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Family planning under social competition

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Great tits trade off future competitive advantage for current reproduction

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ABSTRACT

Quantifying the fitness costs of reproduction is essential to understand the evolution of reproductive behavior. Recent work shows that increased reproductive investment reduced parental survival in more competitive environments. Here we experimentally test the hypothesis that reproductive investment has a negative effect on the ability of parents to compete for resources in later life. In a nest-box population of Great tits (*Parus major*), we manipulated family size by reducing or enlarging broods with two or three nestlings, relative to a control group, in two years (N = 237 broods). Parental feeding effort was positively related to experimental family size but leveled off for the enlarged broods. In the next breeding season we manipulated the nest box quality in early spring by reducing the depth of 80% of the nest boxes (deeper boxes are safer and preferred). We analyzed parents' probability of obtaining a deep breeding box in relation to their previous year's family size manipulation. We found for both years that increased reproductive investment negatively affected the probability of parents to claim a high quality nest box in the subsequent breeding season. We thus confirm that family size has a negative effect on the future competitive ability of parents. Such carry-over effects are important because they show that selection on individual optimal clutch size will depend on 1) resource abundance and the level of competition in the next breeding season and 2) the reproductive investment of the competitors in the current breeding season because it affects their future competitive ability as well.

INTRODUCTION

An individual's relative current performance is shaped by long term effects of its previous history and experiences (e.g. Beckerman et al. 2002; Oksanen et al. 2012; O'Connor et al. 2014). Such carry-over effects are believed to be mediated by changes in the energetic state of the individual which affect an individual's performance in later life stages (Harrison et al. 2011; O'Connor et al. 2014)

In a recent conceptual paper O'Connor et al. (2014) hypothesized that the fitness costs of reproductive investment can be considered as a carry-over effect. Many studies have shown evidence that reproductive investment has long lasting negative effects on the physiological state of the parents (e.g. reduced immunity (Knowles et al. 2010; Christe et al. 2012), higher energy expenditure (Sanz and Tinbergen 1999), more mass loss (Merilä and Wiggings 1997; Verhulst 1998) or lowered plumage quality (Siefferman and Hill 2005a).

Interestingly, even though effects of reproductive investment on the physiological state of the parent are well established, evidence for resulting carry-over effects on the future fitness of parents is equivocal (avian: Linden and Møller 1989; Dijkstra et al. 1990; Stearns 1992; Golet et al. 1998; Parejo and Danchin 2006; Santos and Nakagawa 2012; mammals: Stearns 1992; Hamel et al. 2010). One reason for this discrepancy is that costs of reproduction may be mediated directly by ecological factors such as predation (Zera and Harshman 2001; Speakman 2008; Alonzo-Alvarez and Velando 2012). For example, studies have shown that parents have a higher probability of being depredated if they invest more into reproduction and that parents adjust their reproductive investment to predation (Magnhagen 1991; Martin et al. 2000; Fontaine and Martin 2006). The level of predation in the environment may thus affect the costs of reproduction.

Next to direct effects of ecological factors, it has been suggested that the interaction between ecological factors and the physiological state of the parent may determine the cost of reproduction (Svensson and Sheldon 1998; Speakman 2008; Nicolaus et al. 2012a; Wilson 2014). One important example of a process where such interactions could play a role are density dependent effects on reproductive traits (avian: Newton 1998; mammals: Fowler 1987; Bonenfant et al. 2009; Oksanen et al. 2012). Several studies have found evidence that parents face higher costs of reproduction at increased population densities (Festa-Bianchet et al. 1998; Oksanen et al. 2007) via a potential increased level of competition for resources (Agrell et al. 1995; Newton 1998; Both et al. 2000; Nicolaus et al. 2012a).

In a recent experimental study in great tits, results indicate that costs of reproduction are indeed a function of the level of competition in the environment (Nicolaus et al. 2012a). In this study, the authors found that parents paid a higher survival cost of reproduction in areas with experimentally increased sex ratio (and presumably higher level of intraspecific competition) (Nicolaus et al. 2012a). Selective mortality occurred during the second half of the winter period. We hypothesized that reproductive investment negatively affects the competitive ability of parents and that the level of competition later in life determines whether costs of reproduction are paid (Nicolaus et al. 2012a).

This study aims at testing the latter hypothesis of Nicolaus et al. (2012) in a great tit population. We aimed to measure effects of reproductive investment on the ability of parents to compete in the following breeding season because it was found that survival costs of reproduction were paid between midwinter and the breeding season (Nicolaus et al 2012). Based on this we expect that if competition is induced in this period, differences in the competitive ability of parents as a consequence of their reproductive investment, will become apparent. To test this, we first manipulated reproductive investment via family size in the breeding season and then increased competition for high quality nest boxes just before the following breeding season by reducing nest box depth in 80 % of the available nest boxes. Shallow boxes are less safe against nest predation and may affect other physical aspects of the breeding box (Wesołowski 2002; Czeszczewik & Walankiewicz 2003; Mazgajski 2003; Kaliński et al. 2014; Fokkema pers.obs.). Earlier experiments showed that, when given the choice great tits prefer deep nest boxes (Lohrl 1986, Summers & Taylor 1996).

