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Fighting for fitness

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General introduction and summary of main results

1

H. Martijn Salomons

Life history theory

Life histories lie at the heart of biology; no other field brings you closer to the underlying simplicities that unite and explain the diversity of living things and the complexities of their life cycles... Life history theory is needed to understand the action of natural selection, a central element of evolution, the only theory that makes sense of all of biology.... There is much to be done.

Stephen C. Stearns

In: *The evolution of life histories*

During life, each individual is faced with the fact that available resources (i.e. time and energy) in any particular environment are finite. As a result, resources allocated to one trait, or activity, are no longer available for investment in other traits or activities. This is one of the fundamental assumptions of life history theory and can be seen as the driving force behind natural selection. As a result, individuals are always faced with interactions between numerous processes and behavioral decisions (life history traits). These traits include for example growth, age at first reproduction, condition specific investment in reproduction, number and size of offspring, sex of the offspring and lifespan. When interactions between traits are directly related to fitness they are called trade-offs.

The main aim of this thesis is to broaden our understanding of the mechanisms by which trade-offs shape the life history of individual jackdaws. However, also the interaction of a number of life history traits with social dominance will be discussed to highlight the importance of this trait in the life history of jackdaws. This chapter provides a general introduction as well as a summary and discussion of the main results of this thesis. First, the potential use of telomere length as an indicator of physiological condition, aging and survival probability will be investigated (Chapter 2). Then an experiment where brood sizes were either enlarged or reduced is presented, to find out how environmental conditions during early

development affected the offspring (Chapters 3 and 4), but also how the parents coped with the increase in reproductive effort (Chapter 5). The last part of this thesis covers the importance of social dominance in the life of jackdaws and its interaction with in particular the number, quality (Chapter 6) and the sex of offspring (Chapter 7). In the last chapter (Chapter 8) recent evidence for sex dependent embryonic period from other studies will be discussed including a test whether this also applies to jackdaws, as such a mechanism can potentially have a profound effect on sex allocation.

Trade-offs

Natural selection is expected to maximize the fitness of individuals. In iteroparous species (i.e. having multiple breeding attempts), fitness is the sum of the total reproductive output of each individual over all its breeding attempts, which therefore also includes the reproductive value of its offspring. While reproductive effort within each breeding attempt should be focused on producing as many offspring of high quality (in terms of reproductive value) as possible, there is at the same time a limit to this amount because all resources allocated to the offspring (e.g. food and time) will no longer be available for investment in somatic maintenance and repair. These long term costs, in addition to direct costs like higher mortality risk through increase in foraging activity to feed the offspring, result in lower parental body condition and survival probability. As a

result, the amount of effort invested during each breeding attempt should always be determined by balancing current fitness benefits against the potential decline in fitness benefits of future breeding attempts. At the same time, the total number of offspring per breeding attempt will negatively affect rearing conditions of each individual offspring because this will lead to an increase of competition over the resources provided by the parents. Thus, there exists also an optimal number of offspring in a nest, in the sense that increasing this number would no longer increase reproductive value of the brood and could even lead to a decrease. These two trade-offs between current and future reproductive success and between the number and quality of offspring are the most prominent trade-offs between two life history traits (directly related to reproduction and fitness) in life history theory (see Figure 1.1).

Especially in the wild, the number of offspring at which overall fitness of an individual will be maximized (in birds commonly termed ‘optimal brood size’) is likely to depend on local environment, but most importantly on individual quality (physiological health and reserves). Therefore, correlational studies may hold little value when studying the trade-offs associated with clutch size. Such information can only come from studies that experimentally manipulated reproductive effort. The most popular tool to perform such manipulations is via brood size manipulation, where the number of offspring is either increased or decreased. Although such manipulations have indeed been shown to affect overall fitness of individuals either through decreased body condition, survival or future reproductive value of the parents or the offspring or even both, surprisingly little is known about the mechanisms underlying these effects. The aim of the brood size experiment in this study was therefore to provide more insight into these mechanisms, by assessing its effect on several physiological indicators of body condition and survival.

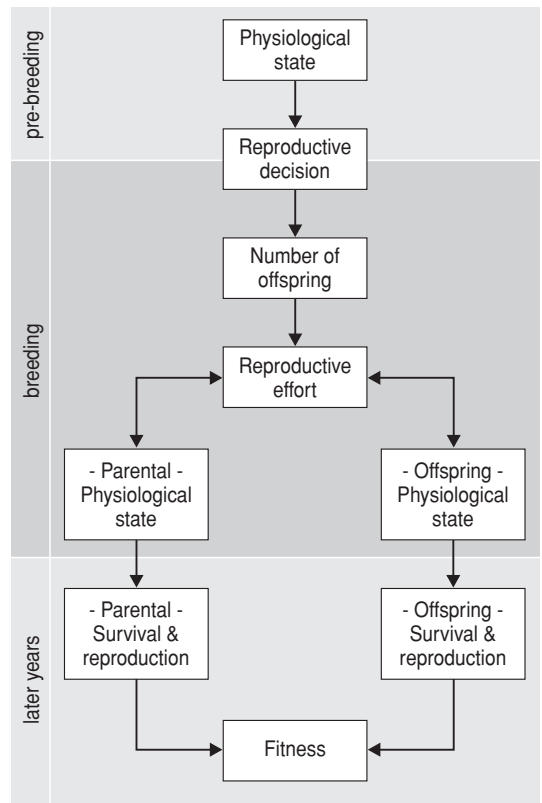


Figure 1.1. Life history of an iteroparous species. Each breeding season a reproductive decision is made on the basis of physiological state. Reproductive effort after this decision is a dynamic process, balancing investment in fitness benefits of the current reproductive effort against the expected fitness benefits of own future reproduction to optimize total fitness.

