Engineering brood size and structure as a conservation tool for altricial birds

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Chapter 1: General introduction

Abstract

Conservation biologists use many methods to increase the population size of threatened and endangered birds. In particular, nestling transfers have been used to increase the probability of survival mainly in precocial species. However, such manipulations of altricial species have rarely been used solely for conservation purposes. The goal of this study was to examine the potential for nestling transfers to enhance the population productivity of altricial birds using red-winged blackbirds (*Agelaius phoeniceus*) as a model system. The protocol used prior knowledge of the relationship between reproductive success and family size to transfer nestlings from situations of low to high survival. Many altricial birds generate brood hierarchies among their offspring by hatching their eggs asynchronously. First-hatched "core" progeny enjoy higher average survival and growth than later-hatched "marginal" nestlings, particularly in larger broods. This creates an opportunity to move marginal hatchlings with poor prospects for survival into broods where they would enjoy a higher expected survival, a technique I refer to as "brood engineering". I transferred single nestlings between nests early in the nestling period to create donor and foster broods. The resulting nest survival was compared to the expected survival for the pre-manipulation brood structure calculated from 11 years of demographic data. Overall, an increased productivity averaging four-tenths of a nestling per transfer over the expected number seen on average for a given brood structure was obtained. As well, the transfers did not measurably reduce the experimental nestling survival. This work suggests that nestling transfers can be used for threatened altricial

species to enhance population productivity. However, certain conditions must be present in order for brood engineering to provide the most benefit, most importantly hatching asynchrony and hatching failure.

Introduction

The principle of allocation dictates that parents trade off offspring number for quality, and fewer higher quality offspring may be preferable to a larger number of lower quality off offspring. Such trade offs appear evident in altricial birds. Parents often create more incipient progeny than they are capable of rearing to independence, and allow family size to be trimmed by a process of brood reduction, that they facilitate by establishing a competitive hierarchy among offspring. This brood hierarchy leads to a differential survival among nestmates, and creates opportunities for wildlife managers to increase populations of threatened species that I explore here.

In chapter 2 of this thesis I review the relevant literature on the regulation of family size in altricial birds. In these species, the development and survival of offspring throughout the nestling period and beyond is dependent on the brooding, provisioning and waste removal of their parents. Thus, parental quality will affect both the size of the clutch laid and the number of offspring surviving to fledging. In addition environmental factors such as weather conditions and food availability are important correlates of nestling survival (Blondel *et al.*, 1998; Tinbergen and Verhulst, 2000; Forbes *et al.*, 2001). Many studies have manipulated brood size and structure in order to investigate the factors that affect the brood size at fledging (Nur, 1984a,b; Dijkstra *et al.*, 1990; Pettifor, 1993).

Second, I also discuss the differential survival of different castes of nestlings. Because incubation begins before all eggs are laid, parents confer an advantage to some offspring in the brood by providing them with a head start over their younger siblings (Clark and Wilson, 1981). Thus, two castes of offspring are created: the core brood with

relatively secure prospects for growth and survival; and the marginal brood with lower average growth and survival (with greater variation) than their core broodmates (Mock and Forbes, 1995). Lack (1947, 1954) was the first to present the logic of adaptive brood reduction. Parents produce an initially optimistic clutch size with a portion of the brood that will survive under favourable ecological conditions. Under poor conditions, however, this class of surplus (or marginal, sensu Mock and Forbes 1995) offspring is eliminated from the brood via brood reduction that is normally the outcome of fatal sibling rivalry.

In chapter 3 of this thesis, I present the results of a two-year field study where I experimentally manipulated brood size and structure of red-winged blackbirds (*Agelaius phoeniceus*) to enhance population reproductive success. This is a technique I refer to as brood engineering, where nestlings are transferred from broods with poor prospects for survival (e.g., last-hatched nestlings from large broods that are likely targets for brood reduction) and moved to situations with better prospects for survival (small broods and particularly those experiencing hatching failure). The purpose of brood engineering is to increase the number of offspring surviving to fledging at a population level by strategic transfers of individual nestlings. Experiments in which a single nestling was moved were used to increase the prospects of survival in 2002 and 2003. I used a large historical data set for this blackbird population to guide the decisions of which nestlings to transfer and where to transfer them. I also used these data to examine the expected survival of experimental nestlings in their original sibship structure (number of core and marginal offspring) to compare to the observed survival of families in both the donor and recipient broods. I discuss the results of these experimental brood manipulations for their potential

to increase population reproductive success. In addition, I suggest guidelines and

limitations for this procedure and provide information on potential study species.

