CHAPTER 1

General introduction

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NATURAL SELECTION HAS A SOCIAL COMPONENT

Evolution is commonly defined as the change in gene frequencies in populations over successive generations, and the process of natural selection has a strong social component because competition is involved (Darwin 1859). As Stephen Stearns (1976) phrased it “fit organisms are defined as those better represented in future generations than their relatively unfit competitors”. The fitness of an individual is thus always measured relative to others. Differences in individual traits often matter in social interactions with others such as the competition for mates, food or breeding sites, and in non-social interactions, for instance one individual may be better to evade predators than others. Overall, such relative differences in the performance of individuals to others result in individual differences in survival and/or reproduction and hereby their contribution to future generations (fitness).

Individual fitness is thus not only determined by individual traits but also by the interplay between those individual traits and the traits of other individuals (Moore, Brodie & Wolf 1997; Wilson 2014). When the level of competition for resources in the environment of an individual is high, such effects of others on the fitness of the individual may be especially important. Under competition, individuals with traits that ensure a relatively higher competitive ability to that of others may benefit from a higher access to resources and consequently have a higher fitness. Competition thus acts as a selective force, favouring individuals with traits that ensure a higher competitive ability.

In this thesis I explore whether competitive ability is affected by individual reproductive decisions with the aim to clarify how competition can affect selective forces on individual reproductive behaviour.

WHY DON’T ORGANISMS PRODUCE MORE OFFSPRING?

The background of my thesis lies in the seemingly simple question: why don’t organisms produce more offspring? Simply reasoned, if the evolutionary goal of life of each individual is to maximize its fitness, why have ‘Darwinian demons’ not evolved that produce infinite amounts of offspring starting right after birth (Monaghan & Nager 1997; Barnes & Partridge 2003)? The theory formulated to answer this question is called life history theory. Van Noordwijk and de Jong (1986) defined life history theory as: “an elaborate answer to the simple question of why having more offspring is not always selected for”.

One central component of life history theory is the concept of trade-offs. The general expectation is that all trade-offs, even if they act on the long-term, are the result of differential allocation of resources between traits. If limited resources need to be allocated over different traits vital to the individual, then a higher investment of an individual to one trait will go at the expense of the other trait(s). Individuals thus face ‘decisions’ in which traits to invest and it is assumed that the long history of evolution has selected the strategy to allocate investment as such that lifetime fitness is maximized (Stearns 1989; Lessels 1991). Two major trade-offs have been formulated that determine the number of
offspring an organism can produce over its lifetime 1) the trade-off between quality and quantity of offspring and 2) the trade-off between fitness from current and future reproduction (Lack 1947; Williams 1966). These trade-offs are thought to be key in determining the life history traits of an individual as its growth, the family size it produces, when and how often it reproduces and its lifespan (senescence, Atema 2017).

**THE TRADE-OFF BETWEEN QUALITY AND QUANTITY OF OFFSPRING**

The idea of the existence of a trade-off between the quality and quantity of offspring was formulated by David Lack (Lack 1947, 1948, for a complete overview of the history see: Birkhead et al. 2014). Lack hypothesised that family size evolves through natural selection resulting in the maximal number of surviving offspring (‘the most productive family size’). He hypothesized that the number of offspring parents can successfully raise is determined by the amount of resources parents can provide. Because resources and time are limited, an increase in the quantity of offspring logically goes at the expense of the quality of each individual offspring. Lower quality offspring often have a lower probability to survive until the following year (i.e. recruit) and therefore the fitness that parents gain by siring more offspring is expected to level off or even decline (Smith and Fretwell 1974; see fig. 1.1, grey lines). Empirically the trade-off between quality and quantity of offspring is well established (Roff 1992; Stearns 1992).