A long-term study on jackdaws

This study was conducted on free-living jackdaws, a hole breeding semi-colonial bird species. The largest part of the data presented here was collected in a colony at the Biological Centre (BC) in Haren (the Netherlands), a semi-urban environment (36 nest boxes). During this project we also established five smaller colonies located in a more rural area 5–10 kilometers south of Haren (5–20 nest boxes each). The BC

colony was established in 1965 after which it was used on and off for research (for example by August Röell in the late 1970's and Cor Dijkstra in 1989) before it was enlarged to 36 nest boxes in 1996 when the study was resumed.

Estimates of survival of jackdaws at the BC were around 80%, indicating an average lifespan of around five years (Chapter 6). Individuals that were over the age of ten years were however no exception, and there was one female that was at least 15 years of age when she sadly died in 2009. Jackdaws are sedentary and, even more noteworthy, highly monogamous. Pairs bond for life and most often return for breeding to the same nest box every year (especially after a successful first year of breeding). Therefore a large number of individuals could be studied over several consecutive years allowing the investigation of trade-offs both within and between breeding seasons. Moreover, free-living individuals face a multitude of trade-offs and behavioral options that are absent in captivity. Therefore, the jackdaw makes an ideal model species for the questions addressed in this thesis.

Brood size manipulations

The number of nestlings in a brood was manipulated when the oldest nestling in the brood was five days old. The parents readily accepted the new nestlings, resulting in an increase in the number of nestlings that they reared. On average parents whose broods were enlarged had to provide for approximately 5 nestlings while parents rearing broods reduced in size only had to take care of approximately 2 nestlings. Furthermore, total brood mass production for 'enlarged' broods between day 5 and day 20 was twice that recorded for 'reduced' broods. Thus, under the assumption that higher brood mass indicates higher parental effort, it can be concluded that parental effort of birds rearing 'enlarged' broods was substantially

increased. From the point of view of the offspring, the higher number of nestlings in enlarged broods was expected to create less optimal environmental conditions during early development as a result of increased competition over the resources provided by the parents. In this study, broods were either enlarged or reduced. As a consequence there were no control broods of natural size. The decision to use this setup was made based on the fact that the main aim of this study was to find out more about the trade-offs in response to brood size manipulations. The addition of a control group would have reduced per group sample size and therefore statistical power to test these effects.

Physiological condition

By definition, measures of (physiological) state can only be considered a condition index when they are associated with fitness (i.e. reproduction and survival). Although it has been recognized that physical condition plays an important role in steering many life history decisions and, as such, is an important concept in evolutionary ecology there is still little knowledge on how different aspects of condition should be measured. In this study a total of six physiological traits were determined, body mass, haematocrit, buffy coat, telomere length and levels of total antioxidant capacity (TAC) and oxidative damage. In the next section each of these parameters will be shortly introduced.

Body mass

Body mass is probably the easiest and most often used index of condition. Corrected for structural measures of body size such as tarsus length, it provides an estimate of the energy reserves of an individual. In general a higher body mass is seen as an indicator of higher body condition. In jackdaws, this was at least true for nestlings. Nestlings that were low in body mass at fledgling had lower chances of surviving the first year (Chapter 6), in line with

other studies showing similar effects (Magrath 1991; Schwagmeyer & Mock 2008). In adults, females that had a lower body mass laid smaller eggs (Chapter 6), also showing that low body mass is an indicator of lower condition. However, (especially for adults) the relation between body mass and (physiological) condition may not be as straightforward. Apart from obvious negative side-effects like those related to obesity in humans, it is now well known that body mass is a dynamic parameter that can also be subject to regulation in response to environmental circumstances, independent of condition. Thus mass can only be reliably used as a characterization of condition when these circumstances are taken into account. Even when mass does predict fitness prospects, additional measures of condition can be of use because combining multiple sources of information in one measure of condition is likely to have higher predictive value than mass alone.

Haematocrit

In the literature there are several indications that a high proportion of red blood cells per volume of blood (haematocrit) is an indication of good condition. Several studies showed that birds that suffered food shortage, were subject to experimentally elevated levels of energetic demand or had an overall lower survivability had lower levels of haematocrit (Svensson & Merilä 1996; Piersma et al. 2000; Møller & Petrie 2002; Verhulst et al. 2004; Sánchez-Guzmán et al. 2004; Kalmbach et al. 2004; Jenni et al. 2006). However, other studies did not find such relations and have argued that although haematocrit may vary in relation to (extreme) changes in condition, haematocrit levels need not always vary with condition when body condition is within the normal range (Cuervo et al. 2007). As haematocrit largely determines the oxygen transport capacity, there is the possibility that haematocrit is regulated as an optimal compromise between the competing demands of oxygen transport and constraint of blood viscosity. This possibility must not be overlooked,

especially when studying effects of like in this study elevated levels of reproductive effort.

Buffy coat

The buffy coat is the proportion of cells other than erythrocytes per volume of blood (primarily leukocytes). A high buffy coat indicates acute or chronic infections (Harrison & Harrison 1986; Gustafsson et al. 1994) and can therefore be expected to be higher in birds with low condition. Although the number of bird studies measuring buffy coat is relatively low, there are a few observational studies on free-living birds that do indeed show a relation between buffy coat and body mass (Verhulst et al. 2002; Møller & Petrie 2002), reproduction (Moreno et al. 1998) and survival (Verhulst et al. 2004). While collared flycatchers *Ficedula albicollis* rearing experimentally enlarged broods had more blood parasites and a larger buffy coat (Gustafsson et al. 1994).