We predict that family size will increase parental feeding effort (a proxy for reproductive effort), reduce parents' competitive ability and subsequently reduce their probability to claim preferred deep nest boxes in the following breeding season.

MATERIALS AND METHODS

Study area

The study was performed in a nest box breeding great tit population in the Lauwersmeer area, in the north-east of the Netherlands (53°23'N, 6°14'E, for map see Nicolaus et al. 2009). Within this area 12 study plots were set up. Each study plot contained 50 nest boxes, spaced 50 meters from each other. The plots consisted mainly of relatively young (approx. 40 years old) deciduous trees (Nicolaus et al. 2009).

Standard protocol

In 2010, 2011 and 2012, all nest boxes were checked during the breeding season on a weekly basis. During these checks laying date and clutch size were recorded. Laying date was back-calculated assuming one egg was laid per day. Expected hatching date was calculated assuming a breeding period of 12 days after the last egg was laid. While breeding, when possible, we tried to identify the female by her unique color ring combination (applied in previous years, see below). To determine the actual hatching date (day 0) nest boxes were monitored daily starting two days before the expected hatching day. When the nestlings were 5 days old, the entire brood was weighed (mass \pm 0.1 g). The following day (day 6), each individual nestling was weighed (mass \pm 0.1 g) and ringed with a unique numbered aluminum ring (standard rings issued by the Dutch centre for avian migration and ecology). Subsequently two or three of the nestlings (depending on the brood size, see below) were swapped between nests of the same age and approximately the same size and mass according to the experimental setup (see below). When the nestlings were 7 days old, both parents were caught in the nest box using a spring trap,

identified on the basis of their aluminum ring and measured. Parents that were not ringed yet received a new combination (one standard aluminum ring and three plastic color rings). Missed parents were caught two days later. Some parents that could not be caught were identified near their nestbox with binoculars (on the basis of the color ring combination that they received at an earlier time point). When the nestlings were 14 days old, they were all individually weighed (mass \pm 0.1 g). 21 days after hatching a final fledge check was conducted to determine if- and how many nestlings had fledged.

Experimental setup

Manipulation of family size

In 2010 and 2011 family size was manipulated (fig. 3.1: experimental setup). The family size of three nests hatching at the same day was altered within 'trios' by -3 , 0 , $+3$ or by -2 , 0 , $+2$ nestlings at day 6. Original nest parameters within trios were chosen as similar as possible regarding initial family size, clutch size and brood weight (overall result per manipulation group: table 3.1). Nests belonging to the same trio were assigned a 'trio-number' to facilitate analysis.

The decision to reduce/enlarge broods by either two or three nestlings was based on the size of the broods involved. If the family size reduction resulted in a brood of less than five nestlings; two nestlings were exchanged (to reduce the probability of brood desertion, Verboven and Tinbergen 2002). In some cases by mistake two nestlings were exchanged although the family size after reduction was above four nestlings, (N=6 trios, initial family size 7–8). For all analyses (see section: analyses) it was checked whether inclusion of these accidental assignments affected our results. The outcome of model selection was similar in both cases.

Within each trio, nest treatment and nestlings to be exchanged were randomly assigned among nests (for the nest treatments the RAND function in Excel was used; a self-written program in VBA code in Access was used to generate a random number for each nestling (Microsoft 2010)). In total four nestlings of the control broods were

Table 3.1: Manipulations were done within a trio of matched nests, in which either two ($-2/0/+2$) or three nestlings were exchanged ($-3/0/+3$). Column two and three show the sample size and the mean original clutch size. Column four and five show the mean number of nestlings- and brood weight before the family size manipulation at day 6.

# of nestlings exchanged	N	Clutch size (SD)	# Nestlings (SD)	Brood weight (g) (SD)
-2	17	8.76 (1.25)	6.12 (0.99)	46.04 (12.57)
0	17	8.47 (1.42)	6.41 (0.71)	47.28 (11.85)
2	17	8.18 (1.70)	6.29 (1.16)	47.71 (13.46)
-3	62	9.16 (1.10)	8.65 (1.07)	72.34 (11.04)
0	62	9.26 (1.24)	8.53 (1.20)	71.49 (12.21)
3	62	9.23 (1.08)	8.31 (1.02)	67.95 (11.76)