**THE TRADE-OFF BETWEEN CURRENT AND FUTURE REPRODUCTION**

One point that Lack did realize, but based on his investigations on great tits (*Parus major*) considered less important, was that parents themselves may face fitness costs of a higher investment in reproduction (Roff 1992). At about the same time, Reg Moreau (1944) studied clutch sizes in altricial birds, and he considered that such costs were important in the regulation of clutch size. Moreau proposed that the strain to raise larger clutches may result in a lower survival of parents. Due to this survival effect parents that would produce smaller clutches may produce more offspring over their lifetime as opposed to parents that produce larger clutches. This idea was later formalized by George C. Williams in 1966, who is generally regarded as the founder of the trade-off between current and future reproduction. Williams hypothesized that a higher investment into current reproduction may go at the expense of the parent’s residual reproductive value or, phrased differently, at the expense of the fitness parents may gain from future reproduction (depicted by the black solid lines in fig. 1.1). The loss in fitness from future reproduction as a consequence of the investment in current reproduction was termed ‘the cost of reproduction’ (dark rectangles in fig. 1.1). Because natural selection favours individuals that have the highest genetic contribution over their entire life-time, parents experiencing such a cost should produce families smaller than the size that would produce the most surviving offspring (Lack’s family size) from a single family as they can still gain fitness
Figure 1.1: Costs and benefits of family size and how they relate to optimal family size. In the panels from A to C the negative impact of family size on parental fitness increases (black solid lines) while the offspring fitness curve (grey solid lines) is assumed unaffected. The maximum (indicated by a *) of the sum of parental and offspring fitness (dark striped line), i.e. the optimal family size, shifts to lower values with increasing negative effects of family size on parental fitness (panel C). This coincides with an increased cost of reproduction at the optimum (darkgrey vertical blocks).

from future reproduction (summed parental fitness depicted by the black striped line in fig. 1.1, the asterisk depicts the optimal family size for the parent).

This idea implies that, if the fitness costs of reproduction are higher, parents should lower their investment in the current reproductive attempt (fig. 1.1, most right figure) and that if the fitness costs of reproduction are lower parents should increase their investment into current reproduction (fig. 1.1, most left figure). This means that any factor that affects the occurrence of fitness costs of reproduction will affect the level of reproductive investment of parents that maximises fitness (Gadgil & Bossert 1970; Charnov & Krebs 1974).

HOW CAN COMPETITION SHAPE REPRODUCTIVE TRADE-OFFS?

Both the trade-off between quality and quantity of offspring and the trade-off between current and future reproduction have been shown to be affected by competition. The trade-off between quality and quantity of offspring was shown to be stronger with high competition: parents had higher fitness when producing smaller families with higher ‘quality’ offspring when competition was high whereas under low competition parents gained more fitness by producing larger families with lower ‘quality’ offspring (Both, Visser & Verboven 1999; Sinervo, Svensson & Comendant 2000). In his thesis Both (1998) hypothesized that potentially juveniles from smaller families have a higher competitive
ability and therefore, under high competition, were better able to recruit into the population the following year.

Though the trade-off between quality and quantity of offspring may thus be an important component determining the reproductive decisions of parents under competition, in this thesis I chose to focus my attention on the influence of competition on the trade-off parents face between current and future reproduction.

In recent years, researchers have started to investigate how competition can affect the trade-off between current and future reproduction and it is in the footsteps of these researchers that I follow in this thesis (Siefferman & Hill 2005a; Oksanen et al. 2007; Nicolaus et al. 2012a). I focus on testing the consequences of reproductive investment on the competitive ability of parents and how under high competition this can lead to fitness costs of reproduction. In the next sections of this introduction, I will first discuss how the cost of reproduction was measured, then the importance of competition in mediating its occurrence and finally the research design of my thesis.

TESTING THE THEORY: HOW TO QUANTIFY THE FITNESS COST OF REPRODUCTION?

Four different empirical approaches have been used to quantify the costs of reproduction 1) phenotypic correlations, 2) phenotypic manipulations, 3) genetic correlations and 4) selection experiments (Lessels 1991; Alonso-Alvarez & Velando 2012). Here I will focus on the first two approaches.

Phenotypic correlations
If a trade-off between current and future reproduction exists, then an increase in allocation to current reproduction will go at the expense of future reproduction. Researchers have tested this idea by studying phenotypic correlations, for instance by regressing components of current reproduction to components of future reproduction. If a trade-off exists one expects a negative correlation, but in many cases such phenotypic correlations were positive (for examples of such studies see: van Noordwijk & de Jong 1986; Lessels 1991). One explanation for this is that negative phenotypic correlations are masked by differences in the ‘quality’ of parents or the ‘quality’ of the environment they are in. Some parents are ‘better’ due to their intrinsic traits or the environment in which they live and therefore are able to produce more offspring seemingly without expense for their future fitness. Due to this potential confounding effect of quality differences between parents, phenotypic correlations are generally regarded as an unsuitable measure of trade-offs (Perrins & Moss 1975; van Noordwijk & de Jong 1986; Lessels 1991).

