

# Family size and competition:

By Livia De Felici Msc Ecology and Evolution, Sept. 2015

**Abstract:** One of the trade-offs on which life history theory is based is the one between current and future reproduction. Investment in current reproduction can be paid off in the future by reduced survival or fecundity. Recent work has shown that only under high levels of competition in the social environment reproductive costs were paid. First evidence now indicates that reproductive effort may negatively affect parental competitive ability in later life. In this work we further test this hypothesis and the consequences of a lower competitive ability for the ability of parents to secure vital resources later in life.. We worked on a great tit (*Parus major*) population that underwent brood size manipulation during the year 2014. To induce competition among the great tit parents, before the beginning of the new breeding season we reduced the availability of nest-boxes in the study area. We used the probability of getting a new nest-box as a measure of competitive ability. If family size has a negative effect on competitive ability, we would expect birds that raised reduced broods perform better compared to the ones who raised enlarged broods. The results showed an effect on survival until the first part of winter but no effect on the probability of getting a new nest-box. Our results thus provide no direct evidence for the hypothesis that family size negatively affects parental competitive ability in later life. The selective disappearance we found before midwinter of parents as a consequence of their brood size manipulation however does indicate that differences in parental competitive ability may have already played a role before the onset of our experiment.

## Introduction:

Life history theory is based on the assumption that animals have limited resources that can be allocated differently among various life traits. This implies the existence of trade-offs in order to maximize the fitness of each individual.

In reproduction, one trade-off is between the quantity and quality of the offspring (Lack 1947). Assuming that reproductive effort of the parents is equally divided between the young, the fitness of each one is expected to decrease as family size increases. On the other hand, with a high number of offspring there are more chances for the copies of parental genes to be successfully transmitted.

Considered important as well is the trade-off between present and future reproduction. In this case it is hypothesized that an increased effort in the current reproductive attempt will be paid by reduced survival or fecundity in the future. This trade-off, also known as the cost of reproduction, has been largely studied in the last 50 years using different approaches, from genetic correlations (e.g. Rose & Charlesworth, 1981) to manipulations of family size in a laboratory setting ( e.g. Stier, Reichert, Massemin, Bize, & Criscuolo, 2012) or in the field ( for review see Linden & Møller, 1989). Manipulation of family size is necessary in

these kind of studies because the number of offspring produced is influenced by the environmental and parental quality (Högstedt, 1980). For instance, in a natural setting the relationship between clutch size and survival may find that parents with larger clutch size also have a higher survival. This positive relationship may be due to a better quality of the parents or of the territory they breed in. These kind of effects can interfere with the studied patterns.

The results from studies using brood size manipulations aiming to quantify the costs of reproduction are mixed. Some studies fail to find a causal relationship between parental effort and future parental fitness, others reveal a negative or sometimes even a positive correlation (for review see Nur, 1987, Dijkstra et al., 1990, Stearns 1992, Barnes & Partridge, 2003; Santos & Nakagawa, 2012). This heterogeneity may be partly attributed to spatial and temporal variation in ecological conditions among studies such as resource availability, predation pressure or temperature fluctuations (Nur, 1987).

Recent findings (Nicolaus et al., 2012) highlight the contribution of social environment in determining the costs of reproduction. Nicolaus performed a series of experiments of brood manipulation in a Great tit (*Parus major*) population. She worked during several breeding seasons manipulating the sex ratio and fledgling densities in the study area in order to create four different environments (low density-female biased, high density- female biased, low density-male biased, high density- male biased). She monitored the fledgling success, parental effort and survival rate of the birds. The results showed that parental survival costs were higher in environments with higher competition (male biased). She hypothesized that this extra-cost was caused by a negative effect of manipulation on parental competitive ability.

