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The effect of family size on the ability
of great tit (*Parus major*) parents
to win competitive interactions over
food in the winter period

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INTRODUCTION

Competition is an important selective force shaping the life history of organisms (Svensson and Sheldon 1998, Wilson 2014). One major life history trade-off influenced by competition, is the trade-off between current and future reproduction. In recent work Nicolaus et al. (2012) showed that only under high levels of environmental competition survival cost of reproduction were paid. Through such effects of competition on survival cost of reproduction the optimal reproductive behaviour of individuals may be affected (Nicolaus et al. 2012a). In recent studies, we investigated the hypothesis that family size negatively affects the competitive ability of parents in later life and that under high competition this can result in a fitness cost of reproduction. To test this hypothesis, we conducted family size manipulations within a great tit (*Parus major*) population and induced competition among the parents in the next winter and spring for nest boxes used respectively as a sleeping- or breeding place. We found evidence that in spring, but not in winter, experimental family size negatively affected the ability of parents to compete for nest boxes. We thus used the outcome of the competition for nest boxes as a measure of competitive ability. The disadvantage of this method is that the process of competition is not directly observed, winners and losers of competition are identified after competition took place. An alternative more direct method is to observe competitive interactions among individuals over resources (Drent 1983, Drent et al. 1996, Verbeek et al. 1999, Lange and Leimar 2001, Dingemanse and De Goede 2004, Vedder et al. 2008). On the basis of such observations winners and losers of competitive interactions can directly be determined.

Differences in parental competitive ability due to previous reproductive effort may matter the most in competitive interactions over food in winter. Access to winter food can have marked positive effects on the winter survival of birds, suggesting that during winter, competition for food is high (Van Balen 1980, Brittingham and Temple 1988, Perdeck et al. 2000, Robb et al. 2008, but see: Arcese and Smith 1988, Crates et al. 2016). In line with this, Carrascal et al. (1998) found that in winter the number of aggressive displacements between great tits increased in areas with low food abundance and with colder local climate conditions.

Here, within a great tit (*Parus major*) population, we tested the hypothesized negative effect of family size on parental competitive ability in competitive interactions over winter food. We performed family size manipulations during the breeding season in 2013. Subsequently at the beginning of October we created feeding locations throughout the study area to attract birds. Until early February, we measured the effect of experimental family size on the outcome of competitive interactions between manipulated parents and other great tits over winter food at these feeding locations.

Competitive interactions among great tits for food involve attacks, ritualized displays or true fights (termed here as 'direct interactions'; Drent 1983, Lange and Leimar 2001, 2003). In many cases competitive interactions can also be more subtle, with birds avoiding direct interactions with one another, birds may wait nearby the food source until their opponent is finished or birds at the food source may leave (flee) as soon as an oppo-

ment approaches (termed here as ‘indirect interactions’; Kaufmann 1983, Korsten et al. 2007). Drent (1983) stated that it is impossible to establish whether indirect more subtle interactions truly are competitive interactions or whether they may have just occurred by chance. We scored both type of interactions in our observations and tested the effect of family size manipulation on the probability of manipulated parents to win in three datasets, one containing exclusively direct interactions, one containing exclusively indirect interactions and one containing both direct and indirect interactions.

Our primary expectation, based on the hypothesis of Nicolaus et al. (2012), was that parents that raised smaller experimental families would win more often in competitive interactions over winter food. If both indirect and direct interactions are competitive interactions, we expected a similar negative effect of experimental family size on the probability of parents to win. If as Drent (1983) stated indirect interactions occurred by chance, we expected a difference in the effect of experimental family size on the probability of parents to win depending on the interaction type, with a negative effect in the direct interactions and no effect in the indirect interactions.

MATERIALS AND METHODS

Study site and model species

The study was performed in a nest box breeding great tit population in the Lauwersmeer area, the Netherlands (fig. B.1). The nest box population in this area was founded in 1993 and from 2004 onwards it has been divided into 12 study plots consisting of 50 nest boxes each (600 nest boxes in total). The study plots consisted mainly of young deciduous trees (max. 50 years old), shrubs and some conifers, interspersed with open grasslands (fig. B.1).

Family size manipulation

During the breeding season of 2013 all nest boxes were checked on a weekly basis. As soon as eggs were detected to be incubated (warm uncovered eggs) we could calculate the expected hatching date (assuming one egg a day was laid and incubation starts after laying the last egg and takes around 12 days, de Heij et al. 2006). Two days before the expected hatching date we checked the nest to determine if it hatched, if not hatched yet we checked the nest daily until it did. If during one of the nest box checks the female was present breeding on the eggs we identified her, based on existing identification rings if possible (one aluminium ring with unique inscription and three plastic colour rings).