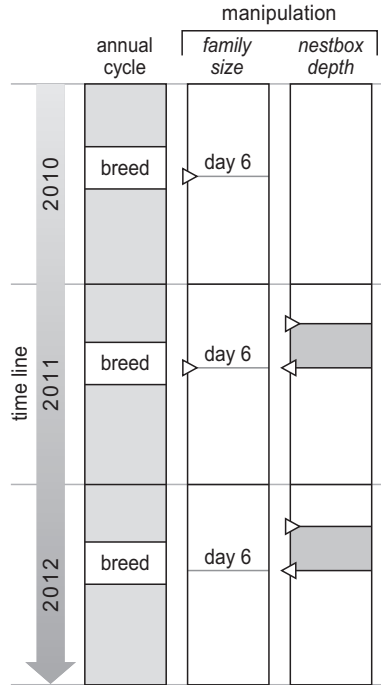


Figure 3.1: Time line of the experiments relative to the breeding cycle. In 2010 and 2011 the family size was manipulated when the nestlings were 6 days old (second column, grey lines with triangles pointing right). In the following year, 2011 and 2012 at the end of February the nest box depth was reduced in part of the boxes (third column, right pointing triangles). In the same breeding season at day 6 nest boxes were restored to their original depth (left pointing triangles). The duration of the experiment is indicated by the grey blocks in the third column. For further explanation see methods.

exchanged with respectively two nestlings of the reduced- and two nestlings of the enlarged broods. The net number of nestlings in the control nest was kept the same. This design ensured that the fraction of own nestlings relative to the total number of nestlings present in the nest remained approximately the same for all manipulation groups and that each nest experienced a similar level of disturbance.

Manipulation of nest box depth

In the original boxes the distance from the bottom to the lowest edge of the entrance hole (nest box depth) was approximately 16 cm. In 2011 and 2012, at the end of February, nest box depth was reduced in part of these nest boxes to respectively ± 12 and ± 7 cm by adding one or two wooden blocks (4.3 cm thick) inside the box.

Within plots we randomly assigned the depth treatment to the boxes (using the RAND function in excel (Microsoft 2010)) in the spring of both study years. Per study plot of 50 boxes 10 boxes were left deep, in 20 boxes the depth was reduced to 12 cm and in 20 boxes the depth was reduced to 7 cm. The randomization procedure generated no differences between parents of the three different family size manipulation groups (reduced,

control, enlarged) in terms of the distance between their original breeding box and the nearest deep box in the following year (linear model: $F_{(2, 123)} = 0.39$, $P = 0.68$; average distance to deep box: 65 meters)

In 2011 we accidentally lost some eggs due to a gap between the wooden block(s) and the side of the nest box (in 3% of the nesting attempts). In 2012 we therefore added a hardboard sheet on top of the blocks that prevented egg loss. In that year we also added a sheet to the nest boxes without blocks. During both study years, blocks were removed when the nestlings were 6 days old, to enable catching of the parents at day 7 (de Jong et al. 2014). After removal of the blocks in 2011 the family size manipulations were carried out (fig. 3.1: experimental setup)

Analyses

We used mixed models to test our prediction that family size manipulation positively affected parental feeding effort and negatively affected the probability of parents to claim a deep nest box in the following year. We additionally quantified whether or not fitness costs of reproduction were paid before competition for deep nestboxes was induced, potentially reducing the experimental effect.

Calculation of response variables:

Parental feeding effort

Effects of family size manipulation on parental feeding effort were estimated using the following two parameters 1) the gain in brood mass from when the nestling were 6 days old (just after manipulation) until they were 14 days old and 2) the number of fledglings produced. The gain in brood mass was calculated as the brood mass at day 14 (the sum of all individual nestling weights measured when the nestling were 14 days old) minus the brood mass at day 6 (the sum of the weights of all individual nestlings in the nest after the family size manipulation when 6 days old). The number of fledglings produced was calculated as the number of nestlings observed when 14 days old minus any nestlings found dead at the fledging check (see standard protocol).

For the analysis of the effect of family size on the gain in brood mass, 15 broods (6% of all manipulated broods) could not be included as all nestlings had died before day 14. These cases were not excluded in the analysis of the number of fledglings produced (N = 237 broods included). To check how this affected our results, the analysis of the effect of family size manipulation on the number of fledglings produced, was also done excluding all nests in which no nestlings fledged (N = 16 broods; 1 extra brood excluded because the nestlings in this brood died after day 14).

Components of future parental fitness

Effects of family size manipulation on two components of parental fitness were analyzed: the probability of parents to start a late brood (for definition see below) during the season and the probability to be recaptured locally in or around the nestbox the following breeding season (see standard protocol; as measure of local survival). Mark-recapture models were not used to estimate parental local survival because the adult detection

probability of survival is high in this population (0.897, SE = 0.055 see: Tinbergen & Sanz 2004; Nicolaus et al. 2012a). For the analysis of local survival N = 474 individuals were included.