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Chapter 2: The regulation of clutch and brood size in altricial birds.

Abstract

The regulation of the number of altricial offspring surviving the nestling period and beyond is affected by many factors. I discuss both proximate and ultimate reasons for the family size produced in many altricial species. Aside from obvious differences across species, clutch size is affected by a wide array of factors that include, but are not restricted to, ecological conditions, parental ability and condition, prior breeding experience and age. The optimal clutch size is affected directly by optimal brood size, and this is influenced by predation risk, thermoregulatory abilities, and the prevalence of hatching failure. Brood size is key for survival and can be both too large or too small depending on current breeding conditions that are often not predictable at the time of egg laying. Indeed, hatching asynchrony and brood reduction may have evolved to tailor brood size to prevailing conditions. Further, the prevalence of hatching asynchrony has generated many hypotheses beyond just adaptive brood reduction. Regardless, hatching asynchrony generates competitive disparities among contemporary broodmates that exert a strong influence on post-hatch survival, though other factors such as brood size and offspring sex may also be important determinants of survival.

Offspring production by altricial birds is underpinned by a trade off between the number and quality of progeny: more is not always better. The constraints on offspring quality arise from many factors, beginning with parental quality and ability, to constraints imposed by the current environment. All else being equal, natural selection should favour parents that produce the most surviving progeny. At the outset, behaviours that

superficially seem to prevent parents from producing the most offspring are in fact present to allow them to do just that. Many species routinely produce more offspring than they can rear or can seemingly produce less than they are capable. As well, they create hierarchies among their offspring, but to what end?

Introduction

What determines clutch size in altricial birds? Egg laying requires energy and thus can constrain the number of eggs laid and hence limit clutch size (Freed, 1981). Initially, a variety of factors can constrain clutch size including timing of breeding, harshness of the preceding winter, the age of the female, pre-breeding feeding by males, as well as incubation efficiency (reviewed in Klomp, 1970; Engstrand and Bryant, 2002; Reid, 2003). Females in better physiological condition can afford to invest more in egg production resulting in a larger clutch size (Slagsvold and Lifjeld, 1990). As well, older females often lay larger clutches (Reid *et al.*, 2003). Female condition can be determined in part in species where the male is involved in feeding his partner before egg laying (Krebs, 1970). Males that provide more food may enable females to lay more eggs. Prior breeding attempts can also affect the number of eggs laid per female (Young, 1996). Females that previously reared a larger brood may produce a smaller one in her next attempt. For species that lay more than one clutch in a breeding season, the number of offspring may decrease in the second attempt (reviewed in Klomp, 1970).

Additionally, time constraints on laying factor into the number of eggs laid per clutch. Altricial birds lay at most one egg per day (Klomp, 1970). If the probability of offspring survival declines throughout the season then laying a larger clutch may not be advantageous as this delays hatching of the young (Perrins, 1965). For species that lay large clutches the effect could be especially apparent. A delay in hatching can have undesirable effects; food may be at its maximum earlier on in the breeding season. This may result in asynchrony between when the food is available and when nestlings are present.

Further, incubation efficiency can affect the number of eggs laid. Size constraints of the female's brood patch determine the number of eggs she can incubate (Engstrand and Bryant, 2002). The brood patch allows for heat conduction between the female's body and the eggs being incubated. Inadequate incubation of eggs may lead to hatching failure and a reduced brood size (Stoleson and Beissinger, 1999). In fact, brood parasites will often remove eggs to, in part, reduce the problems associated with inefficient incubation caused by too large clutches (Wood and Bollinger, 1997).

David Lack originally proposed that female birds lay a clutch size that maximizes the number of surviving offspring, and that brood size is tied to the number of nestlings that can be fed (Lack, 1947). In short, clutch size is governed by a trade-off between offspring number and quality. In many brood manipulation experiments, nestlings from larger broods are often smaller both structurally and in terms of mass than nestlings from smaller broods (Askenmo, 1977; Dijktstra et al., 1990; de Kogel and Prijs, 1996; Young, 1996; Saino et al., 1997; Burness et al., 2000). Reduced offspring quality results from lower per capita provisioning in larger broods (Tinbergen and Verhulst, 2000) or greater expenditure of energy due to sibling competition (Neuenschwander et al., 2003) or both. Often, as brood size increases, parents make more visits to the nest (Young, 1996). However, there is a maximum level to where a female will work; she does not continue to feed her young indefinitely. This ceiling effect has been demonstrated in brood manipulation experiments (Moreno et al., 1995; Tinbergen and Verhulst, 2000). As brood size increases, the amount of foraging may increase but this may not fully compensate for the increase in brood size, thus the amount of food per chick is lower in enlarged broods and starvation may result (Moreno et al., 1995; Tinbergen and Verhulst,

