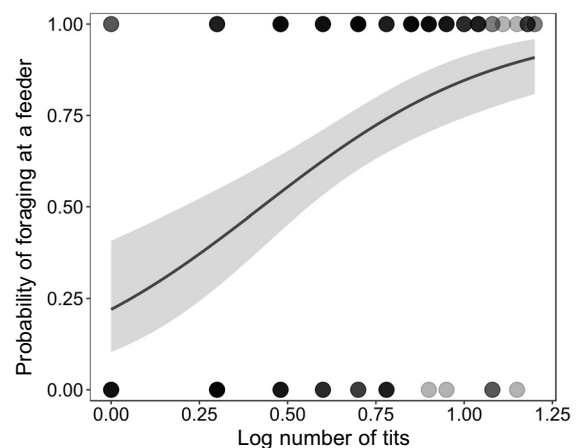


Fig. 1. The relationship between number of tits (log-transformed) and the probability that a bird feeder is used by Great Tits during 120 minutes of observation. Grey bands are standard errors of the fitted function. The darker the colour of data points the more of them are overlapped.

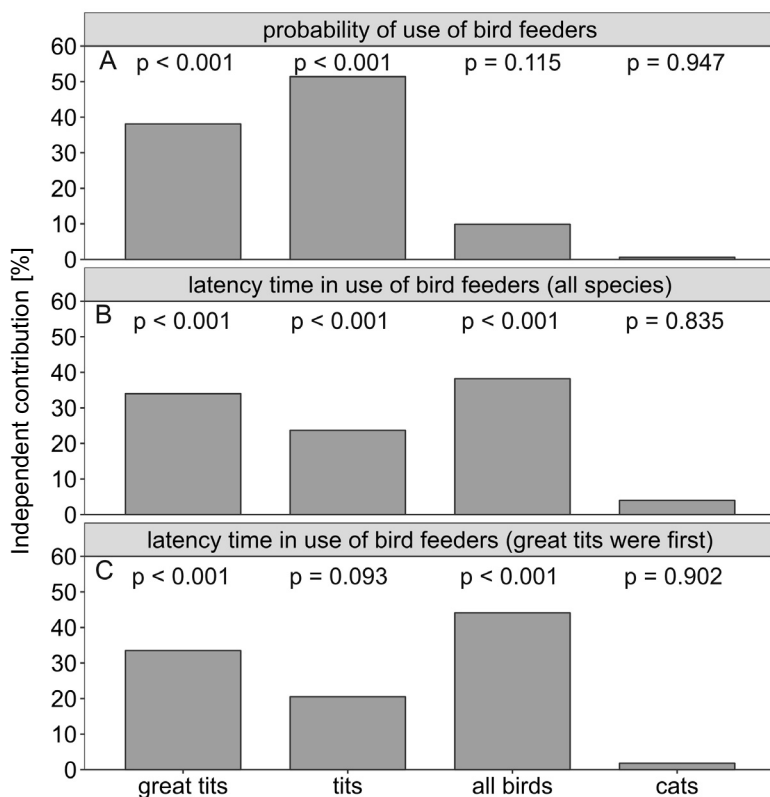


Fig. 2. Decomposition of variance associated with variables describing social context as independent components using the hierarchical partitioning method. The independent contribution of variables to the probability of use of bird feeders (A), and latency between placing food in a feeder and observation of first Great Tits (B, C). Analysis of the latency included cases with other species visiting feeders first (B) or included only cases where Great Tits were the first species at feeders (C). Statistical significance (p) of individual contribution to each variable is given above bars. Explanations: tits — total number of tits other than Great Tits, Great Tits — abundance of Great Tits, all birds — abundance of all other species, cats — presence of cats.