Phenotypic manipulations
Phenotypic manipulations are the primary method developed to quantify trade-offs between current and future reproduction by controlling for potential differences in the ‘quality’ of parents and/or their environment. Here the investment into current reproduction of the parent is manipulated by the researcher independently from the ‘quality’ of the
parents or their environment. Phenotypic manipulations of family size can be divided in indirect and direct manipulations. For indirect manipulations family size is manipulated indirectly, for instance through supplementary feeding of the female avian clutch size was increased, and the subsequent fitness consequences were analysed (Lessels 1991). Direct manipulations are manipulations where the family size that parents have to raise is manipulated by taking away or adding eggs (in the case of egg laying species) or offspring. One way a researcher can for example do this, is by manipulating the family size that parents have to raise by taking away a fixed or variable number of offspring of some randomly selected families and adding them to other families. A third set of randomly allocated nests are then often kept as a control (e.g. Perrins & Moss 1975; Blondel et al. 1998; Koskela et al. 1998; Parejo & Danchin 2006). A more balanced method to account for potential quality variation, employed also in this thesis, is to match three families with as much a similar background as possible (e.g. same initial family size, same laying date, same offspring weight prior to manipulation) and exchange young between two families, reducing one and enlarging the other and keeping the other as control (e.g. Sanz & Tinbergen 1999; Fokkema, Ubels & Tinbergen 2016). By doing such direct manipulations researchers thus create different manipulation groups and for the average parent of such a group, researchers subsequently quantify the effects of the manipulated family size on their future survival and/or fecundity (Lessels 1991). The general assumption in both indirect and direct manipulations is that parents respond to the manipulated family size as if it was their own family size decision.

A critique of the method of manipulation within a matched trio of nests is that enlarged broods in matched trios of the larger natural sized broods and reduced broods in matched trios of the smaller sized natural broods, will end up outside the natural range of normal brood sizes. In the method of random assignment of manipulations this can be circumvented by always enlarging the smallest natural broods and always reducing the largest natural broods. This means however that the random manipulations of family size will not be independent of the original natural family size of the parent. Furthermore, one can argue that from an individual perspective every manipulation of family size, even within the natural population range of family sizes, results in a family size outside the natural range for that individual.

**Mixed empirical evidence for fitness costs of reproduction**

Reviews of studies in which family size was experimentally manipulated (see above) show that the evidence for the trade-off between current and future reproduction is mixed. While some studies indeed find that parents pay costs of reproduction others do not (avian: Linden and Möller 1989; Dijkstra et al. 1990; Stearns 1992; Roff 1992; Golet et al. 1998; Parejo and Danchin 2006; Santos and Nakagawa 2012; mammals: Stearns 1992; Hamel et al. 2010). In a meta-analysis of avian studies Santos and Nakagawa (2012) showed that males in response to increased reproductive effort suffered an approximate decrease of 26% in the probability of survival compared to control males, whereas
females with increased reproductive effort survived equally well as control females. This suggests that the sexes may also differ in whether they pay fitness costs of reproduction. It seems surprising that costs of reproduction are often not found, because in empirical studies often individuals produce smaller families than the most productive one, and hence an extra selection pressure should be involved (Klomp 1970; Vanderwerf 1992).

Most of these reviews were based however on studies that tested effects of family size on fitness components of future reproduction rather than a lifetime fitness estimate. This might have led to wrong conclusions on the presence or absence of a cost of reproduction (Daan & Tinbergen 1990). Furthermore the different conclusions on the existence of cost of reproduction between studies may have been caused due to differences in the traits of the investigated study species and the methods used to manipulate family size. One important trait of the investigated study species is lifespan. Hamel et al. (2010) showed that a species lifespan can determine which fitness components are affected by family size. Based on a review the authors showed that longer-lived ungulates paid reproductive costs of reproduction (future fecundity costs) more frequently while shorter-lived rodents paid survival cost of reproduction more frequently. Depending on the lifespan of the study species and the fitness components analysed, studies may thus arrive at different conclusions regarding the occurrence of costs of reproduction.