Telomeres

Telomeres are regions of non-coding but highly structured DNA at the end of linear eukaryotic chromosomes, consisting of a tandem repeated highly conserved DNA sequence (5'-TTAGGG-3')_n. In this study, the length of telomeres was determined in red blood cells, which are nucleated in birds. After the DNA was extracted, and digested using restriction enzymes, each sample was separated by pulsed field gel electrophoresis (see Figure 1.2). This method, although laborious, has the advantage that it provides estimates of genome-wide distributions of telomere lengths for each sample (Baird 2005), but perhaps most importantly in the case of bird studies one can avoid the problem of interstitial telomeres (in combination with a probe that only binds to the 3' overhang structure of the telomere). Evidence accumulates that telomeres shorten during life, and that telomere shortening in particular reflects life style and predicts remaining lifespan. However, few studies until now have investigated telomere dynamics and its relation to survival

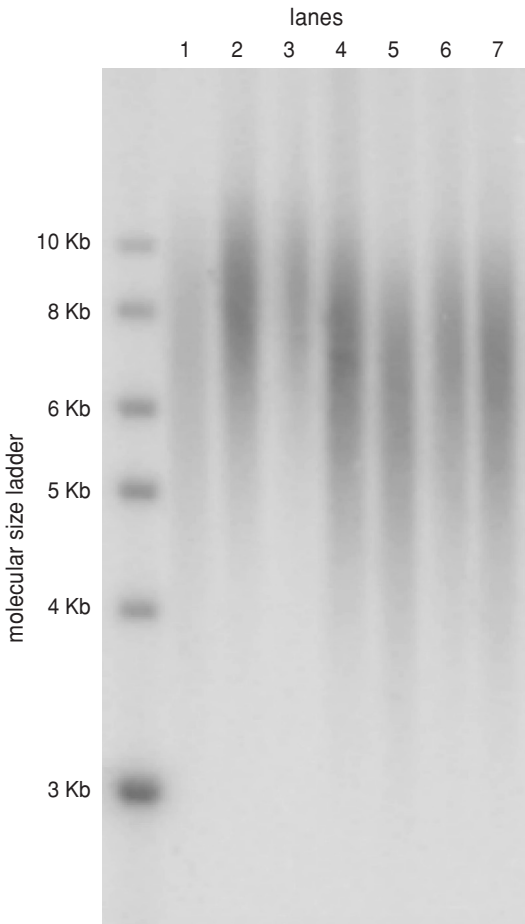


Figure 1.2. Picture of representative pulsed-field gel showing the molecular size ladder and the first 7 lanes with smears representing telomeres of individual samples.

under natural conditions. In fact there is currently only one study on telomere dynamics related to age and survival in a free-living animal, the alpine swift (Bize et al. 2009). In this study it was shown that telomeres shortened with age and moreover that, initial telomere length and telomere shortening rate were both better predictors of survival probability than age itself. Telomere shortening occurs primarily as a consequence of oxidative stress (see

below). Because oxidative stress also causes damage to other physiological components of an organism, it is as yet unclear whether telomere length or shortening rate has a direct (causal) effect on survival, or whether it should be seen as a biomarker of somatic deterioration due to these damaging processes.

Oxidative stress

Oxidative stress results from an imbalance between pro-oxidant (ROS) production (e.g. free radicals and peroxides) and the capability of an individual to defend itself against and/or repair damage caused by these ROS. Because of their high reactivity ROS can do damage to lipids, proteins and nucleic acids (DNA). They are the inevitable byproducts of aerobic metabolism, and therefore any increase in energy turnover should in theory lead to an increase in ROS production and consequently to oxidative stress in the case of an insufficient defensive system. These antioxidant defense systems are made up of enzymatic antioxidants such as superoxide dismutase and catalase that work primarily within mitochondria at the site of free-radical production and micromolecular antioxidants such as vitamins E and C, uric acid and glutathione that function both in tissues and in the bloodstream. Antioxidant protection is assumed to entail costs and has been shown to be reduced in birds with increased reproductive effort (Wiersma et al. 2004). Because of its damaging potential, oxidative stress leads to physiological deterioration and has been linked to aging and senescence (Beckman & Ames 1998; Finkel & Holbrook 2000). Levels of TAC and oxidative damage were determined in the plasma. ROS production can not be determined directly due to the high reactivity, instead the concentration of reactive oxygen metabolites (ROM) in the plasma was determined. ROM's are formed through the interaction between reactive oxygen species and somatic tissue (primarily lipids) and can be used as an indicator of ROS and especially oxidative damage.

Number and quality of offspring

Effects on growth and physiology

In line with earlier studies, manipulating brood size affected the growth and body condition of offspring (Chapters 3 and 4; see Figure 1.4 for a summary of the observed effects). This indicates that the actual number of offspring does indeed play a role in determining the quality of offspring.

Both measures of growth (body mass and tarsus length) were lower in nestlings reared in 'enlarged' broods (Chapter 3). Thus, enlarging brood size is likely to have had a substantial effect on offspring survival prospects. These effects were stronger in daughters compared to sons and therefore, assuming that a possible mass * sex interaction with respect to survival was weak, it could be anticipated that survival was stronger affected in daughters than in sons. On the basis of growth, it seems therefore justified to conclude that daughters are more vulnerable to brood size effects than sons.

In contrast, the effect of brood size manipulation on the level of DNA damage, estimated by telomere length, was found to be highest in sons (Chapter 4). Between the age of 5 days and 30 days (just before fledging), sons reared in 'enlarged' broods lost on average almost double the amount of base pairs compared to sons reared in reduced broods (Figure 1.4). At the same time, telomere shortening was found to be independent of brood size manipulation in daughters (Figure 1.4). This is an important finding, because not only do these data provide evidence for a trade-off between growth and somatic maintenance and repair and an apparent difference between the sexes in the outcome of this trade-off, it provides valuable information on the link between environmental conditions during early development and fitness prospects.