When the young in the nest were 5 days old, we again visited the nest boxes to weigh the whole brood and count all nestlings present. Using this information, we matched sets of three nests with a similar number of nestlings, similar clutch size and similar average nestling weight (hereafter called ‘trios’). Within these trios of nests we performed family size manipulations when the nestlings were 6 days old. The treatment of each nest and the nestlings to be exchanged were randomly assigned. One nest was enlarged in size by adding three nestlings and one nest was reduced in size by removing three nestlings. The

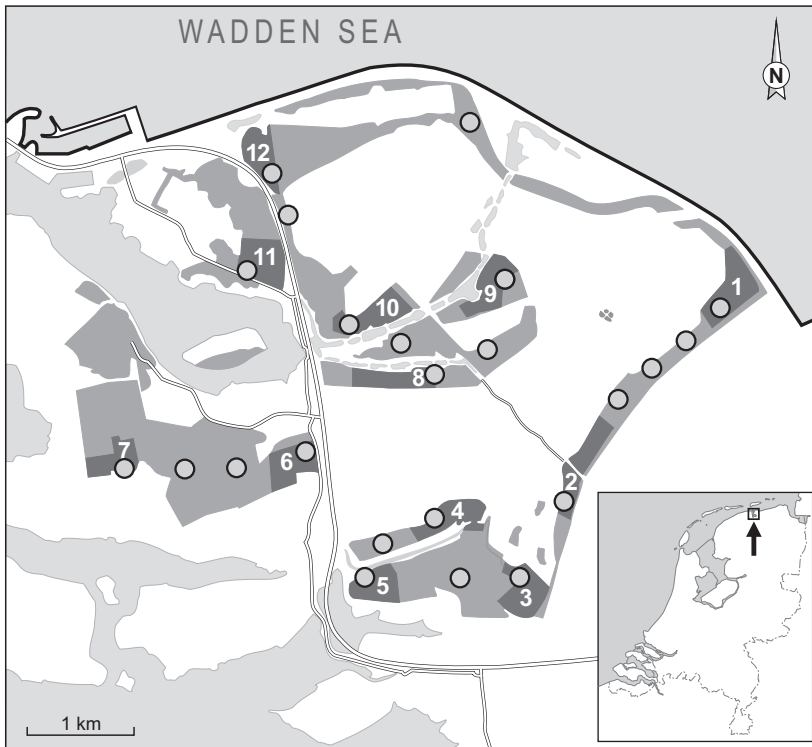


Figure B.1: Map of the study area with the 12 study plots indicated in black. Each plot consisted of 50 nest boxes. The grey circles with the black outline depict the locations of the 23 feeders. Dark grey areas are woodlots without any nest boxes. The light grey area represents the Lauwersmeer lake (on the left side of the map) and the Wadden sea (at the top of the map). The white areas are non-woody surroundings, mostly consisting of grass or agricultural lands. Near the top left corner of plot 11 and the top right corner of plot 7 respectively two villages were located.

control nest was not changed in size but four nestlings were exchanged with respectively two nestlings of the reduced brood and two nestlings of the enlarged brood. In some matched trios of nests with low original brood sizes ($N = 4$ trios), we exchanged two nestlings instead of three, to prevent brood desertion when the brood becomes too small (Verboven and Tinbergen 2002). In total over the breeding season 75 broods were manipulated, consisting of 25 broods of each manipulation group (for further details see: Fokkema et al. 2016).

Identifying the parents and providing them with a transponder ring

The day after family size manipulation we attempted to catch both parents using spring traps and identify them based on their existing ring combination (see above). If not successful a second attempt was made two days later. If this failed we attempted to identify the parents using binoculars around the nest box based on their colour ring combination.

For most parents, when caught, we altered their colour ring combination slightly and replaced one plastic colour ring by a transponder ring (EM4102 bird PIT tag 2.6mm, manufactured by: IB technology, Eccel Technology Limited). If not yet ringed we provided the parents with a set of identification rings and a transponder ring. In total 138 parents (of the 150 manipulated parents) were provided with a transponder ring (8 were not caught and 4 were accidentally not transponder ringed when caught). The transponder ring allowed us to measure 1) the number of feeding visits in relation to family size manipulation and 2) to identify manipulated parents that made use of supplementary food at our feeding stations in winter (see below). The number of feeding visits indeed increased with family size manipulation (see also appendix chapter 2).