This hypothesis was tested in the work of Fokkema et al. (Fokkema et al., submitted) on the same population. During two study years, brood size manipulations were conducted. As measure of competitive ability competition was induced among the tits for high-quality deep nest-boxes just before the following breeding season (e.g. deep nest-boxes are preferred by great tits and may lower predation risk- Löhrl 1986, Summers & Taylor 1996 Kaliński *et al.* 2014). Fokkema et al. found that family size manipulation negatively affected the ability of parents to claim a deep nest box.

These results are thus in line with the hypothesis raised by Nicolaus et al (2012), reproductive investment indeed seems to negatively affect parental competitive ability later in life. This shows that reproductive costs are set in interaction with the level of local competition in the parents environment.

In this study the consequences of brood size manipulations on competitive ability are further investigated. The same nest-box population of great tits as in the study of Nicolaus et al. (2012) and Fokkema et al. (submitted) is used as study model. Again brood size manipulations were carried out. Just before the onset of the following breeding season the number of breeding boxes available was reduced by 80%. The probability of a parent to acquire a breeding place during the breeding season was used as a measure of competitive ability. From the study of Drent (Drent, 1987) it is known that nest-boxes are preferred breeding sites for Great tits, so the expectation is that when locally the availability of nest boxes is reduced,

competition will increase. If family size negatively affects the competitive ability of parents, we thus expect a negative effect of experimental family size on the probability of parents to secure a nest-box under high competition.

#### Materials and methods:

##### Study area:

The study was carried out in a nest-box-breeding population of Great tits in the Lauwersmeer area, in the northern part of the Netherlands (53°23'N, 6°14'E, see fig 1 for the map). About 90 square kilometres were reclaimed from the Waddensea in 1969 and now consists of wetlands, reeds and on the higher parts forests populated by young trees, mostly deciduous and few conifers.

The measurements took place in 12 plots of roughly 10 ha distributed over the forests. Before the nest-box reduction experiment, each plot contained 50 nest boxes attached to trees at breast height (approx. 1,20 m) and separated 50 m from each other in a grid.



Fig.1 Study plots in the Lauwersmeer.

##### Brood size manipulation:

During the breeding season of 2014 a brood size manipulation experiment was carried out (for details see Fokkema et al. (submitted), De Jong 2014). The original family size of 111 broods was altered by -3, 0 or +3 nestlings 6 days after the hatching date. In 3 cases 2 nestlings were swapped instead of 3 to prevent

desertion of the brood by the parents due to too small a brood size (initial family size of trios: 6-7 nestlings). "Trios" of nests with similar initial conditions (clutch size, brood size and weight of the nestlings) were matched and nest treatment and nestling to be swapped were randomly assigned so that each trio contained reduced (-3,-2), control (0) and enlarged (+3, +2) broods. 204 out of 222 of the parents of these broods were provided with an external transponder ring. Four different colours were available for the transponder rings which were either fitted on the left or the right leg without other rings. On the other leg an aluminium ring and coloured plastic ring was attached in a unique combination. This enabled identification of the manipulated parents without catching.

#### Winter roost checks:

In December 2014 a first night check was performed. The birds were caught while sleeping in the boxes, the location of where they were sleeping was noted, the birds were identified by ring number, the sex of the bird was noted and next the birds were measured for weight (mass  $\pm 0,5$  g), tarsus (length  $\pm 0,1$  mm) and primary third feather (length  $\pm 0,5$  mm). Unringed birds were ringed with an aluminium ring and three coloured plastic rings for further identification.

#### March roost check:

In the first half of March a night-check was carried out. In order to minimize disturbance for the birds and possible subsequent movements between boxes, handheld transponder readers were used. In this way the presence of transponder birds could be detected without opening the boxes. The readers were held from outside the nest-box close to the bottom and to the sides of the boxes and the transponder number was shown on the display and noted down for identification. No biometric measurements were taken this time.

#### March observation:

Before removing the nest-boxes for the experiment, observations to identify birds were carried out in the study plots. Focus was on the 8 plots in which most of the manipulated birds were seen roosting during the night checks in March. These plots were visited at least 6 days in the period from February to March. The remaining 4 plots were visited at least 2 days. The observation was performed by one person per plot starting from the early morning until the early afternoon (approx. 8 hours). The birds were identified by their unique colour combination and their exact location was noted down in Amersfoort coordinates. Furthermore it was noted down whether the bird was male or female, whether it was seen with a partner and the behaviour displayed at the time of the observation.