A different point regarding the lifespan of species is that the relative importance of the trade-off between current and future reproduction versus the trade-off between quality and quantity of offspring may differ. For instance, for very short-lived species in which future breeding attempts yield no or little addition to the individual's lifetime fitness, reproductive decisions may only be governed by the trade-off between quality and quantity of offspring. In such cases fitness costs of reproduction may not occur (i.e. every adult dies after reproduction).

One important methodological aspect by which studies differ is the reproductive phase in which family size is manipulated. In avian species, researchers have manipulated the family size that parent have to raise by 1) forcing parents to lay new eggs by removing each egg after it has been laid, 2) adding or removing eggs during the incubation phase or 3) adding or removing nestlings either right after or a few days after hatching. Visser & Lessells (2001) showed that survival costs of reproduction were most severe for females in which family size had already been manipulated during egg laying, followed by the females whose family size was manipulated during the incubation phase and lowest for the females whose family size was manipulated during the nestling phase. In a different study de Heij and co-workers (de Heij, van den Hout & Tinbergen 2006) also showed that when extra fitness costs of family size incurred by parents during incubation are taken into account this can make a marked difference in the conclusions on the selective pressures on individual family size.

To check whether the mixed evidence for fitness cost of reproduction was the result of 1) the focus on measuring effects of family size on distinct fitness components rather than a lifetime fitness estimate and 2) differences in the methodology and investigated species between studies, I performed a review focusing on studies investigating similar study species (Parus spp) and in which family size was manipulated using a similar method
(manipulations during the nestling phase). I chose for these study species and method of family size manipulation because of the relevance for my own research (discussed further below). Eight of the studies I reviewed could be assigned as having a complete estimate of lifetime fitness (table 1.1, last column) and overall the evidence of these studies proved mixed.

Table 1.1: The effect of experimental family size on the fitness costs of reproduction reported in 15 reviewed studies using a similar method of family size manipulation for similar study species. $SB_p =$ probability of starting a second brood in year $x$, $S_p =$ survival probability to year $x+1$, $B_p =$ clutch size in year $x+1$. If left blank the fitness component was not measured in the study. The last three columns indicate respectively if second broods were known to occur in the area (present or absent), whether the study can be regarded as complete in terms of fitness measured (1 = complete or 0 = incomplete) and the overall fitness estimate of the cost of reproduction for the complete studies. Superscript: 1: Only for second calendar year female birds; 2: Only in environments with male biased sex ratio. F = females only, M = males only, no effect found in the other sex.

<table>
<thead>
<tr>
<th>Study: reference</th>
<th>Study area</th>
<th>Study species</th>
<th>$SB_p$</th>
<th>$S_p$</th>
<th>$B_p$</th>
<th>SB present</th>
<th>Complete</th>
<th>Fitness sum</th>
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</thead>
<tbody>
<tr>
<td>Blondel et al.  (1998)</td>
<td>Corsica (FR)</td>
<td>Blue tit (Cyanistes caeruleus)</td>
<td>0</td>
<td>0</td>
<td>-</td>
<td>absent</td>
<td>1</td>
<td>0</td>
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<td>Parejo &amp; Danchin (2006)</td>
<td>Parc Regional (FR)</td>
<td>Blue tit (Cyanistes caeruleus)</td>
<td>-</td>
<td>0</td>
<td>+</td>
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<td>Horak (2003)</td>
<td>Tartu (EST)</td>
<td>Great tit (Parus major)</td>
<td>+(F)</td>
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<td>absent</td>
<td>0</td>
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<td>Linden (1988)</td>
<td>Gotland (SE)</td>
<td>Great tit (Parus major)</td>
<td>-</td>
<td>-</td>
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<td>present</td>
<td>0</td>
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<tr>
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<td>Revinge area (SE)</td>
<td>Great tit (Parus major)</td>
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<td>Stjernman et al. (2004)</td>
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<td>Orell &amp; Koivula (1988)</td>
<td>Oulu (Fl)</td>
<td>Willow tit (Parus montanus)</td>
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<td>Orell et al. (1996)</td>
<td>Oulu (Fl)</td>
<td>Willow tit (Parus montanus)</td>
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<td>Sanz &amp; Tinbergen (1999, 2004)</td>
<td>Lauwersmeere (NLD)</td>
<td>Great tit (Parus major)</td>
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<td>Great tit (Parus major)</td>
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<td>Great tit (Parus major)</td>
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THE IMPORTANCE OF THE MECHANISMS BEHIND FITNESS COSTS OF REPRODUCTION

To understand why costs of reproduction have been found in some study systems in some study years and not in others, knowledge of the mechanisms behind the occurrence of fitness cost of reproduction is essential. As Derek A. Roff (1992) phrased it:

“The question is not whether there are costs but under what circumstances and what ways a cost is exhibited”.