Identification of the opponents

To be able to identify local competitors of the manipulated parents, we attempted to also catch all non-manipulated parents in the breeding season 2013 and provide them with a unique set of colour rings if not yet ringed (one aluminium and three plastic colour rings). Further we also provided all offspring from nest boxes (from both manipulated and not manipulated broods) with a set of identification rings.

Besides the local breeding birds and their offspring, in our study system in the non-breeding season there is an influx of non-ringed great tits (mostly juveniles). To be able to identify these great tits as well, we performed two roost checks in December. The first roost check was conducted in the evening of the 9th and 10th of December and the second roost check in the evening of the 17th and the 18th of December. During such checks, roosting birds were taken from the nest box and if not yet ringed, provided with a unique colour ring combination. Some of the manipulated parents encountered in the roost checks, which had received a transponder ring in 2013, had developed injuries (see chapter 2 for more details). These parents were treated by removing the transponder ring. Non-injured birds with a transponder were treated by removing the colour ring from the same leg as the transponder ring. We made sure that birds were still uniquely identifiable (only some birds that were resident in study plots far apart were allowed the same colour ring combination).

Feeding locations

During autumn (early October 2013) 23 feeding locations, as used in earlier work (Radersma 2011), were re-created at approximately the same locations throughout the study area both inside and outside the study plots (fig. B.1). The distance between feeding locations was approximately 600 meters. We distributed the feeding locations in a way that birds could potentially visit multiple feeders in their local area. This would 1) help to estimate potential effects of distance to the territory on the dominance of birds at feeding stations (Dingemanse and De Goede 2004, Korsten et al. 2007) and 2) potentially promote the number of interactions we could record between manipulated parents and others at different locations.

At each location we placed a feeder providing striped sunflower seeds and a feeding table with a net with peanuts attached to the centre of the table. To attract birds, per loca-

tion also three extra fat balls were provided attached to branches of surrounding trees or bushes. Food was replenished approximately once a week. Feeders were placed if possible near shrubs to facilitate cover from predators for the great tits to make the feeders more attractive for the birds.

Monitoring feeder visits

To measure which feeding locations were visited we used transponder readers (type: LID665, version V804, manufactured by Dorset identification b.v.). Feeders were made of plastic drain pipes and at the lowest end of the drain pipe a feeding compartment was fitted. Around the entrance of this compartment the antenna of the transponder reader was placed. We had 12 readers for 23 feeder locations at our disposal. We therefore used a rotation scheme to quantify the number of manipulated parents visiting the different locations. The transponder readers were equipped to read the code emitted by the transponder ring earlier provided to the manipulated parents. The data on feeding visits to the feeders by the manipulated parents collected using the readers were downloaded using a laptop with LID 650/665/1260 V804 software (Dorset Identification b.v). Using this data we allocated our observation effort to the feeding locations by concentrating at those feeders where more manipulated parents were recorded (see also below).

Observations of competitive interactions

Based on the visitation rate to the feeders we allocated no observation sessions on competitive interactions between great tits to 3 locations, 1–2 observation sessions to 11 locations and between 3–11 observation sessions to 9 locations in the period from the beginning of November 2013 until the beginning of February 2014. We worked with a team of three observers until midwinter and two observers after midwinter (1 observer per location). In total we performed 86 observations sessions, 79 of 3 hours and 7 of 2 hours).

The observation protocol was as follows. Before an observation session at a feeding location was started, all food at the feeding location was removed, except a single peanut bag placed at the centre of the feeding table. An extra nylon mesh bag was added around the peanut bag to make it more difficult for the birds to remove food and fly away, thereby increasing the number of interactions on the feeding table. Each table was observed using a telescope (20×60) from a movable observation hide (Stealth gear, high altitude) placed approximately 7 meters away from the feeding table. Voice recorders (Olympus VN-711PC and Philips model DVT1100) were used during the observations to record the competitive interactions. When an interaction took place between two individuals it was scored, when possible, which individual great tit won (gained/maintained access to the food) and which great tit lost (lost access to the food/did not gain access to the food). All interactions were at least one of the opponents could be identified based on its colour ring combination were recorded. We also scored the type of behaviour involved in the competitive interaction. Competitive interactions among great tits for food involve direct interactions (display, attacks or fights) or indirect interactions (waiting or fleeing for an opponent). We scored both type of interactions in our observations and analysed the direct and indirect interactions separately in our analyses.