2000). Additionally, an increased demand affects the quality and quantity of food resulting in an increased parasite load or reduced health of nestlings (Willis and Baker, 1981; Westerterp *et al.*, 1982;). Immune system function is tied to food quantity. Supplementing protein-rich foods increases the level of immunocompetence (Saino *et al.*, 1997).

As well, overcrowding in the nest can squeeze smaller nestlings to the bottom resulting in smaller nestlings being trampled or squashed and may cause nestlings to fledge earlier (Fautin, 1941). Nest sanitation can become a problem as brood size increases, as parents may not be able to adequately remove fecal sacs (Westerterp *et al.*, 1982). Smaller broods avoid these problems. They receive more food per capita in most instances (Saino *et al.*, 1997) thus reducing sibling competition (Ohlsson and Smith, 1994).

Feeding activity by parents and/or noisier begging by nestlings, both more common in larger broods, may attract predators (Slagsvold, 1982). In general, higher predation favours smaller clutch size (Lundberg, 1985, Gotmark, 2001). In areas that experience high predation, smaller clutches may be favoured, in part to reduce the energy cost of whole-brood loss. Having "reserves" left over to produce another clutch would provide the greatest benefit (Slagsvold, 1984).

Although there are obvious costs to large clutches and broods, there may be benefits beyond just producing more progeny. For example, there is a critical brood size for thermoregulation in altricial birds (Yarbough, 1978). Larger broods have a lower surface area to volume ratio, thus the rate of heat loss during parental absences is reduced (Olson, 1992). Maintenance of high body temperature is important, as growth rate affects

when the nestlings fledge and body weight at fledging. Reductions in body temperature will lower the metabolic rate since altricial birds are ectothermic during the early stages of nestling life. Larger broods also reach brood endothermy before smaller broods, thus the parent(s) can spend less time brooding and more time foraging (Westerterp *et al.*, 1982). Attaining brood endothermy may be especially important during cooler weather early in the breeding season in some areas. Brooding must increase as temperatures drop. Larger broods may require less brooding (Sanz and Tinbergen, 1999). In some species, the food intake of smaller broods may actually be greater than that for larger broods as they are not as able to assimilate food as well when their body temperatures fall during parental absences (Westerterp *et al.*, 1982). As well, larger brood sizes may enjoy greater survival than smaller broods due to superior thermoregulatory abilities (Yarbough, 1970).

Environmental stochasticity may render the optimal clutch size in a given breeding season unpredictable. The challenge grows when the conditions at egg laying do not predict those during brood rearing. For example, in red-winged blackbirds (*Agelaius phoeniceus*), weather conditions at egg laying are uncorrelated with those during brood–rearing (Forbes *et al.*, 2001). Nur (1984b) found that blue tits (*Parus caeruleus*) often do not rear the most productive brood size in a given year. Rather, they could raise more offspring. In an experimental study, he found that parents would have been more productive had they attempted to raise a larger brood. However, the most productive brood size differed across years, being larger in good years, and smaller in poor years. In a more variable island population of the same species, nestling manipulations did not affect the number of recruits produced in a given breeding season (Blondel *et al.*, 1998). The same number of recruits was produced independent of brood

size. Again, the average number of recruits differed across years and larger broods were associated with lower quality offspring (Blondel *et al.*, 1998). Thus, producing a larger clutch size may not be optimal in order to ensure offspring quality in all years. The optimal clutch size differs between years because of variability in environmental conditions.

If parents cannot forecast forthcoming conditions, the optimal clutch size will reflect the long-term balance of ecological conditions. Smaller clutches will be favoured, for example, if "poor" years are common (Konarzewski, 1993; Young, 1996). Gene flow across populations can prevent natural selection from finding local optima for clutch size. For example, a "leakage" of genes from populations in low quality habitats may result in sub-optimal clutch sizes in productive habitats. Birds using decision rules for a more productive habitat in a poorer locale were less successful in one study of blue tits (Rytkonen and Orell, 2001). A reduced brood size produced the same number of young as enlarged and unmanipulated broods. Thus, the reduced brood size was optimal in one habitat type that had less food available for feeding while the other brood sizes suffered brood reduction (Rytkonen and Orell, 2001).