In Chapter 2 longitudinal data are presented on telomere dynamics in nestling and adult jackdaws. These data show that telomeres shortened with age and that there was indeed

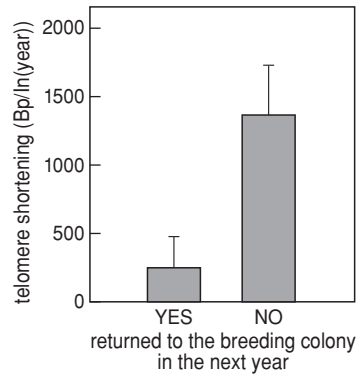


Figure 1.3. Telomere shortening rate (base pairs / ln (year)) (mean \pm standard error) for individuals that did or did not return to the colony the next year.

selective disappearance of individuals with short telomeres at any given age. Moreover, these data in particular show that not only the length of telomeres within individuals was important, but that the rate at which the telomeres of an individual shortened in particular predicted the survival of that individual (Figure 1.3). This was in agreement with the results from the recent study on alpine swifts by Bize et al (2009). As in most other species studied so far, telomere shortening early in life

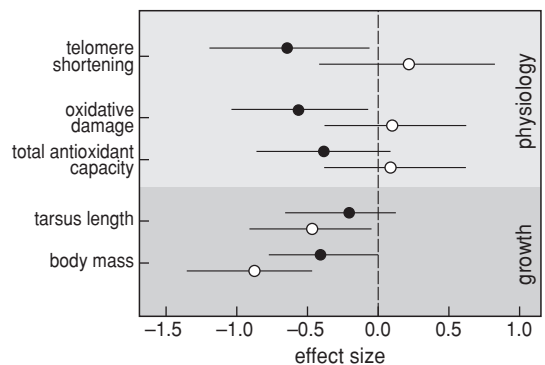


Figure 1.4. Comparison of the effect size of the brood size manipulation for different parameters in daughters (open dots) and sons (closed dots). Dashed line indicates no effect.

was markedly higher compared to that in adults. In jackdaws, the rate at which telomeres shortened between ages 5 and 30 days was up to 100 times higher than the rate recorded in adults (Chapter 2). Obviously, telomere length during adult life is predominantly affected by the amount of telomere loss in early life. Therefore, the observed effect of experimentally manipulated environmental conditions on telomere shortening in the offspring could provide a link between these conditions and fitness of the offspring through its connection with life expectancy (Chapter 2).

The next step would be to understand what causes the increased rate of telomere shortening in sons reared in enlarged broods. As mentioned above, the main known determinant of telomere shortening is damage resulting from oxidative stress. As such, differences in telomere shortening rate between individuals are likely to be the result of a higher resistance to the damaging potential of pro-oxidants produced in the body. Data on the level of TAC and oxidative damage in nestlings reared in either enlarged or reduced broods revealed that these oxidative stress parameters were indeed also affected by brood size manipulation. Furthermore, they show that these effects also differed between daughters and sons. Although for TAC there was no significant interaction between sex and manipulation, the effect size for sons was substantially larger than it was for daughters (Figure 1.4). This could indicate that nestlings (sons in particular) reared in 'enlarged' broods allocated fewer resources to defense mechanisms against oxidative damage. This was supported by the fact that the effect of the manipulation on levels of TAC could be entirely explained by differences in body condition (residual body mass over tarsus). However, instead of an expected lower level of oxidative damage due to a higher protection, oxidative damage levels were also higher in sons reared in reduced broods. In daughters, there was no discernible effect of brood size manipulation. It is worth mentioning here that this finding clear-

ly illustrates the necessity for studies concerning levels of oxidative stress to estimate both sides of the equation, if only because it was previously suggested that levels of oxidative protection can also be up regulated as a consequence of increased levels of ROS (Barja 2002, Costantini 2008) and measuring just either one would have led to opposite conclusions.

The mechanism causing a higher level of oxidative damage in sons reared in reduced broods is unclear, especially considering that these levels seem to contradict our finding of lower telomere shortening rates in these nestlings. Differences in mass and size between nestlings reared in 'reduced' and 'enlarged' broods could explain the increase in oxidative damage in 'reduced' broods. However, although tarsus length was correlated to levels of oxidative damage, it did not explain the brood size manipulation effect. Moreover, within treatment groups there was a negative correlation in sons, i.e. oxidative damage was lower in larger nestlings. This, in combination with the finding that the effect of manipulation on oxidative damage was only observed in sons, whereas growth estimates were instead most affected in daughters, makes it less likely that growth *per se* affected levels of oxidative damage.

Most likely, the higher level of oxidative damage in these nestlings was the result of increased free radical production through higher daily energy expenditure. For instance, it could be that nestlings in 'reduced' broods allocated more resources to immune function and that, in experimentally enlarged broods, the immune function competes with other physiological functions, such as growth. Here this should then result in differential allocation of energy towards somatic maintenance between nestlings in 'enlarged' and 'reduced' broods. Indeed, levels of RMR were found to be higher in nestlings in 'reduced' broods (Chapter 3). However, when RMR was corrected for body mass, to allow comparison with oxidative damage (which is measured as a concentration), the brood size manipulation effect

on RMR could be completely explained by differences in body mass between the treatment groups. Note however that, even though it is the only available proxy of energy expenditure in this study, RMR comprises only a small part of total daily energy expenditure (DEE) and it is not unlikely that the relation between RMR and DEE differs between treatments as was for instance found in starlings working for food (Wiersma et al. 2005).

Sex dependent environmental sensitivity

Even though the relation between telomere shortening and levels of both TAC and oxidative damage in nestlings did not quite reach significance, and also that the results regarding levels of oxidative damage seemed to contradict the observed difference in telomere shortening, these data provide evidence for a sex dependent differential allocation of resources towards growth and somatic maintenance and repair in response to limited resource availability.