We analyzed the effect of family size manipulation on the probability of parents to produce a late brood later during the same season on the basis of all manipulated females (N = 236 females; 1 female of the manipulated broods was excluded as she could not be identified, see standard protocol). A late brood is defined as either a repeat clutch (following a first brood that produced no fledglings) or a second clutch (following a first brood with at least one fledgling). In addition we analyzed the probability that a first brood did not produce fledglings (N = 16 broods failed), and for the broods that did produce at least one fledgling, the probability to produce a second brood (N = 221 broods).

Probability to claim a deep nest box

In total 126 experimentally manipulated parents were seen again breeding in deep or shallow boxes in the next breeding season. In this dataset, each parent was coded 1 when it bred in a deep nest box and 0 when it bred in either a nest box with one or two blocks (the latter two classes were taken together as almost none of the great tits bred in two block boxes, N=4 parents). All 126 parents with manipulated broods thus also those excluded in previous analyses (see: 'Parental feeding effort'; parents of broods in which all nestlings died before fledging) were included in the analysis of the probability of parents to obtain a deep breeding box.

Predictor variables:

Family size manipulation

We included manipulation of family size as a continuous variable in all analyses because our expectation was directional (directional statistical test; for overview of statistical approaches used in brood size manipulation studies see Knowles et al. 2009). In all analyses we tested whether family size manipulation had a quadratic effect (see: 'model selection and statistics used').

Post hoc the results for the parents of manipulation trios in which two nestlings were exchanged to acquire a deep nest box seemed to differ from the main part of the data (manipulation trios in which three nestlings were exchanged, fig. 3.2C). When tested this difference proved to be not significant (see results). The sample size of the manipulation trios in which two nestlings were exchanged was however limited. Furthermore, although we could not show a difference between them, the manipulations in which two nestlings were exchanged may have responded different to the family size manipulation than the manipulations in which three nestlings were exchanged due to a difference in the average original clutch size in these groups (i.e. lower reproductive investment, see table 3.1). We therefore decided to also present our analyses for the main part of the data separately.

Study year and sex of the parent

In all analyses study year and the interaction between manipulation, manipulation² and

year were included. In the analyses of local survival and the probability to claim a deep nest box, additionally sex and the interaction between manipulation, manipulation² and sex were added to the model.

We included both sexes separately in the analysis of the effect of the probability of parents to claim a deep box. The exact role of both sexes in the process of nest box selection is complex and far from understood. Behavioral research indicates that the male competes to claim a high quality territory (i.e. with deep nest boxes) and the females compete for the males with high quality territories (Hinde 1952). Based on this we assumed that the effect of family size manipulation applies to both sexes.

Random variables:

Trio ID, brood ID in the year of manipulation, and ring number of the parents (individual ID) were included as random effects in the analyses of the probability of parents to claim a deep box. Trio number was included to correct for non-independence between nests. Brood ID accounted for the common history of parents (only 11 of the 109 pairs stayed together, for most of the pairs which split-up only the male or the female was seen again: 88 pairs). Ring number accounted for repeated measures of some individuals in 2011 and 2012 (N = 11 parents seen in the period 2010–2011 and 2011–2012). In the analyses of parental feeding effort and fitness from late broods within the same season only trio ID was included as a random effect. In the analyses of the local survival to the following breeding season, trio ID and ring number were included (N = 43 parents raised broods in which the family size was manipulated in both 2010 and 2011). The random effects were always kept in the model during model selection.

Model selection and statistics used

Analyses of parental feeding effort were done using LMER with Gaussian errors (Linear Mixed Effect Models). For the analyses of the probability of parents to start a late brood within the same season, the local survival probability of parents and the probability of parents to claim a deep nest box, a GLMER (Generalized Linear Mixed Effect Models) was fitted with a binomial error structure. Model selection was done using the backwards elimination procedure. First the interactions between the quadratic term of manipulation with all other included predictor variables were eliminated in order of significance. Next the interactions between the linear term of manipulation and all included predictor variables were eliminated in order of significance. We next tested whether the quadratic term could be eliminated and proceeded by eliminating all other predictor variables according to their significance. Model comparison was first done using likelihood ratio tests and next repeated on the basis of AIC (Akaike Information Criterion) values. The outcome of model selection did not differ between both methods, so the outcome of model selection of the basis of the likelihood ratio tests is reported.

All analyses were performed in R 3.2.0 (R core team 2015). R package lme4 was used for the mixed-effects analysis. Figures were created using the R package 'ggplots2'. The solid and dotted line in figure 3.2A-C were calculated using the predict function of the package 'lme4' (predict.merMod). This was done using the selected models including the

random effects. For the analysis of the probability to claim a deep box, the effect size was calculated using the package ‘pwr’ (Cohen 1988).

RESULTS

Parental feeding effort

Parental feeding effort was successfully altered by the manipulation of family size. The number of fledglings produced was found to increase with manipulation and level of for the enlarged families (quadratic effect). A similar, though just not significant effect was found of family size manipulation on the gain in brood mass (fig. 3.2A-B; table 3.2). Within the same analyses, for both measures of parental feeding effort a stronger positive effect of family size manipulation was found in 2011.