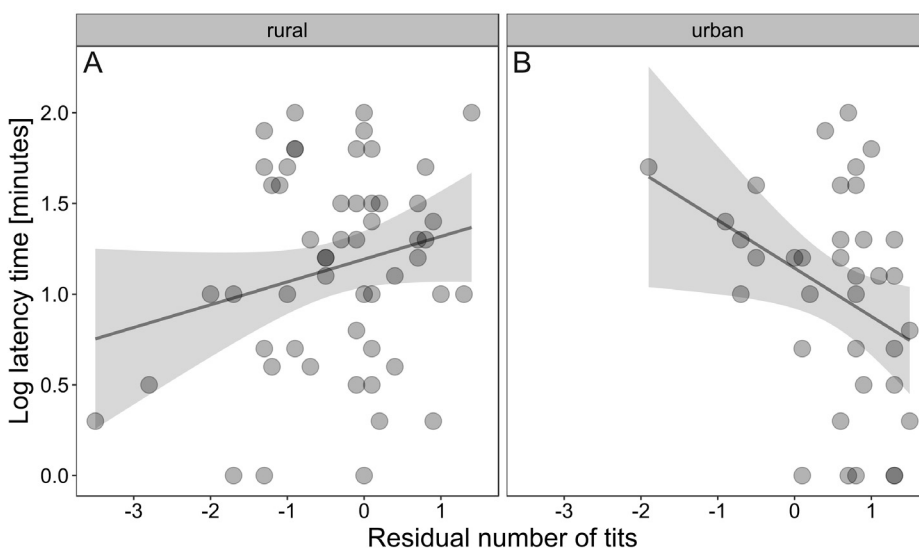


Fig. 3. The relation between number of tits (residual) and latency (both log-transformed) in use of bird feeder in rural (left panel) and urban environments (right panel). The number of tits is residuals not explained by total number of individuals of all birds (the relationship: number of tits = 4.3 + 0.06×number of all birds, $r^2 = 0.10$, $p = 0.030$). The lines are the linear regression lines while the bands are the 95% confidence intervals. The negative and positive values of residuals indicate that the number of tits was smaller and larger than predicted by total number of birds, respectively. For further explanations, see Fig. 1.

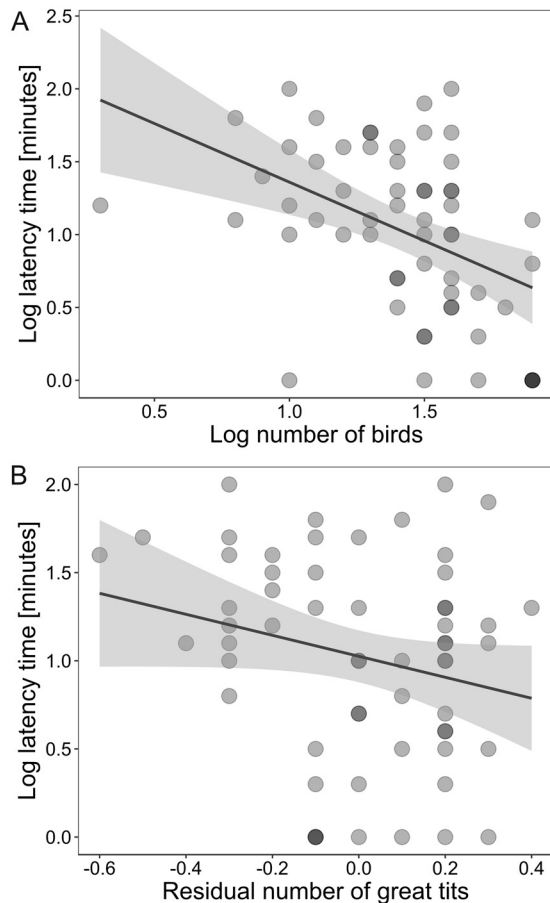


Fig. 4. The relationship between latency and (a) total number of individuals of all bird species and (b) the number of Great Tits during point counts. All data are log transformed. The number of Great Tits is residuals not explained by total number of individuals of all birds (the relationship: number of Great Tits = $4.6 + 0.07 \times \text{number of all birds}$, $r^2 = 0.14$, $p = 0.002$). The lines are the linear regression lines while the bands are the 95% confidence intervals. Negative and positive residuals indicate that the number of Great Tits was smaller and larger than predicted by total number of birds, respectively. For further explanations, see Fig. 1.

the number of all birds had statistically significant negative effects on latency (Fig. 4, Table 2). The function slope was the steepest for number of Great Tits (Table 2). Hierarchical partitioning indicated that the number of Great Tits and the number of all birds had statistically significant individual contributions (Fig. 2). Finally, the individual contribution of number of all tits seemed substantial but was only marginally significant (Fig. 2).