Sex dependent effects of environment during early development have repeatedly been reported. For instance in zebra finches it was shown that final body mass and growth rates of females were lower in conditions of restricted food when compared to males, in the absence of parent-offspring and sib-sib interactions (Martins 2004; see Råberg et al. 2005 for a review of other examples). However, the sex that was most susceptible to the manipulation varied between species and most importantly also between studies on the same species. Such patterns of sex dependent sensitivity to environmental conditions during early development could facilitate the evolution of sex allocation, because they will affect the fitness benefits of investing in a particular sex depending on the state, condition or environment of the parents. At first glance also in this study one of the sexes seemed more affected by brood size manipulation than the other. Daughters in 'enlarged' broods had lower growth rates whereas sons were seemingly less affected. Nonetheless, daughters were not the only sex

suffering from brood size enlargement as sons were found to pay, less visible, costs in terms of physiology.

Although it remains to be tested whether there was a difference between the sexes in the effect of the experiment in terms of actual fitness, the observed differences in response between the sexes does provide further support for the hypothesis that the observed effects were the result of differential energy allocation in the trade-off between growth and somatic maintenance. Such a trade-off could very well result from selective pressures forcing sons to invest most in growth, under sub-optimal conditions at the expense of physiology. These selective pressures would arise for example through an effect of body size on social dominance. In jackdaws, dominance rank has been shown to affect future survival and reproductive success (see below) and the rank of a breeding pair is primarily dependent on the status of the male. Hence, by investing in growth under sub-optimal conditions at the expense of other physiological parameters, jackdaw sons may increase their fitness prospects. For daughters on the other hand, body size may be less important and more resources are allocated towards physiological maintenance and repair.

These results show that studies on the effect of rearing conditions can be highly dependent on the parameter of interest. Moreover, they show that the use of only a limited number of parameters could lead to false conclusions when certain other parameters that could have an opposite effect on fitness are overlooked. Ideally, one should focus not only on the direct short-term effects of brood size manipulation, but also on effects at the level of survival and fitness. Unfortunately, studies showing such data are extremely rare and inconclusive. Clearly, more studies are needed to test whether sexes do differ in sensitivity to environmental conditions during early development in terms of actual fitness, the most relevant parameter in this context.

Current reproductive effort

Parents rearing 'enlarged' broods had to provide food for a higher number of nestlings. Thus, it would seem justified to conclude that the workload of these parents was increased. Nonetheless, the effects on (physiological) condition of the parents were rather weak (Figure 1.5). This raised suspicions about whether brood size manipulation really did increase reproductive effort. However, the finding that cumulative brood mass production was substantially higher for parents rearing 'enlarged' broods seemed to confirm an increase in effort in response to brood size enlargement. Of course this can only be true under the assumption that brood mass production is an indicator of parental effort (i.e. the total amount of provisioning), however given the substantial difference between treatment groups this assumption seems justified.

There could be several reasons for the apparently small effects of increased reproductive effort on the parents. First of all, there is a possibility that the data had insufficient power to detect the actual effect. Especially in the case of the measures of oxidative stress there seemed to be an, albeit small and insignificant, effect in the expected direction. Another reason, from a practical point of view, may have been that the wrong parameters were measured or that the timing of the measurements was not optimal. All parameters were only measured once around fifteen days after brood size manipulation. Although brood size was still larger at that moment for broods in the 'enlarged' treatment, most nestlings had already reached their final body size as the peak in growth rate of nestling jackdaws was around a week earlier. Therefore it is possible that the largest effect of the manipulation would also have been earlier.

Assuming that parents indeed did not experience negative effects on their physiology in response to increased reproductive effort, this suggests that the jackdaws under 'normal' con-

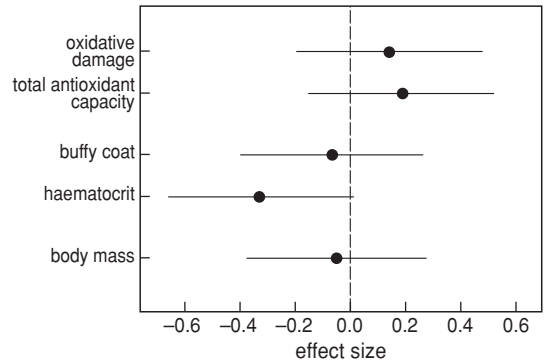


Figure 1.5. Comparison of the effect size of the brood size manipulation for different parameters in parents. Dashed line indicates no effect.

ditions are not performing at their maximal effort and could in fact work harder without detrimental effects on their physiology (Figure 1.6). A possible explanation could be that the increase in reproductive effort incurred by the brood size manipulations of this study was not large enough, allowing parents to fully cope with the increased workload. However, the effects of the manipulations on the offspring seem to contradict this. The quality of off-

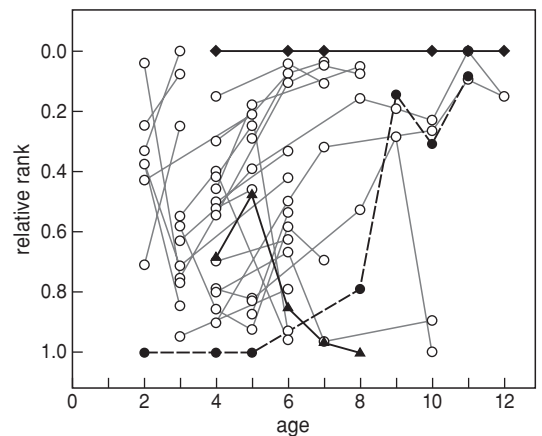


Figure 1.6. Relation between male age and social dominance. Lines connect data of separate individuals. Low rank indicates high dominance.

spring, in terms of growth and physiology, was significantly reduced when brood sizes were enlarged. This indicated that parents did not provide optimal rearing conditions for these offspring. Thus, in other words, even though parents whose brood was enlarged did increase their effort, this increase was insufficient and this affected the quality and (presumably) fitness prospects of their offspring.