When the same analysis was repeated, excluding the 16 nests in which no nestlings fledged, the non-linear effect of family size manipulation on the number of fledglings produced was marginally significant (manipulation²: $\chi^2_{d.f.1} = 2.93$, $P = 0.08$).

When the above analyses were redone but excluding the manipulation trios in which two nestlings were exchanged, the outcome of model selection was similar (fig. 3.2A-B dotted line).

Components of future parental fitness

(1) Probability to fail the first clutch

We found a strong trend that the probability of nest failure in 2011 was lower than in 2010 (mixed model: intercept: -2.34 ± 0.30 ; year 2011: $\beta = -1.12 \pm 0.66$, $\chi^2_{d.f.1} = 3.08$, $P = 0.08$). Controlling for these year differences, no effect of family size manipulation on the probability of parents to fail their first brood was found (manipulation: $\chi^2_{d.f.1} = 1.21$,

Table 3.2: Model summary of the final linear mixed effect models describing the effect of family size manipulation on different aspects of parental feeding effort: the weight gain in grams of the brood from manipulation (day 6) until day 14 ($N = 222$ broods) and the number of fledglings successfully reared per brood ($N = 237$ broods). The variance of the random effect trio ID was 62.8 for the brood weight gain analyses and 1.36 for analyses of the number of fledglings. For the factor year, 2010 was the reference category.

	Brood weight gain day 6–14 (grams)					Number of Fledglings				
	β	SE	$\Delta\chi^2$	d.f.	P	β	SE	$\Delta\chi^2$	d.f.	P
Intercept	55.55	2.61				6.37	0.32			
Manipulation	0.45	0.77				0.23	0.09			
Manipulation ²	-0.72	0.32	4.85	1	<0.05	-0.09	0.04	5.30	1	<0.05
Year	13.77	3.17				1.79	0.40			
Manipulation x year	4.63	1.14	15.93	1	<0.001	0.62	0.13	21.53	1	<0.001

Rejected terms: manipulation² x year (d.f.1)

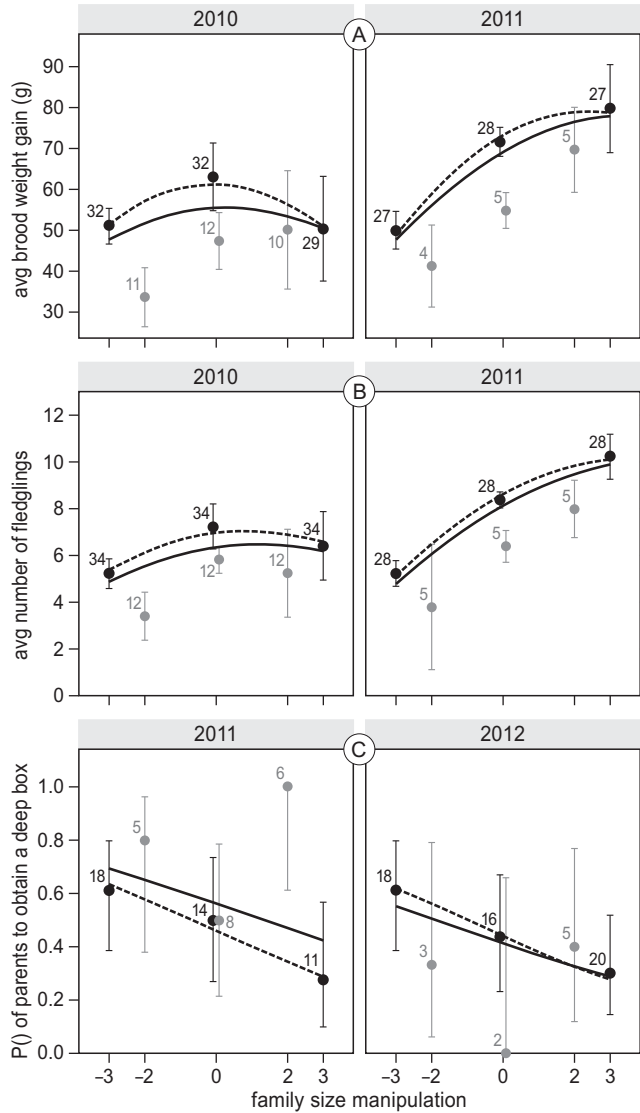


Figure 3.2A-C: The effect of family size manipulation on A) the weight gain of the brood in grams after manipulation, B) the number of fledglings successfully reared per brood and C) the probability of parents to obtain a preferred deep nest box in the following breeding season. Sample size is indicated by symbol size and the numbers next to the error bars. Error bars for figure A-C depict 95% confidence intervals. The solid line depicts the predicted response (see methods). The dotted line depicts the predicted response when the manipulation trios in which two nestlings were exchanged were excluded from analyses.