The expected slope of the relationship between log latency and log abundance is -1.000 . For the number of Great Tits the observed slope did not differ significantly from -1.000 ($t_{57} = -1.395$, $p = 0.168$). In contrast, the observed slope for

all birds was significantly less steeper than -1.000 ($t_{57} = -3.068$, $p = 0.0033$).

The effect of sex

Males started foraging at birdfeeders significantly faster than females ($3.41 \text{ minutes} \pm \text{SE} = 0.54$ vs. $5.76 \text{ minutes} \pm \text{SE} = 0.51 \text{ min}$, $t_{57} = 3.015$, $p = 0.004$). This difference amounted to a 40% reduced latency in males compared to females.

DISCUSSION

We investigated the behaviour of birds at novel food sources placed across urban and rural habitats in Poland. Latency to arrival by Great Tits at feeders was strongly predicted by the local abundance of Great Tits and the local abundance of all birds according to point counts conducted in the very same locations as where the novel feeder was placed. There was a stronger effect of conspecifics than heterospecifics on latency. The effect of conspecifics was as expected from their abundance, while that was not the case for the effect of heterospecifics, which had a weaker effect than expected from their abundance. Great Tit males had a much shorter latency to arrival than females, which may be driven by males taking greater risks than female, but other factors like experience, body mass and location in the hierarchy of flocks cannot be excluded. Interestingly, we did not detect any statistically significant effect of predator presence (cats) on the use of novel bird feeders.

Resource limitation is common both during the non-breeding and the breeding season (Newton 1998), resulting in intraspecific and interspecific competition (Alatalo 1982, Dhondt 2011). Here we have provided empirical evidence consistent with intraspecific and interspecific competition by showing that latency until arrival at novel feeders strongly depends on the number of individual Great Tits, but also on the number of individuals of other bird species. The steeper slope for conspecifics than for heterospecifics may imply that intraspecific competition is more intense than interspecific competition, as is usually the case (Dhondt 2011). We consider that early arrival at a feeder implies significant costs because early arrival is traded against assessment of potential risks of predation. Indeed, we have previously shown that flight initiation distance (FID) at feeders was positively correlated with FID elsewhere, implying that different species maintained

their ranking in terms of anti-predator behaviour in the presence and the absence of feeders (Møller et al. 2015). FID was generally shorter in the presence of feeders than in their absence, and the reduction in FID in urban compared to rural habitats was positively correlated with the reduction in FID in the presence of feeders compared to their absence (Møller et al. 2015). Thus, risk-taking behaviour by birds was independently affected by the presence of feeders and by urban habitats.

Male Great Tits had surprisingly short latency until arrival compared with females with the average being 3.4 minutes for males and 5.8 minutes for females. This difference amounted to 40%. An obvious reason for such a sex difference in behaviour is that males are larger and hence need more food than females. Cramp & Perrins (1993) reported mean weight from Norway of 19.1 g in males and 17.9 g in females and values of 18.9 g and 17.7 g from Eastern Germany. This amounts to a 7% difference, which is considerably smaller than the 40% difference in latency documented in the present study. Hence, the effect of body mass could not entirely account for the sex difference in latency. Zahavi et al. (1997) suggested that males may take greater risks than females as a means of showing off to competitors. An example of such risk taking is described for Hooded Crows *Corvus cornix* in which more dominant males take greater risks when approaching a potential predator (Slagsvold 1984, 1985). Because males compete over access to females for reproduction, we should expect greater variance in male behaviour and shorter latency to arrival at feeders than in females. This is indeed the pattern that we found. Finally, males have been shown to be higher in the hierarchy of foraging flocks in an experimental study of Great Tits (Saitou 1979, Sandell & Smith 1991).

Superabundant and novel food resources may release birds from predation pressure since predators (cats) must also find these new locations where birds aggregate in large numbers (Baker et al. 2008). Thus, there is most likely a time lag between finding novel food resources by birds and subsequent behavioral and numerical responses of predators. This may explain the lack of statistically significant effects of cats in our short-term experiments. Furthermore, this suggests that innovative foraging behaviour may possess fitness benefit in terms of lower predation risk as innovative birds may constitute a more unpredictable food resource for predators.