Analyses

The effect of family size manipulation may differ according to the interaction type (see end of introduction for expectations). To test whether family size manipulation had a negative effect on the probability of parents to win competitive interactions over winter food we therefore used two datasets that distinguish between interaction types. One dataset contained exclusively direct interactions and one exclusively indirect interactions.

The dataset containing only direct interactions consisted of 445 interactions involving 28 manipulated parents (8 R, 9 C, 11 E). The dataset containing only indirect interactions consisted of 484 interactions involving 30 manipulated parents (9 R, 9 C, 12 E). In both datasets we only included manipulated parents which we had at least 5 times visually identified in an interaction. We did not include interactions of manipulated parents with other parents of the same manipulation category as we were interested in the difference in the performance of parents of the manipulation groups relative to others.

In most of the recorded interactions manipulated males were involved (382 in the direct interactions; 413 in the indirect interactions), whereas manipulated females were far less often observed in the interactions. In addition in interactions where the opponent could be identified (351 interactions in the direct interactions, 412 in the indirect interactions), most interactions were between manipulated parents and juveniles (279 interactions in the direct interactions, 330 in the indirect interactions).

We analysed the datasets of both interaction types separately and combined. The analysis was done using R (version 3.3.1, R Core Team 2016). We used generalized linear mixed models with a Binomial error structure. We included an individual identification number for the manipulated parents and an identification number for the observer as random effects in the model to correct for non-independence.

To explain the probability of winning a conflict we included as explanatory variables, apart from family size manipulation (as a continuous variable), a factor coding for the sex of the parent, the natural logarithm of the distance between the feeding station and the parents previous breeding location (nest box) (as shown to matter by: Dingemanse and De Goede 2004, Korsten et al. 2007) and the period in which the interactions were observed (before midwinter: Nov–Dec or after midwinter: Jan–Feb). We included the period because previous research has shown that effects of family size manipulation on the occurrence of survival cost of reproduction under competition occurred only after midwinter (Nicolaus et al. 2012a). In the combined dataset for both interaction types we included interaction type as an explanatory variable (direct or indirect).

Model selection was based on likelihood ratio tests using a backwards elimination procedure. We first eliminated the interactions between family size manipulation and the predictor variables if possible. Next we tested whether family size manipulation, sex of the parent, period, distance or the type of interaction (in the combined dataset) could be eliminated by order of significance.

RESULTS

The effect of experimental family size on the probability of parents to win an interaction over winter food

In the dataset containing direct interactions only, the effect of family size manipulation significantly differed between the observation periods (table B.1). When controlled for effects of sex of the parent, experimental family size had a negative effect on the probability of a parent to win a competitive interaction after midwinter, while before midwinter no clear effect existed (table B.1, fig. B.2). We found no evidence that the effect of family size manipulation differed between the sexes. The probability to win a direct interaction did not differ with the distance of parents to their former breeding box, also not in interaction with family size.

Based on the dataset containing indirect interactions only, controlled for an effect of sex of the parent (higher probability of males to win) we found a trend that family size manipulation positively affected the probability of parents to win in indirect interactions (intercept: -1.83 ± 0.56 , family size manipulation: $\beta = 0.20 \pm 0.11$, $\chi^2_{d.f.1} = 2.92$, $P = 0.087$). The effect of family size manipulation did not differ depending on the time period, the sex of the parent nor the distance to the parent's territory. Time period or distance to the parent's territory also had no main effect.

In the combined dataset including both direct and indirect interactions we found that the effect of family size manipulation on the probability to win significantly differed between the types of interaction. For the direct interactions a stronger negative effect of

Table B.1: Outcome of the generalized linear mixed effect models fitted to a dataset consisting of direct competitive interactions to describe the effect of family size manipulation on the probability of parents to win in the observed competitive interactions for winter food. Corrected for effects of sex of the parent, we found a significant difference in the effect of family size manipulation on the probability of parents to win in competitive interactions with others in the observation period before and after midwinter. The variance explained by the random effect individual id was 0.83 and the variance explained by the random effect observer ID was 0.04.

