SUMMARY

The subject of this thesis is whether conditions during early ontogeny affect reproduction and survival of offspring later in life and **how** they may affect these fitness components. The approach taken in this laboratory study is to manipulate brood size experimentally and assess effects on offspring after their independence.

These questions originate from two lines of research. Firstly, it has become clear from a number of long-term field studies on bird populations that there are large differences between individuals in lifetime reproductive success. Estimates of the proportion of individuals that do not at all contribute to the next generationn vary from 62 to 87 percent. This is partly caused by the fact that a large proportion of fledglings die before they can reproduce and in part because the individuals that do reproduce vary greatly in reproductive success. The question is how such extreme differences in lifetime reproductive success are caused. The importance of genetic variation is considered limited because it can be expected theoretically that genetic variance is low in traits closely related to fitness because such traits would be subjected to a strong selection pressure. However, ontogenetic circumstances are considered potentially important determinants of individual differences in lifetime reproductive success because of the long term effects they may have on the adult phenotype.

The second line of research departs from the prediction that individuals will behave in such a way that their fitness is maximized, this is called optimal behaviour. This hypothesis can be tested by manipulating the behaviour experimentally and subsequently measuring the consequences for fitness. If organisms behave optimally it is expected that every manipulation of the behaviour will result in a fitness reduction. A number of studies have tested these ideas by manipulating the size of the brood or clutch, a behaviour which can be manipulated relatively easy by adding or removing eggs or young. These studies have provided evidence that individual birds lay the number of eggs which maximize their lifetime reproductive success. In the studies mentioned it was found that offspring reared in enlarged broods generally grow less well and have a higher chance of dying during the nestling phase and as fledglings, than offspring reared in broods of normal size. They are also less likely to be recaptured as a breeding bird and in two studies it was found that they produced fewer offspring.

Effects of brood size on offspring after their independence deserve more study. In the first place because up to now not effects of brood size on the survival and reproduction of offspring once they are adults have not received much attention, while the incorporation of such data in estimates of optimal brood size should improve their accuracy. However only when such data are gathered in the field where natural selection operates, can they be used for this purpose. This subject is therefore not within the scope of the project which is confined to the laboratory. Nevertheless, laboratory experiments can be used to answer relevant questions. Another important reason to study long term effects of brood size more extensively is that little is known about how effects of brood size on components of fitness of offspring could emerge. Such effects may arise in different ways. For instance offspring from large broods may

be less likely to be recaptured as breeders because they are less likely to survive. Survival is often measured in field studies as recapture rate and this may be determined by mortality but also by the extent to which individuals emigrate. Other possible causes of a lower recruitment rate in birds from enlarged broods may be that they are less capable to acquire a mate or less able to defend a nest site. Studying effects of brood size on the ethological functioning of offspring may help answer this type of questions. This is the approach taken in the study reported in this thesis. The laboratory setting provides better possibilities than the field for the detailed study of behaviour needed. The findings may give more insight in to the processes that could play a role in the field in causing effects of rearing conditions on fitness. The aim of the experiments described in this thesis was to contribute to this insight. To this end effects of brood size manipulation on fitness components (mortality and aspects of reproduction) of offspring were assessed as well as effects on characteristics which may mediate such effects (morphology, sexual attractiveness and social dominance). Throughout I have compared natural siblings (brothers or sisters) which were artificially reared apart in small broods (two young) and large broods (six young).

In Chapter 2 an assessment is made of long-term effects of brood size on the morphology and mortality of offspring. Birds of both sexes reared in small broods were consistently larger and heavier as adults, which confirms and extends the results of brood size manipulations in the field. Effects on some traits were temporary, individuals reared in large broods had shorter wings as young adults but caught up on wing length later. In addition, males from small broods had redder beaks as young adults, a trait correlated with sexual attractiveness in this species, but this difference disappeared later in adulthood. A sex-specific effect on mortality of offspring was found: females but not males from large broods were more likely to die. The effect occurred in adult offspring well after the manipulation and under *ad libitum* feeding conditions. This suggests that brood size may have an even stronger impact on mortality under natural circumstances which are likely to be harsher than those in the laboratory. If confirmed under natural circumstances, the findings may imply that optimal brood size depends on offspring sex ratio. Further study of effects of brood size on the physiology and aggressive interactions of male and female offspring may shed more light on the mechanism mediating the higher vulnerability of females.