$P = 0.27$; manipulation²: $\chi^2_{d.f.1} = 1.50$, $P = 0.22$; average probability to fail = 0.06). The effect of manipulation did not differ between years (manipulation \times year: $\chi^2_{d.f.1} = 1.28$, $P = 0.26$; manipulation² \times year: $\chi^2_{d.f.1} = 0.10$, $P = 0.76$). The variance of the random effect trio ID was 0.

Excluding the manipulation trios in which two nestlings were exchanged did not affect the outcome of model selection.

(2) Probability to start a late brood

The probability to start a late brood (repeat or second clutch) was lower in 2011 than in 2010 (mixed model: intercept: -0.21 ± 0.21 ; year 2011: $\beta = -0.89 \pm 0.35$, $\chi^2_{d.f.1} = 6.75$, $p < 0.01$). Controlling for these year differences, the probability of females to start a late brood tended to decline with family size manipulation, but this trend was not significant (manipulation: $\chi^2_{d.f.1} = 2.25$, $P = 0.13$; manipulation²: $\chi^2_{d.f.1} = 0.85$, $P = 0.36$; average probability to start a late brood: 0.38). The effect of family size manipulation did not differ between years (manipulation \times year: $\chi^2_{d.f.1} = 0.44$, $P = 0.55$; manipulation² \times year: $\chi^2_{d.f.1} = 0.34$, $P = 0.56$). The variance of the random effect trio ID was 0.53. Similar results were obtained when the females that failed their first brood (repeat clutches) were excluded. The earlier reported effect of year on the probability to start a late brood disappeared when the manipulation trios in which two nestlings were exchanged were excluded (year 2011: $\beta = -0.60 \pm 0.37$, $\chi^2_{d.f.1} = 2.61$, $P = 0.10$). Besides the latter difference the outcome of model selection was similar to the analyses in which the manipulation trios in which two nestlings were exchanged were included.

(3) Parental local survival probability

Parental local survival probability differed between years, with an estimated higher local survival in 2011 than 2010 (mixed model: intercept: -1.16 ± 0.15 ; year 2011: $\beta = 0.51 \pm 0.21$, $\chi^2_{d.f.1} = 5.83$, $P < 0.05$). Controlling for these year differences, there was no effect of family size manipulation on the local survival probability of parents (manipulation: $\chi^2_{d.f.1} = 0.002$, $P = 0.96$; manipulation²: $\chi^2_{d.f.1} = 0.15$, $P = 0.70$; average survival probability: 0.28). The sexes also did not differ in their survival probability ($\chi^2_{d.f.1} = 0.68$,

Table 3.3: Final model of the effect of the family size manipulation in the preceding year on the probability of parents to claim a deep breeding box the following year ($N = 126$ parents). The variance was 0.11 for the random effect trio ID, 0.42 for the brood ID and 0 for ring number (individual ID). For the factor year, 2011 was the reference category. For the factor sex, the males.

Variable	Estimate β (\pm SE)	$\Delta \chi^2$	d.f.	P
Intercept	-0.05 (0.21)			
Manipulation	-0.19 (0.09)	4.64	1	<0.05
Rejected terms:				
manipulation ² \times sex (d.f.1), manipulation ² \times year (d.f.1), manipulation \times sex (d.f.1), manipulation \times year (d.f.1), manipulation ² (d.f.1), sex (d.f.1), year (d.f.1)				

$P = 0.41$). The effect of family size manipulation further did not differ between the years (manipulation \times year: $\chi^2_{d.f.1} = 1.05$, $P = 0.31$; manipulation² \times year: $\chi^2_{d.f.1} = 1.50$, $P = 0.22$) or the sexes (manipulation \times sex: $\chi^2_{d.f.1} = 0.09$, $P = 0.76$; manipulation² \times sex: $\chi^2_{d.f.1} = 0.72$, $P = 0.40$). The variance of the random effect trio ID was 0.02, the variance of the random effect ring number was 0.

Similar results were obtained when manipulation trios in which two nestlings were exchanged were excluded.

Probability of a parent to claim a deep nest box

Family size manipulation had a negative effect on the probability of a parent to claim a deep breeding box in the following breeding season (effect size between parents that raised reduced- and parents that raised enlarged families: 0.67; fig. 3.2C; table 3.3). Year in which the nest box depth experiment took place and sex of the parents had no significant effect on the ability of parents to claim a deep nest box. The effect of family size manipulation further did not differ between years or depending on the sex of the parent (no interaction between manipulation/manipulation² and sex or year).

Some parents were observed twice in both experimental rounds (11 parents raised a manipulated brood in 2010 and 2011 and claimed a deep/shallow nestbox in 2011 and 2012; see fig. 3.1). Excluding the second observation of these individuals (year 2011–2012) did not affect the outcome of model selection.