Variable	Estimate β (\pm SE)	Chi2	d.f.	P
Intercept	-1.10 (0.53)			
Family size manipulation	0.06 (0.13)			
Sex of the parent		6.10	1	< 0.05
Male relative to female	1.45 (0.57)			
Period				
After midwinter relative to before midwinter	0.38 (0.36)			
Family size manipulation x Period		4.10	1	< 0.05
Family size manipulation x Period: after midwinter	-0.25 (0.12)			
Rejected terms:				
Family size manipulation x sex of the parent (d.f.1), Log Distance (d.f.1), Family size manipulation x Log Distance (d.f.1)				

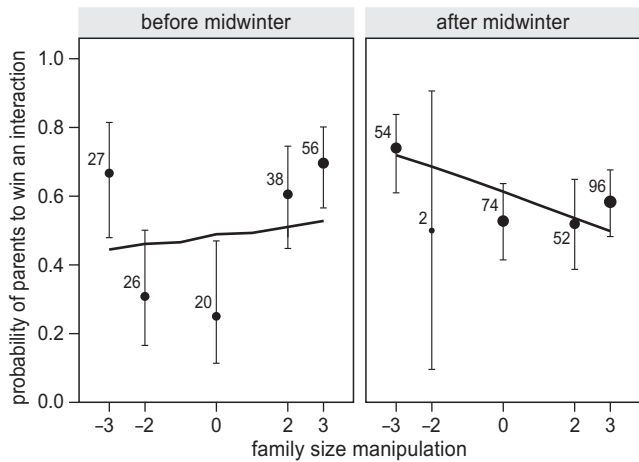


Figure B.2: The effect of family size manipulation before- and after midwinter on the probability of parents to win in competitive interactions for winter food, based on the dataset containing direct interactions only. We found a difference in the effect of family size manipulation before- and after midwinter. Before midwinter there was no clear effect of family size manipulation on the probability of parents to win competitive interactions, while after midwinter we did detect the expected negative effect of family size manipulation. The dots represent the raw averages per manipulation group with 95 percent confidence intervals. Sample size (the number of interactions observed) is depicted by the size of the black dots. The solid line depicts the predicted response calculated on the basis of the final selected model.

family size manipulation on the probability to win existed (intercept: -1.81 ± 0.51 , family size manipulation \times type of interaction: direct relative to indirect: $\beta = -0.23 \pm 0.07$, $\chi^2_{d.f.1} = 10.07$, $P < 0.01$), consistent with the separate analyses.

DISCUSSION

The aim of this study was to test the hypothesis raised by Nicolaus et al. (2012) that family size negatively affects the competitive ability of parents in later life. We focussed our study on competitive interactions over winter food involving great tit parents whose family size had been manipulated the previous breeding season. In our analyses we differentiated between direct competitive interactions in which either display, attacks or fights were involved and indirect interactions in which more subtle interactions as waiting or fleeing while an opponent approaches were involved. We did this because of the claim of Drent (1983) that indirect interactions cannot be used evaluate dominance relations between birds as it cannot be excluded whether such behaviour may just occur by chance. We indeed found a difference in the effect of experimental family size on the probability of parents to win depending on the interaction type. For the direct interactions, after midwinter we found evidence for the expected negative effect of experimental family size on the probability of parents to win. Within indirect interactions the effect tended to be

positive, the latter was unexpected as we hypothesized that if indirect interactions would occur by chance, effects of experimental family size would be absent.

Parents raising smaller experimental families thus waited more often while their opponents had access to the food (the majority of the indirect interactions consisted of 'waiting' interactions) but after midwinter were also the ones who won more often in direct interactions involving display, attacks or fights. It could be that we observed this pattern because parents raising smaller experimental families could, due to their competitive superiority, gain access to the food for longer time periods (e.g. Cole and Quinn 2012). Therefore these parents may have been able to afford to rest more often nearby the feeding table, while being (unjustly) recorded as losers of indirect competitive interactions. Within this scenario, indirect interactions would thus not be a good measure of competitive ability.

If we conclude that the outcome of direct competitive interactions are the best reflection of parents competitive ability, why then did the effect of experimental family size on the probability of parents to win differ before and after midwinter? Nicolaus et al. (2012) showed that survival costs of reproduction in areas with high levels of competition were only paid after midwinter. These authors hypothesized that differences in parental competitive ability due to previous reproductive effort may have played a role in this period. Our results are consistent with this explanation. Especially after midwinter the need for supplementary winter food may have been great thus increasing the motivation for all manipulated parents to compete (Jansson et al. 1981, Andersson and Åhlund 1991, Lemel and Wallin 1993, Renner et al. 2012). After midwinter, under such higher levels of competition, differences in parental competitive ability due to parent's previous reproductive effort may have mattered in determining their probability to win competitive interactions.

Overall, based on the recorded direct interactions, our study shows that after midwinter experimental family size negatively affected the probability of parents to win in direct competitive interactions over winter food. This is consistent with the hypothesis that family size negatively affects the competitive ability of parents in later life. Such negative effects of family size on the competitive ability of parents could provide a causal explanation for the occurrence of fitness cost of reproduction under high level of competition.