Effects of brood size on subsequent pair formation of offspring are the subject of Chapters 3 and 4. In Chapter 3 the main question is whether brood size affects sexual attractiveness of young adult offspring. In choice tests, in which birds of the opposite sex could indicate there preference for an individual reared in a small or in a large brood by sitting seeking its proximity, it was found that males reared in small broods sang more and were more attractive to females. Male beak redness was correlated positively with female preference. Attractiveness may have important consequences for the reproductive success of males. Attractive males may be the first to pair and females may invest more in reproductive effort if paired to an attractive male. Females from small and large broods did not differ in attractiveness. In Chapter 4 the question asked is whether males from small and large broods at an older age still differ in success at

acquisition of a breeding partner. This was the case although at this age the initial differences in beak redness and song rate had disappeared by then. This indicates that the differential mating success is not a transient effect which disappears with maturation.

In Chapter 5 it is investigated whether brood size affects social dominance of adult offspring. In Experiment 1 dominance with respect to food was assessed. In this experiment a food container was used from which only one bird at a time could feed. In Experiment 2 social dominance of males from small and large broods was investigated. To this end a female was presented behind wire mesh, which was sufficient to provoke fights between the males with usually one obvious winner. No effects of brood size on social dominance were found in either context. The results suggest consistently that social dominance is not affected by brood size in this species.

The subject of Chapter 6 is the subsequent reproductive success of offspring reared in small and large broods. In one experiment some aspects of female egg production are assessed. Females reared in small broods layed larger eggs, but there were no effects on timing of the first clutch, clutch size or total number of eggs produced. In a second experiment the reproductive behaviour of offspring of both sexes was investigated. The birds were kept in small groups in a semi-natural situation (an aviary). No effects of the experiment on production of offspring were found. Possibly there were no adverse effects of brood size in this species on the reproductive parameters studied. Of course, this negative result under *ad libitum* feeding conditions in the laboratory does not preclude that such effects do occur in the wild. It is possible that the analysis of genetic parenthood would reveal differences in the number of offspring produced by individuals reared in small and large broods. For this purpose blood samples have been taken of all birds. It was however not feasible within the scope of the project to analyse them.

In conclusion, in offspring of both sexes an effect of brood size occurred which teaches us more about the way in which brood size might in nature affect the fitness of offspring. Females reared in small broods had a lower mortality later in life and males reared in small broods had a higher mating success than their siblings reared in large broods. It is obvious that both are likely to have substantial fitness consequences. However, the socalled "negative" results reported above, the failure to find an effect of brood size on traits of offspring during adult life may also be important. Patterns of effects that brood size or other rearing conditions have on the phenotype may vary between species or sex-age classes. For instance, rearing conditions could affect mainly the success of the first reproductive attempts of young adults, or effects of rearing conditions on competitiveness could be most prominent in species in which social dominance depends on body size.

Finally in Chapter 7 a review is presented of the current experimental evidence for long-term effects of brood size or food availability on offspring in birds and in rodents. The results clearly indicate that conditions during early ontogeny can affect components of lifetime reproductive success and several traits that may mediate such effects. In birds survival of independent offspring was affected by rearing conditions in

about half of the species studied and reproductive success (measured as number of offspring produced that became breeding birds themselves) was affected in all species studied but the number of studies was very small. In rodents effects of rearing conditions on reproduction are more established than in birds and more is known about mechanisms that may mediate effects of rearing conditions, but less than in birds is known about effects of rearing conditions on survival after independence. Taken together, the currently available evidence suggests a multitude of causal chains of events which would lead to consistent inter-individual variations in fitness traceable to early rearing conditions.