#### Reduction in number of breeding boxes:

During the 17th, 18th and 19th of March 2015 80% (40 out of the 50) of nest boxes present in each plot was removed. The boxes left in the plot were randomly selected; they were cleaned and moved 35 m north-east from their original location to mitigate potential prior residency effect (Harvey, Greenwood, &

Perrins, 1979). Whenever it was not possible to shift the boxes to the northeast, they were moved south-east, otherwise north-west or finally south-west. All the boxes were hung at breast high, facing east.

Standard protocol:

From the beginning of the breeding season (April 2015) weekly plot-checks were carried out. Nest boxes were checked for the presence of eggs, the initial laying date was established with a back calculation assuming one egg was laid per day, final clutch size was recorded. The start of the incubation period was assessed checking whether the eggs were warm and uncovered by nest material. Colour combination of females incubating was read whenever possible during the checks without taking the bird out of the nest-box. Hatching date was determined by checks around 12 days after the start of incubation and was referred to as day 0. On day 6 the nestlings were ringed with an aluminium ring and weighed ( $\pm 0,5$  g). On day 7 parents were caught by means of spring traps, identified and measurements of weight ( $\pm 0,5$  g), tarsus ( $\pm 0,1$  mm), and third primary feather ( $\pm 0,5$  mm) were taken. When the catch was not successful a new attempt was made after two days. In case catching was unsuccessful the identification of the birds was based on, whenever possible, the data available from the observations or, for the females, using the ring reading data gathered when they were incubating.

Measurements of weight ( $\pm 0,5$  g), tarsus ( $\pm 0,1$  mm) and primary third feather ( $\pm 0,5$  mm) were also taken of young on day 14. Around day 21 the nest-boxes were checked to see if the young had fledged. In case they were, the boxes were cleaned and the nests inspected for dead chicks, if not they were visited again some days later until the brood was fledged.



Fig.2: Original setting of the study plots before reduction in number of nest-boxes (50 per plot).



Fig. 3: new setting of the study plots after reduction in number of nest-boxes (10 per plot).

Data selection and sample size:

Different data sets were available to analyze the survival rate and the probability to get a box for the manipulated birds.

A “maximal set” contained lists of all the individuals considered to be alive during a determined phase of winter or spring (see table A).

A “reduced set” contained manipulated parents exclusively seen in the area in determined phases of winter or spring, excluding individuals that were not seen in that moment, but were seen alive later (e.g. for the survival until December 2014, parents that were not seen during December night-check but that were seen during the March night-check were excluded ).

A last “minimal set” excluded from the lists birds that were seen during one period but not in the previous one (e.g. parents that were seen in the March night-check but not in December night-check were excluded).

The results obtained using these different sets were similar to each other, but only the results obtained from the “maximal set” are presented in this paper.

The number of individuals contained in the lists used for the analysis is shown in table B, in tables C and D the same individuals are sorted by sex.

To have a complete overview of the survival rate during the year see figure 3.

	List of manipulated birds	description
1	Breeding season 2014	Birds from manipulation experiment of 2014
2	Alive until December 2014	Birds found during the night-check in December 2014 or seen in later time points (March night-checks, March observations or breeding season 2015)

3	Alive until March 2015	Birds found during night-checks in March, during March observations or in the breeding season 2015.
4	Breeding in season 2015	Birds breeding in nest-boxes during breeding season 2015.

Table A: lists of birds used in the analysis.

	Breeding season 2014 (1)	Alive until Dec 2014 (2)	Alive until March 2015 (3)	Breeding season 2015 (4)
reduced	74	36	23	12
control	74	31	26	7
enlarged	74	21	11	5
tot	222	88	60	24

Table B: The number of manipulated birds from the breeding season 2014 (*Breeding season 2014*) alive in different phases of the winter and spring.