It could be that reproductive effort of parents with 'enlarged' broods was less than optimal from the point of view of the offspring because the parents valued their own future reproductive output higher than the expected fitness benefits through their current offspring. Assuming that further increase in their effort would have resulted in a decrease in their own condition. This would be in line with theoretical predictions of the outcome of the trade-off between current and future reproductive success for species with low extrinsic mortality. Although it is of course tempting to conclude this from the combined effects of brood size manipulation on parents and offspring in this study, the lack of data directly linking brood size manipulation to actual fitness benefits does not allow such a conclusion. Perhaps in the near future, data on recruitment rate and survival of individuals manipulated in this study will fill in the bottom half of the scheme presented in Figure 1.1 and provide the answer.

Social dominance

Living in groups, jackdaws spend a large proportion of the day interacting with other members of the colony. These interactions can be beneficial or neutral for the involved individuals for example in the case of sharing information on foraging opportunities in communal roosts or predator alert, promoting coloniality. However, especially around the breeding season, a large proportion of the interactions are the result of competition over resources (e.g. food, nest boxes, nesting material and mates).

These interactions are often resolved via non-physical displays. Sometimes such displays are not enough however, and in these cases fights occur that can sometimes become quite severe and even result in injuries (ranging from a removed tail feather to damage to the cornea of an eye (personal observations)). At the population level, it is thought that the principle of social dominance and especially social hierarchies in colonial species has evolved to lower the amount of physical fights and thus the risk of injury. Subordinates will know which individuals are more dominant over them, making the outcome of fights more predictable and they will be more likely to leave without a fight.

Social dominance was determined by observing interactions over an artificial food source. The number of times an individual won or lost an interaction through displacement (loser leaves when the other approaches), threat (loser leaves when the other performs a threat display) or physical fights or when an individual was obviously waiting for the other to stop eating was scored. To stage conflicts, food was offered in small pits (diameter 10 cm). At these pits, only one jackdaw or a jackdaw pair could eat at a time. From these interactions a rank order was calculated. A strong linear dominance hierarchy exists, in the sense that jackdaws rarely lose a conflict with an individual with lower social status (Tamm 1977; Röell 1978; Wechsler 1988). The outcome of a conflict can of course be state dependent; hungrier birds may, for example, win more conflicts over food. Earlier studies in the same colony had already shown however, that jackdaws that were successful in interactions over food also had primary access to available nest boxes and succeeded in defending more nest boxes during winter (Röell 1978). This information, together with the observation that the hierarchy is highly stable over successive years, indicates that dominance in competition over food reflects resource-holding potential, rather than some transient effect of state.

Reproductive success

Because socially dominant individuals, by definition, have priority of access to resources, it is generally assumed that these individuals also attain the highest reproductive success. Besides lowering the frequency of physical fights, the fitness advantage to socially dominant individuals is crucial in understanding the existence of dominance hierarchies. Dominants have to invest in acquiring and maintaining social dominance. Such investments are, for example, costly signals used in agonistic interactions (Zahavi & Zahavi 1997) and harmful side-effects of high androgen levels (Folstad & Karter 1992; Frank et al. 1995; Packer et al. 1995; Buchanan et al. 2001), while the increased number of interactions that dominant individuals are involved in (Chapter 6) consume time and energy and increase the risk of an injury. If dominants did not benefit, these investments would be wasted (Pusey & Packer 1997).

Indeed studies reporting positive effects of dominance on reproductive success (reviewed in Ellis 1995) by far exceed those that find either neutral or negative correlations. However, the majority of studies that do not find a positive correlation are based on animals in captivity where the benefits of being dominant may be less pronounced through for instance the ad lib availability of food. Therefore, (inspired by the data collected by Röell at the BC colony in the 1970's) the effects of being dominant in this colony were investigated. It was found that social dominance was associated with low fledgling production and low fledgling quality (deduced from a lower body mass, indicating a lower survival probability; see Chapter 6). At least part of the low success rate of dominant pairs was explained through maternal effects. Females paired with dominant males had poorer condition and produced smaller eggs. The decrease in reproduction was not compensated with greater longevity, because survival was independent of social dominance. As in jackdaws the frequency of extra-pair fertilizations is practically zero

(Liebers & Peter 1999; Henderson et al. 2000). These findings led us to conclude that dominant jackdaws in the BC colony had lower fitness than did subdominants.

This study was the first to show that in free-living animals high ranked individuals can have lowest fitness. This was not a general pattern found within all colonies of jackdaws. Henderson and Hart (1995), in their study on a colony of jackdaws in Leicestershire, found that the most dominant individuals did produce the most offspring. Hypotheses that explain low fitness of dominant birds in the BC colony are based on one of two assumptions. Either it is assumed that there is a causal relation between dominance and reproductive success, or it is assumed that a third factor causes both high dominance and low reproductive success. One possible external factor is senescence, when aging is associated with a decline in reproductive success and an increase in dominance. Although there was no relation found between social dominance and age in the data presented in Chapter 6, more recent data (including data collected between 2005 and 2008) do suggest that dominance rank increases with age in some, but not all, individuals (Figure 1.7). However, it would seem unlikely that such an aging effect could explain the pattern of reduced fitness in dominant jackdaws, not in the least because the decreased reproductive success of dominant individuals was extremely pronounced over a long period of time within individuals. For instance, the most dominant pair in the colony between 1998 and 2007 produced only a total of five fledglings in 1996 and 1997 combined, but no fledglings in all the years afterwards, until the male disappeared in 2008. It is highly unlikely that an individual that is fully capable of maintaining the top position in the hierarchy would be too senescent to produce offspring over a period most likely to be more than half its entire lifespan.