Knowledge of the mechanism can further help to make better quantitative predictions of fitness effects of individual reproductive decisions (Stearns 2011). Such predictions are necessary, because it is impossible to measure the fitness consequences of family size manipulations experimentally year round and for every situation.

Physiological mechanisms
Fitness costs of reproduction may be mediated both by physiology or ecology or a combination of both (Lessels 1991; Zera & Harshman 2001; Speakman 2008). The focus of most studies has primarily been on physiological mechanisms behind fitness costs of reproduction. These studies show that reproductive effort entails physiological costs as depletion of energy stores, depletion of micronutrients, physiological stress, oxidative stress, immunosuppression and costs to maintain neuroendocrine control systems (discussed in: Alonzo-Alvarez & Velando 2012). In turn these physiological costs can result in effects on the future fitness of parents (survival or future fecundity). While these physiological mechanisms tell us something about how cost of reproduction are being paid, they do not answer why in some study populations costs of reproduction have been detected and not in others.

Ecological mechanisms
Predation
Knowledge of the ecological mechanisms likely provides more insight in the occurrence of costs of reproduction. Studies on ecological selection pressures behind the occurrence of fitness costs of reproduction have up to now focused mostly on the relationship between reproductive effort and the predation risk of parents and their offspring. Several empirical studies have demonstrated that a higher reproductive investment increases the risk of predation of parents and/or their offspring within the breeding season (discussed in: Lessels 1991; Roff 1992; Alonzo-Alvarez & Velando 2012). Other studies have shown that parents reduce their reproductive effort when the local level of predation is higher (Magnhagen 1991; Martin, Scott & Menge 2000; Fontaine & Martin 2006). Depending on the local level of predation, parents may thus pay costs of reproduction and thus be selected for having a lower reproductive investment.

Such physiological and ecological mechanisms responsible for fitness costs of reproduction can act independently, but may also interact with one another. Parents in physio-
logical worse condition due to increased parental effort may for instance have a reduced ability to escape predators (Alonso-Alvarez & Velando 2012).

**A role for social mechanisms: competition**

Intra- and interspecific competition is a major ecological selection pressure that, along with predation, could mediate the costs of reproduction. Researchers have long been aware of the potential importance of competition in determining the outcome of parental reproductive decisions. In many populations a negative relationship between clutch or litter size and population density has been found (e.g. birds: Kluijver 1951; Perrins 1965; Both et al. 2000; Nicolaus et al. 2013; mammals: Morris 1989, Koskela et al. 1999, Bonenfant et al. 2009). Several proximate mechanisms have been formulated to explain these density dependent effects on family size, most of them related to higher levels of competition for resources as food or territories at high population densities (Kluijver 1951; Newton 1998). Correlational evidence shows that cost of reproduction are higher at high population density and presumably competition (Festa-bianchet et al. 1998; Oksanen et al. 2007). Due to increased costs of reproduction at high population density parents may be under selection to produce smaller family sizes. Experimental studies in which the occurrence of fitness costs of reproduction under competition are investigated are however scarce. A likely reason is that such a study involves not only manipulating the family size that parents have to raise, but also the level of competition in the parents’ local environment.

Nicolaus et al. (2012a) measured the cost of reproduction under different competitive regimes within a great tit population. Together with her co-workers, she manipulated the competitive environment by changing plot fledgling sex-ratio and density, and additionally measured the cost of reproduction on the basis of family size manipulations. Only in the (presumed) most competitive environments (with a male-biased fledgling sex-ratio) parents paid a survival cost of reproduction. Interestingly, this survival cost was paid well after the breeding season, namely in winter. Nicolaus hypothesized that parents that raised reduced families may have survived better under high competition, because their competitiveness was less compromised as a result of reproductive investment. Under increased competition parents with a lower reproductive investment may thus benefit later in life from a higher access to essential resources (such as nest boxes or mates) which in turn may result in a higher fitness (fig. 1.2). Such carry-over effects (Harrison et al. 2011; Williams 2012; O’Connor et al. 2014) of reproductive effort on a parents competitive ability could provide a mechanism to explain the trade-off between current and future reproduction. This is an important idea, because if reproductive investment negatively affects parental competitive ability and subsequent fitness, the level of competition in a parents’ local environment can exert a selective pressure on parental reproductive investment (fig. 1.2). This could provide an adaptive explanation for the inverse relationship between family size and population density and also explain why studies differ in the detection of fitness cost of reproduction.