FEMALE				
reduced	37	16	10	5
control	37	16	13	2
enlarged	37	8	1	0
tot	111	40	24	7

Table C: same data as table A, but for females only.

MALE				
reduced	37	13	13	7
control	37	15	13	5
enlarged	37	20	10	5
tot	111	48	36	17

Table D: same data as table A, but for males only.

#### Statistics:

Analysis of the effect of brood size manipulation on the probability of parents to survive and the probability of parents to acquire a box were done using GLM (generalized linear model) with a binomial error distribution. Manipulation and sex were considered as categorical variables. The interaction between sex and manipulation was included in the analysis.

In case of significant results a post hoc analysis was conducted to see which categories among reduced, control and enlarged actually differed from each other. The analysis was conducted with a Tukey's HSD test in the R package multcomp (Hothorn, Bretz and Westfall, 2008).

All analyses were performed using R 3.2.0 (R core team 2015).

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#### Local survival effect:

The results from the analysis for the first part of the winter (from breeding season 2014 to December 2014) show significant manipulation effects ( $\chi^2_{d.f.2} = 6,71, p < 0.05$ ; see table 1. Fig. 3). No interaction effect of manipulation and sex could be found so both sexes were affected equally. Post hoc comparison revealed that survival rate differed significantly between reduced and enlarged (z-value= -2,51; p-value= 0,03), but not between enlarged and control (z-value=-1,72; p-value= 0,20) or reduced and control (z-value= -0,83; p-value=0,69).

For the survival in the second part of the winter (from December 2014 to March 2015) a borderline effect of the interaction between manipulation and sex was found. This was due to a significant difference in the survival between males and females of the enlarged category (see figure 4).

#### Probability to get a nest-box:

The probability to get a box during the breeding season 2015 was not affected by the manipulation of the brood size in the previous year. Also no interaction between manipulation and sex nor an effect of sex showed up (see table 3 and figure 3).

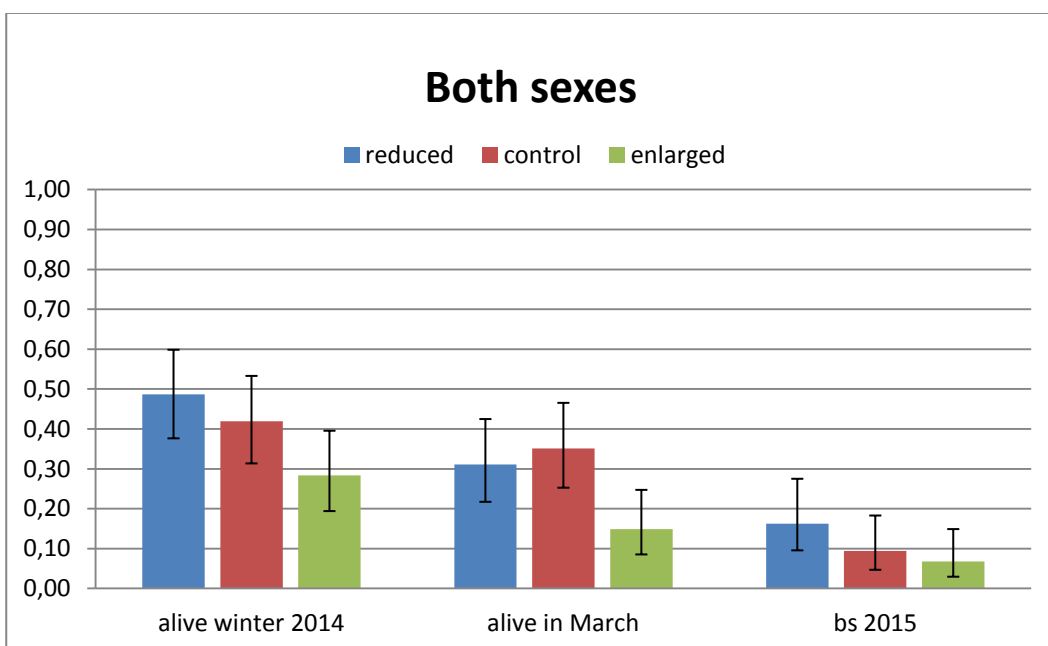


Fig 3: fraction of birds on the initial sample size (n=74) alive in different phases of the year.