The variation in fitness consequences of dominance can also be dependent on food availability and to which level dominant indi-

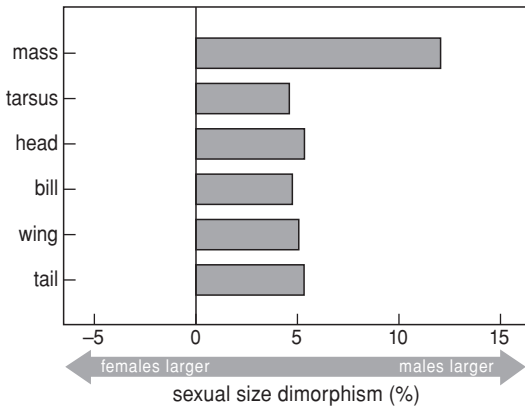


Figure 1.7. Sexual size dimorphism for several parameters of body size in the jackdaw. Solid line indicates no difference, positive values indicate that males are bigger.

viduals are able to monopolize resources (Ellis 1995). In agreement with this proposition, Henderson & Hart (1995) found in jackdaws that dominance had a stronger effect on fledgling production in years when overall success was low and in the common raven *Corvus corax* it was found that increase in the effort needed to monopolize a food source decreased the net benefits of high ranked individuals (Heinrich 1994). Using simple optimality reasoning, this proposition can logically be extended to explain a negative association between dominance and reproductive success: when costs are associated with acquiring and maintaining dominance, and these costs are not compensated with increased resource access (because resources are abundant regardless of status), the net effect of dominance on reproductive success will be negative. Although fledgling production at the BC was approximately equal to that found in the colony studied by Henderson & Hart, the other colonies in this study were doing much better in terms of number and quality of offspring. This difference seemed, especially in the later years, to be due to a lower availability of food suitable for the offspring (mostly invertebrates) at the BC.

Thus, high resource abundance is unlikely to explain the negative association found between dominance and reproductive success.

The question remains why dominant individuals at the BC would 'choose' to participate in interactions and attain a high position in the dominance hierarchy when the benefits associated with such a position are in terms of fitness apparently outweighed by the involved costs. It is possible that such a 'decision rule' has evolved as a consequence of increased fitness benefits at a global scale as illustrated by the study of Henderson & Hart. This rule may however become maladaptive in certain situations like those at the BC. It remains unclear what characteristic makes this colony less suitable for dominant individuals. A comparison with the colony studied by Henderson & Hart revealed that apart from a woodland environment the most pronounced difference was the proximity of neighboring nest boxes in the colony in Leicestershire. Nest boxes in Leicestershire were approximately 8 m apart where nest boxes at the BC were around 1.5 m up to a maximum of 3 m apart. It is possible that the closer proximity induced an increase in the number of interactions. Considering the fact that dominant jackdaws were found to participate more in agonistic interactions (Chapter 6), it is possible that a density dependent increase in such interactions would be strongest in these high ranked individuals. Potentially, this could affect breeding success for instance through a reduction in parental care as a result of increased levels of testosterone associated with agonistic interactions. Alternatively, it could also be that male provisioning rates, essential during incubation and the early rearing period, were lower for high ranked individuals, due to a higher tendency of these males to stay close to the breeding area as a result of higher levels of territoriality. So far, there is however no data to test both these hypotheses (although blood samples have been collected allowing for an analysis of hormone levels).

Sex allocation

Evidence for biased sex allocation in birds has accumulated in recent years. An increasing number of studies report effects on sex allocation of parameters related to environmental conditions and/or of parental body condition, quality or attractiveness in relation to differential resource allocation between daughters and sons (see Pike & Petrie 2003; Alonso-Alvarez 2006 for reviews). These patterns can especially be expected when the net fitness benefits of investment in offspring varies between sons and daughters in different circumstances.

Jackdaws are moderately sexually size dimorphic at fledging, with males being 5-10% larger than females (Figure 1.8), suggesting that higher costs are involved in producing male offspring. Moreover, in jackdaws sexes differed in their response to environmental conditions (Chapter 3 and 4). Although more data are needed to determine the consequences at the level of actual fitness, these two findings increase the likelihood that optimal sex allocation in jackdaws depends on parental resource access and therefore social dominance.

There are several mechanisms via which parents can preferentially increase the quality and survival chances of either sons or daughters. For instance in birds, females may vary the volume of their eggs, and thereby the available resources, or differentiate the amount or quality of food delivered to the nestlings depending on sex.

Since offspring survival probability usually decreases with hatching order in species with brood-reduction (like the jackdaw), parents can also vary the position in the laying order or in the hatching order via variation in embryonic period between the sexes. Whereas there was the aforementioned difference in the response to environmental conditions between the sexes, there was no evidence that survival chances until fledging differed between sons and daughters (Chapter 3). Although data on preferential food provisioning towards sons and daughters were not available, there were no