If the cost of reproduction depends on both individual investment and the competitive environment, this implies that individual fitness is not only the product of individual
**Figure 1.2:** Schematic overview how competition within the social environment can affect the fitness consequences of individual family size decisions. On the left hand side of the figure the traditional view on the fitness consequences of individual reproductive decisions is depicted. Individual family size decisions are expected to affect both the fitness parents gain from current reproduction (recruitment and future fecundity of the offspring) and from future reproduction (future survival and future fecundity of the parent). Selection is expected to shape individual family size decisions as such that the individual fitness is maximized (optimal family size). In this thesis I investigate a potential mechanism behind effects of family size on the fitness parents may gain from future reproduction (right hand side of the figure). Nicolaus et al. (2012a) hypothesize that reproductive effort may negatively affect the future competitive ability of parents: parents with a lower reproductive effort are expected to have a relatively higher competitive ability than other parents in their local environment. When the level of competition in the parents’ environment is high these differences in parental competitive ability due to previous reproductive effort may affect the fitness of parents. In turn these fitness effects of family size may cause a selective pressure on individual family size decisions, and hence the optimal family size decision does also depend on the decisions taken by future competitors.

Reproductive decisions, but also depends on the reproductive decisions (and hence the competitive ability) of other individuals within the same population (fig. 1.2). If for instance an individual invests more into current reproduction, then this is especially detrimental if other individuals in its local environment invest less into current reproduction, because the focal individual pays the higher reproductive costs when competing with individuals with a relatively higher competitive ability. Such frequency dependent effects of the social environment would imply that family size decisions should be viewed in a

**FAMILY SIZE AND COMPETITIVE ABILITY: THE EXPERIMENTAL APPROACH**

This thesis aims to obtain empirical evidence for the importance of competition in understanding the costs of reproduction, in the hope to contribute to the fundamentals of life-history theory. My main aims were to test whether 1) family size negatively affects the competitive ability of parents in later life and 2) whether under competition this leads to fitness cost of reproduction. To this end, I manipulated the family size that great tit parents had to raise and subsequently tested the ability of the parents to compete during the following winter or spring over resources. I manipulated competition among the parents in winter by inducing competition for a) supplementary winter food or by b) the number of roosting sites available and in spring by inducing competition for breeding sites by either c) reducing the quantity or d) the quality of the nest-sites available.

**Study population and conducted research**

I conducted my studies in the Lauwersmeer great- and blue tit (*Cyanistes caeruleus*) nest box breeding population (for map of study area in 2005–2014 see fig. 1.3). The area was reclaimed from the sea in 1969 after which it was partly planted with mostly deciduous trees and some conifers. The nest box population was established by the ’Rijksdienst IJsselmee Polders’ around 1980 after the trees had grown large enough. In 1993, Joost Tinbergen took over the population at that point living in 80 nest boxes spread over 7 plots. Over time as research progressed the number of nest boxes was expanded first to 200 boxes in 1994-2003, then 400 boxes in 2004 and finally 600 nest boxes in 2005-2014. In the last period the nest boxes were concentrated in the north of the Lauwersmeer area and divided over 12 study plots (fig. 1.3). The study population expanded in concert with the number of nest boxes over time (see fig. 1.4 for overview of nest box numbers and occupation over time). In 2015, for the breeding box competition experiment we reduced the number of boxes from 600 to 120 (see next section).