#### Results



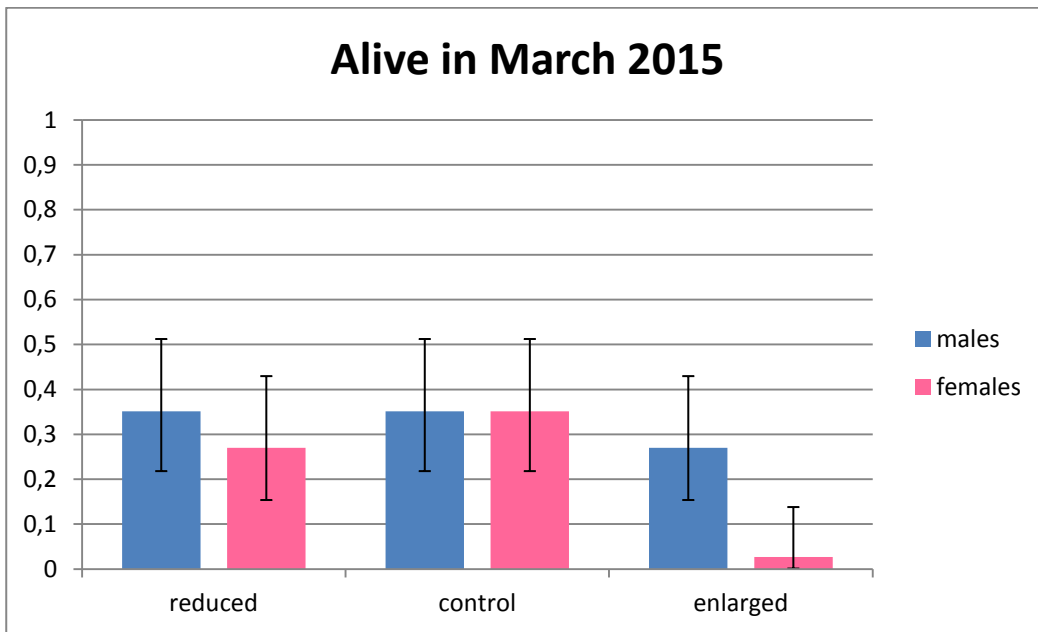


Fig 4: fraction of birds alive in March 2015, divided per categories and sex.

Table 1: final model of the effect of manipulation on the survival of birds from the breeding season 2014 to December 2014

variable	Estimate ( $\beta$ )	SE	Deviance	DF	p-value
intercept	-0,05	0,23			
manipulation			6,71	2	<b>&lt;0,05</b>
control	-0,27	0,33			
enlarged	-0,87	0,35			
Rejected terms: manipulation $\times$ sex (DF2), sex (DF1)					

Table 2: final model of the effect of manipulation and sex on the survival of birds from December 2014 to March 2015.

variable	Estimate ( $\beta$ )	SE	Deviance	DF	p-value
intercept	0,51	0,52			
manipulation					
control	0,96	0,82			
enlarged	-2,46	1,19			
sex					
male	0,11	0,7			
manipulation $\times$ sex			5,77	2	<b>0,06</b>
control:male	0,30	1,21			
enlarged:male	3,04	1,44			
Rejected terms: -					

Table 3. Probability to get a box in the breeding season 2015 for the birds alive in March 2015.

variable	Estimate ( $\beta$ )	SE	Deviance	DF	p-value
intercept	0,76	0,23			

Rejected terms: manipulation  $\times$  sex (DF2), sex (DF1), manipulation  $\times$  sex (DF2)

Discussion:

The aim of the study was to test the hypothesis that family size negatively affects parental competitive ability in later life. The obtained results provide no evidence for this hypothesis, family size manipulation did not affect the probability of parents to acquire a breeding box under high competition.