Post hoc analysis indicated that parents from the manipulation groups in which two nestlings were exchanged and in which three nestlings were exchanged did not differ in their probability to acquire a high quality box (fig. 3.2C; mixed model: manipulations in which three nestlings were exchanged: $\beta = -0.60 \pm 0.52$, $\chi^2_{d.f.1} = 1.45$, $P = 0.22$). Excluding the manipulations in which two nestlings were exchanged also did not affect the outcome of model selection.

DISCUSSION

We tested whether increased parental reproductive investment in one season negatively affected parental competitive ability later in life (Nicolaus et al. 2012a). We indeed found that this was true in the case of competition for high quality breeding sites in spring. Family size manipulation reduced the likelihood that parents occupied a preferred but scarce deep nest box in the following breeding season. Such carry-over effects are important because they show that selection on individual optimal clutch size will depend on 1) resource abundance and the level of competition in the next breeding season and 2) on the reproductive investment of the competitors in the current breeding season because it affects their competitive ability in the future as well.

Was parental feeding effort affected?

Experimental manipulation of family size is based on the assumption that parents cope with the family size manipulation as if it was their own decision. In our experiments

parents did adjust their feeding effort to family size as judged from the positive effects of family size manipulation on brood weight gain and the number of fledglings produced. Consistent with that, earlier work in the same population has shown that the energy expenditure of parents was positively related to family size (Sanz and Tinbergen 1999). The slope of the effect of family size manipulation on our indexes of parental feeding effort differed between the study years. In both 2010 and 2011 the feeding effort increased with family size manipulation, but also in both years and especially 2010 the indexes of feeding effort levelled off with brood enlargement (fig. 3.2A-B). This suggests that the increase of feeding effort with manipulated brood size may have been non-linear in line with the evidence found for an 'energetic ceiling' (Tinbergen and Verhulst 2000).

Overall we conclude that as predicted family size manipulation positively affected parental feeding effort and likely by this the energy expenditure of parents.

The probability of parents to obtain a high quality box

In line with our prediction, we found that reproductive investment negatively affected the ability of parents to compete for high quality nestboxes in later life. This effect was consistent over both study years. We found no indication that the probability of acquiring a high quality nest box was non-linearly related to the brood size manipulation, as expected on the basis of our feeding effort estimates. The sample size is here likely limiting. For the manipulation trios in which two nestlings were exchanged the effect of family size manipulation on the ability of parents to claim a high quality box was less consistent but could not be shown to differ from the manipulation trios in which three nestlings were exchanged (fig. 3.2C). Exclusion of the trios in which two nestlings were exchanged also did not affect the outcome of our analyses.

Potentially different mechanisms can explain the negative effect of family size manipulation on the probability of parents to acquire a high quality box in later life.

(1) Physiological effects

Parents with enlarged broods had to work harder to feed their young, thereby allocating more energy to feeding (Sanz & Tinbergen 1999, same population) possibly leaving less energy for subsequent breeding (e.g. second broods; Nicolaus et al. 2012a same population), repair (Moult: Nilsson & Svensson 1996; Immune response: Knowles, Nakagawa & Sheldon 2009; Knowles, Wood & Sheldon 2010) or to produce bright competitive plumage (Siefferman and Hill 2005a). Similar physiological trade-offs may affect competitive ability later in life and thus the outcome of competition over a preferred breeding site.

(2) Strategic decisions: asset protection

Changes in allocation that explain effects of family size on later parental competitive ability may involve an individual strategic decision to maximize fitness. It has been proposed (Clark 1994; Wolf et al. 2007) and confirmed empirically (Nicolaus, Tinbergen et al. 2012) that parents with high future fitness expectation (i.e. high future 'asset') should behave more cautiously to increase the chance of harvesting their asset. Hence, parents with a reduced family that may have a higher future fitness payoff may be more

inclined to compete for deep nest boxes that reduce predation risk (Lohrl 1986; Summers & Taylor 1996; Wesołowski 2002; Kaliński et al. 2014). The payoff and thus the degree to which assets need to be protected would in this situation depend on the level of competition and the level of predation risk. Asset protection thus could provide a functional explanation for the pattern found.

(3) Strategic decision: perceived predation risk

An alternative explanation is that parents may have perceived the sudden reduction in family size through manipulation as a predation event. Parents may have in response to the experimentally decreased number of nestlings, besides from adjusting the amount of food brought, also have responded to a “perceived” higher predation risk. We would then expect the parents who raised reduced families to, in the future, more prefer the deep safer boxes than the parents of control broods, while no clear expectation for the parents of enlarged families can be given (for review of behavioral adaptations to predation see Magnhagen 1991). Such an effect of predation weakens the technique of brood size manipulation as a means of measuring effects of family size on the cost of reproduction.