The findings that we have reported here for birdfeeders during winter have implications for future research. Given that feeders provide plenty of reliable food, thereby alleviating food shortage during the part of the year when mortality reaches a peak, there must be fitness consequences for birds from attending feeders. Previous studies have suggested that feeder use advances timing of reproduction and increases clutch size (e.g. Norris 1993, Robb et al. 2008). However, the situation is not clear. A recent study investigating individual-level feeder usage (Crates et al. 2016) found no influence of limited-term feeders on fitness, and moreover in some other studies even a negative impact on fitness was reported (Harrison et al. 2010, Plummer et al. 2013). Therefore, we can ask what are the limits to feeder use? A recent review suggested that contagious disease may severely impact on individuals frequenting feeders (Becker et al. 2015), and even general negative effects on viability. In addition, risk of predation may be a significant cost of feeder use in the long term when predators learn about the whereabouts of feeders (Møller 1988, Suhonen 1993, Tvardíková & Fuchs 2011, 2012).

In conclusion, we have shown that exploitation in terms of feeder use is consistent with expectations for intraspecific and interspecific competition and also that males take much greater risks than females by arriving considerably earlier at birdfeeders than females due to sex differences in variance in fitness. However, these competitive interactions may depend on habitat.

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STRESZCZENIE

[Wewnątrz- i międzygatunkowe zagęszczenia ptaków wpływają na wykrywanie nowych źródeł pokarmu przez bogatki w okresie zimowym] Nieprzewidywalnie pojawiające się zasoby pokarmowe w środowiskach sezonowych powinny sprzyjać innowacyjnym osobnikom, potrafiącym je odnaleźć i wykorzystać. Jednym z takich zasobów jest pokarm wykładany w karmnikach w okresie zimowym, co było przedmiotem wielu wcześniejszych badań, zarówno obserwacyjnych, jak i eksperymentalnych. W niniejszej pracy testowaliśmy pytanie, czy zagęszczenie liczebności bogatki jest silniejszym predyktorem wykrycia nowego źródła pokarmu przez ten gatunek, niż zagęszczenie wszystkich gatunków obecnych w środowisku, jak i potencjalne ryzyko drapieżnictwa. Jako zmienna opisującą wykrywanie nowego źródła pokarmu, potraktowano czas po jakim pierwszy osobnik rozpoczął żerowanie w specjalnie skonstruowanym karmniku eksperymentalnym. Dane zbierano zimą 2013/2014 r. w ośmiu miastach i pobliskich wsiach w całej Polsce. Analizy przeprowadzono wykorzystując uogólnione modele liniowe, hierarchiczną separację wariancji i wnioskowanie oparte na selekcji najlepszych modeli na podstawie kryterium informacyjnego Akaike'a.

Wyniki wskazują, że prawdopodobieństwo rozpoczęcia żerowania przez bogatki w nowym karmniku, było pozytywnie skorelowane zarówno z zagęszczeniem bogatek, jak i wszystkich gatunków sikor łącznie obserwowanych w pobliżu karmników (Tab. 1, 2, Fig. 1, 2, 4). Wpływ liczby innych sikor był zależny od środowiska; liczba sikor dodatkowo korelowała z opóźnieniem wykorzystania karmnika na obszarach wiejskich, natomiast relacja ta była negatywna na terenie miast (Fig. 3). Samce bogatki szybciej rozpoczynały żerowanie w nowo ustawionym karmniku niż samice. Zaskakującym jest brak statystycznie istotnego wpływu kotów na zachowanie ptaków (Tab. 2, Fig. 3). Podsumowując, czas wykrycia nowego źródła pokarmu przez żerujące zimą bogatki jest przewidywany przez lokalne zagęszczenia ptaków (zarówno wewnątrz-, jak i międzygatunkowe), a zależność ta jest modyfikowana przez środowisko, natomiast nie zależy istotnie od zagęszczenia kotów w miejscu lokalizacji karmnika.