Here potential reasons for the absence of an effect are explored.

Was parental effort affected by family size manipulation?

It can be argued that the manipulation did not actually have any effect on parental effort during the breeding season 2014. The measurements on parental effort taken after the manipulation experiment of 2014, show a positive relationship between the number of nestlings and the visits the parents pay to the nest (Oomen, unpublished, 2014). Therefore, it is reasonable to say that parents of enlarged broods had a greater workload compared to the other birds and that manipulation had an effect of parental effort.

Were costs of reproduction already paid?

The lack of any effect on the probability to get a breeding box could be the consequence of the fact that costs of reproduction may have been paid before the beginning of the breeding season 2015.

The survival effect that was detected in the first part of winter was not found by Nicolaus et al. (2012) in plots under natural conditions (control plots). So in the same period of the year also under natural condition Nicolaus et al (2012) did not find an effect in the same study population. This discrepancy in the occurrence of survival cost of reproduction has been observed earlier (see intro essay Fokkema for review) and is also were the hypothesis of Nicolaus et al (2012) on the interaction between the occurrence of fitness costs of reproduction and the level of competition in the environment fits in. The fact that Nicolaus et al (2012) did find survival costs of reproduction in plots with high competition during the second half of the winter led them to hypothesize that differences in competitive ability between parents played a role after midwinter. The authors also argued that in this period competition due to adverse natural conditions would have been enhanced. In our case however it may have been that the level of competition under natural conditions was already so high before midwinter, that differences in competitive ability in parents already played a role then which caused the selective disappearance we observed.

Did competition for nest-boxes really occurred?

To assess if competition was truly enhanced by the reduction of breeding sites, it should be measured. Unfortunately it is not easy to directly measure competition. What has been occasionally observed as sign of fight, like feathers, blood or dead birds around or inside the nest-boxes, cannot be certainly addressed as a direct consequence of intra-specific competition. Furthermore, the lack or inaccuracy of data from the past years regarding this kind of observations don't allow any comparison.

The presence of natural cavities as alternatives breeding sites and the rate of occupancy have been also investigated but are not discussed in this paper.

Was sample size too limited?

One limitation that could have biased the analysis regarding the probability of gaining a nest-box is the small sample size. Post hoc power analysis indicates quite low power (a difference between probability of 0,62 in the reduced category and 0,29 in the enlarged could have been detected with a power 58%).

Interaction between sex and manipulation during the second part of winter:

Females of the enlarged category had a lower survival to the second half of winter (from December 2014 to March 2015). The analysis does not show a strong effect but the result is still significant. The reasons for this can be the result of behavioural differences. Females that raised enlarged broods could happen to be less territorial and more prone to migrate elsewhere in case of scarcity of breeding places (Perrins, 1979). The migration rate has not been investigated in details in this study, therefore there are no evidences to prove this hypothesis.

The other option is that females raising enlarged broods die more easily for the consequences of the increased parental effort. However, there are no indication that manipulation had more severe effects on females rather than on males that could explain this difference in survival.

Conclusion:

The importance of the ecological context

The general results of this study are in line with the theory that family size negatively affects parental fitness later in life. This is supported by the evidence that birds that reared enlarged broods in the previous breeding season had a lower survival in the first part of winter, in contrast to earlier work. The absence of any effect of manipulation on the probability of parents to acquire a nest-box during can be found measured in the breeding season suggests that differences in competitive ability may have already played a role before midwinter and that the costs of reproduction have already been fully paid in this period.

The fact that this results differ from others from studies on the same population taken in different years (Nicolaus et al., 2012), shows the influence of ecological conditions. Variations in temperature, predation pressure or other ecological variables can influence how and when costs of reproduction are paid off.

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