Yet, contrary to the expectation if the parents would avoid predation, the general pattern is that parents of reduced broods actually do produce more second clutches (Linden 1988; Smith Kallander & Nilsson 1987; Tinbergen et al. 1987; Parejo and Danchin 2006; Nicolaus et al 2012; similar to the tendency in this study). Also parents caring for enlarged broods increased their feeding effort (Sanz & Tinbergen 1999; Knowles, Wood & Sheldon 2010; Nicolaus et al. 2012a; De Jong et al. 2014; This study) suggesting that the observed patterns are not entirely governed by the perceived predation risk.

What are the consequences?

(1) Can differences in the competitive ability of parents affect the costs of reproduction?

In a study by Siefferman & Hill (2005a) similar effects of family size manipulation on the ability of parents to claim resources were found. The plumage of male Eastern Bluebirds (*Sialia sialis*) that had raised experimentally reduced broods significantly increased in brightness in the following year. Males with brighter plumage in the following year mated with females that initiated egg laying earlier in the season, which may indicate better condition or more experience than the females who lay later. The authors argue, on the basis of previous work, that one reason why these higher quality females chose for the more brightly colored males is that they are better able to gain access to nest cavities (Siefferman and Hill 2005b). For the male, having a higher quality female may yield direct fitness- and indirect fitness benefits (for a recent study and overview of literature on the subject see: Ihle et al. 2015). These results indicate that reproductive investment through affecting the ability of parents to claim resources such as cavities and mates can affect their subsequent breeding success.

In our study next to potential effects of family size manipulation on the quality of the partner obtained, shallower boxes may have also affected breeding success through increased nest predation or altered physical properties of the box (Wesołowski 2002;

Czeszczewik & Walankiewicz 2003; Mazgajski 2003; Kaliński et al. 2014; Fokkema pers.obs). Given our current experimental setup however it was not possible to assess the effects of nestbox depth (or quality of the partner, see above) on breeding success independently from the effect of family size manipulation. For this, an experiment is needed in which nest box depth is experimentally altered after the nestbox choice of the breeding bird.

Next to effects on breeding success, increased competition for nestboxes could lead to a lower local survival of the parents. This could be either due to direct mortality effects caused by severe competition over nest boxes or by a reduced probability for parents to reproduce locally (perhaps also causing parental movements after lost competition over a nest box, potentially with reduced fitness as a consequence). We found no effects of family size manipulation on the local survival of the parents until the breeding season, suggesting that survival costs of reproduction were not directly paid as a consequence of the increased competition for deep breeding boxes. If less or no shallow boxes would have been provided to the parents, we expect that competition would have been more severe and that negative effects of family size on the local survival of parents would have become apparent.

(2) Potential mechanism explaining density dependent effects on family size

If family size mediated differences in competitive ability among parents affect their future fitness this could provide a mechanism explaining density dependent effects on reproduction. In many populations (e.g. avian: Kluijver 1951; Perrins 1965; Both et al. 2000; Nicolaus et al. 2013; mammals: Morris 1989; Koskela et al. 1999; Bonenfant et al. 2009) a negative relationship between the annual mean family size and population density has been found. These density effects stabilize population numbers and are thought to be caused by increased competition for resources (Newton 1998). Our findings indicate how at high population density competition for resources could select for reduced reproductive rates. Under increased competition parents that invest less in reproduction, may benefit from a higher competitive ability. It may thus be adaptive for parents to lower their family size in the face of expected high competition (see also: Nicolaus et al. 2013: clutch size-density reaction norms).

Such mechanisms imply that the fitness consequences of family size are not just related to parents own individual reproductive investment, but also to the individual investment of future competitors. In other words, the decision on family size becomes frequency dependent because the competition in future will depend on the choices the other parents in the population make with respect to family size (see also: Wilson 2014).

The degree to which anticipated future competition is expected to affect reproductive decisions made by the parent should depend on the life history characteristics of the parent. For long lived species fitness gained from future reproduction is likely more important than for short lived species (e.g. Hamel, Côté, et al. 2010). We expect for this reason that under competition, negative effects of family size on parental competitive ability and potentially future fitness, could result in a stronger negative selective pressure on the reproductive investment of long lived species.

Conclusion and future outlook

Our study provides empirical evidence that parental investment in reproduction can carry-over to affect the ability of parents to compete for resources in later life. Depending on the level of competition within the social environment this could in turn feedback to the occurrence of fitness costs of reproduction. This indicates an important condition dependent aspect of the occurrence of carry over effects of current reproduction on future reproduction (as hypothesized by O'Conner et al. 2014). The challenge for future research now is to test the generality of the negative relationship between reproductive investment and the competitive ability of parents in later life and whether or not this provides a mechanism to explain the occurrence of costs of reproduction at high levels of competition in the environment (i.e. density dependent effects on reproduction).

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