Since its start in 1993, the focus of the research of Tinbergen and his co-workers has been on experimentally measuring the fitness consequences of reproductive decisions of parents on family size and sex ratio in the nest in the context of the social environment. Their main aim was to test ideas about optimal clutch size and optimal sex allocation under competition. In the first years (1995, 1997 and 1998), Tinbergen worked among others with J.J.Sanz. In contrast to other study populations (Tinbergen & Verhulst 2000) the number of feeding visits and the daily energy expenditure in the Lauwersmeer population increased with experimental brood size and did not level off (Sanz & Tinbergen 1999). The selective pressure for family size was positive: parents raising enlarged families had a higher fitness (Tinbergen & Sanz 2004). Because the experiments focussed on the nestling phase, thereby missing potential costs of reproduction during the incubation
Figure 1.3: Map of the study area (2005–2014) with the 12 study plots indicated in black. Each plot consisted of 50 nest boxes. 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 are located.

phase, during her thesis de Heij focused on incubation costs. She proved with experimental work in the same population that when costs of incubation were taken into account, the positive selective pressure as established by the family size manipulations changed into stabilizing selection (de Heij 2006). Thus demonstrating that to understand optimal clutch size, the selective pressure in all phases of the reproductive cycle needs to be taken into account. In the years 2005, 2006 and 2007 Nicolaus and Michler designed an intricate experiment to investigate the fitness consequences of parental reproductive decisions on sex-ratio and family size in a variable social environment (Nicolaus 2009; Michler 2010). Based on family size manipulations they showed that while selective pressures on family size in the first period of research in the Lauwersmeer were positive (1995, 1997 and 1998, see above), they had stabilized in the period over which they conducted their studies (2005, 2006 and 2007). In 2008 and 2009 Radersma continued the work on the ecological and evolutionary consequences of brood sex ratio variation (Radersma 2011). He showed that offspring of broods with experimentally manipulated equal sex-ratios had the highest fecundity in their first year of reproduction and he inves-
Figure 1.4: Overview of the number of nest boxes available in the Lauwersmeer area since the start of the research in 1993 until its end in 2015. The number of boxes occupied by blue tits and great tits, in the area are depicted. In rare cases boxes were occupied by other species, but this was a negligible amount.

tigated the mechanisms underlying this effect, among which the effect of sex-ratio on the social networks of offspring in later life. Besides the above work, Dingemanse and Nicolaus pioneered in the population with their work on the personalities of great tits and how the environment and population density in particular can shape the variation in personalities (Dingemanse et al. 2012; Nicolaus et al. 2012b, 2016). All work in the Lauwersmeer study population aimed at quantifying selection pressures on individual traits such as family size and personality in a social context. My thesis continues in this long tradition of experimental work.

OUTLINE OF THE THESIS

Part I. Parental competitive ability in winter
In the first part of this thesis (chapter 2) we tested whether experimental family size negatively affected the ability of great tit parents to claim a nest box for roosting in winter. We drastically reduced the number of roosting boxes available for a short period in winter during two study years. Next, we measured whether parents were able to claim a roosting box depending on their previous year’s reproductive investment and hence whether this brief period of increased competition for roosting sites resulted in a subsequent survival cost of reproduction.

In box A we investigate whether experimental family size negatively affected the ability of parents to compete for food during the winter period. During one study year, from October until February we provided supplementary food at locations throughout the study area. At these feeding locations we performed direct observations on competitive interactions involving manipulated parents.
Part II. Parental competitive ability in spring
In the second part of this thesis, we used the confirmed preference for deep nest boxes by great tits in our study area (chapter 4) as a tool to test whether family size negatively affected the ability of parents to compete for deep nest boxes in the following breeding season (chapter 3). We induced competition for deep nest boxes, by reducing their availability and offering shallow boxes as an alternative. This approach allowed us to identify the parents who lost out in the competition for deep nest boxes because they were more likely to occupy an abundant shallow box. In chapter 5, we estimated the fitness consequences of breeding in a deep or shallower box within the blue tit population, focusing especially also on measuring the supposed lower predation risk of deeper cavities. We did this using an experimental framework in which effects of nest box depth on breeding success could be estimated separately from effects caused by potential differences in the ‘quality’ of parents inhabiting deep and shallow nest boxes.

In chapter 6 we further investigated the hypothesis that family size negatively affects the competitive ability of parents in spring. We induced competition for nest boxes among the great tits, by drastically reducing the number of breeding boxes just before the breeding season. Since few natural holes are available great tits were forced to compete for a box to breed in. During the breeding season we measured which great tits were able to claim a breeding box.

In the final chapter of this thesis (chapter 7) I synthesize our findings. I discuss the evidence we obtained for the hypothesis that family size negatively affects the competitive ability of parents in later life and the consequences for their future fitness. Using the data we gathered, I evaluate how competition in the local environment of parents may pose a selective pressure on their reproductive investment and discuss the implications and generality of our findings.
PART I
Parental competitive ability in winter