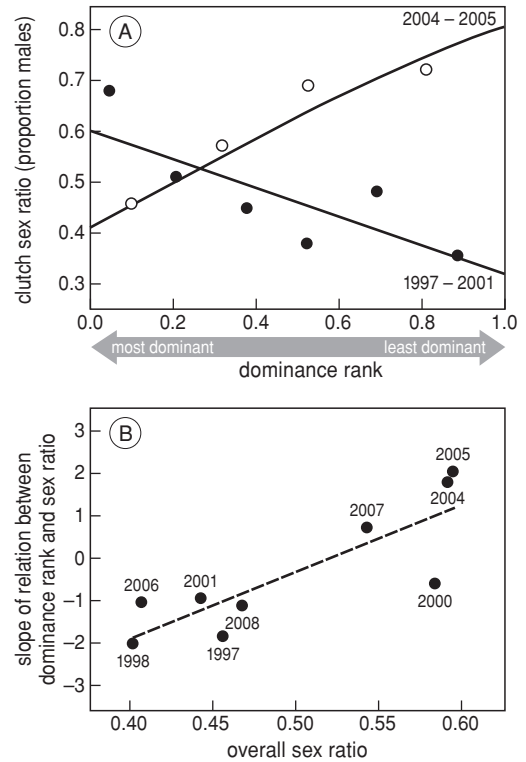


Figure 1.8. (A) Social dominance and sex ratio in two year-groups. Data were pooled for 1997, 1998, 2000 and 2001 (solid dots, each dot represents 9 or 10 clutches, $N = 58$) and 2004 and 2005 (open dots, each dot represents 5 or 6 clutches, $N = 23$) respectively. For statistics see Chapter 7. (B) The relation between sex ratio of all nestlings born in a year and the slope of the relationship between social dominance and sex ratio.

indications that resource allocation in the form of egg volume differed between eggs containing male or female embryos (Chapter 7). Also, the order in which nestlings hatched within a nest was not dependent on their sex as there were no differences in laying order (Chapter 7) or embryonic period (Chapter 8) between sons and daughters. Thus, it would seem that there is no evidence for sex dependent resource allocation in jackdaws, at least through these mechanisms.

However, the most direct strategy to modify sex allocation is through adjustment of the primary sex ratio of offspring (Fisher 1930; Charnov 1982; Pike & Petrie 2003; Alonso-Alvarez 2006). Of all hatchlings at the BC between 1996 and 2008 (except for 2002 and 2003) sex was determined from their DNA. Overall 376 sons were born against 365 daughters, as would be expected when offspring sex determination in these jackdaws was random with probability 0.5. Nonetheless, in none of these years separate was the sex ratio ever really close to 1:1. This may suggest that sex determination in jackdaws was not such a random process after all. Indeed, it was found that clutch sex ratio was strongly associated with social dominance. The effect was very strong compared to most avian sex ratio studies, with a sex ratio difference of 30-40% between the most and least dominant pairs. However, the direction of this effect varied between years. Dominant jackdaws produced more sons during the first years of the study, but fewer sons during the last years (Figure 1.8A) and this effect seemed persistent within individuals.

Attempts to explain the relation between social dominance and offspring sex ratio, and especially the shift in this relationship between years, have thus far not been successful (Chapter 7). Maternal condition, although related to social dominance, did not predict the primary sex ratio. While on the other hand more sons were born early in the season, but social dominance was not related to laying date. Nonetheless (a change in) environmental condition and/or body condition is still the most likely candidate to explain the observed patterns.

The addition of three more years of data from the years after the period in which the data presented in Chapter 7 was collected revealed that the relation between social dominance and offspring sex ratio continued to shift. After 2005 the relation shifted again towards more males being born in high ranked individuals in 2006, this was also true for 2008 but not

for 2007 where these individuals produced more daughters. Therefore, these data make the possibility that there was a permanent change in the environment between 2001 and 2004 less likely because of the rapid shifts in recent years. Interestingly, these extra data revealed a pattern that the direction of the slope of the relation between social dominance and offspring sex ratio in a certain year was related to the sex ratio of all the offspring born in that same year (Figure 9B). As such, the most dominant individuals in the colony each year produced more of the rare sex. Potentially, this could result in higher fitness benefits through a higher reproductive value of these offspring. The existence of such a causal relationship between these two parameters is however extremely unlikely, not in the least because such a mechanism would require that individual jackdaws can predict the sex of all the offspring produced in the colony. Thus, overall sex ratio at the population level provides neither a mechanistic nor a functional explanation of the observed relation between social dominance and offspring sex ratio. It seems more likely that both parameters were affected by the same (as yet unknown) factor, therefore resolving the questions related to the shift in the effect of social dominance on sex ratio may be one step closer.

Concluding remarks

First of all, the data presented in this thesis show that telomeres and, perhaps even more importantly, their shortening rates can be used as a biomarker of aging and survival probabilities of individuals. Using information on telomeres in combination with other parameters associated with (physiological) condition evidence for trade-offs at various levels and in various traits related to the life history of jackdaws was presented here.

Although the plasticity in the decision remains unclear, jackdaws make decisions

about pursuing a high position in the local hierarchy. Dominant individuals will have higher resource holding potential, but there are also costs involved presumably as a result of the effort needed to attain a high rank. As was shown here, in terms of fitness these costs can even outweigh the benefits associated with social rank.

There was also evidence for parental control on the investment in sons and daughters in the sense that parents seemed to be able to adjust offspring sex ratio. Although evidence for (adaptive) sex allocation in birds is accumulating, extremely little is known about the mechanism via which sex determination could occur. This makes it even more difficult to speculate about what causes the observed link between social dominance and sex ratio, let alone the possibility of a causal link between these two parameters. More research on the observed relationship with overall sex ratio at the population level and also on the differences in the sex dependency of environmental sensitivity during early development should bring us closer to answering these questions.

With regard to the trade-off between current reproductive effort (which includes the investment in number and quality of offspring) and future reproduction to maximise fitness, the data presented here suggest that parents shunt most of the costs resulting from an experimental increase in the cost of reproduction onto their offspring. As such it would seem that jackdaw parents favour their own survival and expected reproductive value over that of their offspring. However, the data presented in this thesis do not warrant such a conclusion because for this information on actual fitness is crucial. Therefore, it is good to know that the continuity of the jackdaw project was assured for the coming years, so that more information on the individuals that were manipulated in this study will become available. With this information the gap that for the moment remains in the bottom half of the scheme presented in Figure 1.1 can then be filled.