Sub-optimal clutch sizes may reflect costs of reproduction. For example, larger clutches/broods may compromise future fecundity and survival (Nur, 1984a; Murphy, 2000; Reid *et al.*, 2003, but see Pettifor, 1993a). Small clutches also prevent investment beyond what the female is capable. Feeding of the young can result in mass loss but females may regulate the amount of mass they will lose so as not to affect their future survival. There seems to be a balance between the costs and benefits of reproduction in many cases (Nur, 1984a; Orell *et al.*, 1996). In some species, the larger the adjusted

brood size, the greater the amount of mass she will lose (Askenmo, 1977; Westerterp *et al.*, 1982; Nur, 1984a but see Orell *et al.*, 1996). Female mass has been shown to affect the probability of recapture due to reduced survival (Nur, 1984a). Mass reduction can affect the over-wintering survival of the female as well as future breeding attempts both within the same season as well as the next (Young, 1996; Murphy, 2000; but see Orell *et al.*, 1996). However, this is not always the case, females may experience a reduction in weight during breeding and in one study this occurred mostly during the egg laying and early-nestling period (Freed, 1981). Thus, weight reduction occurred before the demands of the begging brood were the greatest. It was also suggested that the reduction in weight could also be adaptive as it could reduce flight costs and increase foraging ability for nestlings. Thus, a reduction in female body mass does not necessarily indicate a cost of reproduction unless, the weight loss negatively effects her subsequent survival.

The optimal clutch size may also differ across individuals. Under the "individual optimization" hypothesis individual females lay a clutch that optimizes their personal optima (Pettifor *et al.*, 1988): the number of eggs laid is the number of nestlings capable of being raised by the female. Experimental support for the individual optimization hypothesis has been obtained in great tits (*Parus major*) and yellow-headed blackbirds (*Xanthocephalus xanthocephalus*) (Pettifor *et al.*, 1988, 1993b and Barber and Evans, 1995). Experimental studies of Great tits and starlings provide strong empirical support for the individual optimization hypothesis (Westerterp, 1982; Slagsvold and Lifjeld, 1990; Pettifor 1993b).

Similarly, other studies have shown that birds that lay a larger clutch fledge more young. In yellow-headed blackbirds, the level of brood reduction is the same in both

three and four egg clutches (Richter, 1984). Thus, four-egg clutches fledged more young, had greater productivity and the parents are inherently better able to produce more young. In the same species, in another study, the entire brood rarely survived, brood reduction occurred in almost all nests (Barber and Evans, 1995). Females that lay more eggs were more productive as they inevitably end up with a larger brood size than females with a smaller initial clutch size. Brood reduction is very common in some species, in these instances, as in the yellow-headed blackbird, a larger clutch size accounts for insurance. Further, in many species, females lay more eggs than they normally expect to rear as a hedge against hatching failure (Tinbergen and Both, 1999). If all eggs hatch, surplus offspring can be eliminated by brood reduction or raised alongside the remainder of the brood (Lack, 1947; Forbes, 1990; Krebs, 1999).

Why hatching asynchrony?

One of the most common behaviours seen in altricial birds is hatching asynchrony; caused by the early onset of incubation prior to the clutch being completed (Clark and Wilson, 1981). The adaptive benefit of this widespread behaviour has often been disputed. Many birds practice routine brood reduction: the brood size at fledging is smaller than the brood size at hatching, with the attrition due to fatal sibling competition. David Lack (1947, 1954) suggested that parents may track uncertain food supplies by laying an optimistic clutch size and reducing the brood as feed conditions warrant. Lack further proposed that hatching asynchrony may avert whole-brood loss by ensuring a swift, efficient elimination of the last—hatched offspring, while the whole brood could be reared when conditions are plentiful. Further, often unpredictable weather conditions for

most species at the start of incubation, predicting the conditions when the chicks hatch may not be possible in some species, thus, brood reduction adjusts the brood to the appropriate size when needed (Siikimaki, 1996). In oystercatchers (*Haematopus ostralegus*), the degree of hatching asynchrony varies with environmental conditions, with greater asynchrony in lower quality territories when conditions predict a poor year (Heg and van der Velde, 2001).

In some species, surviving brood members benefit via an increased growth rate and greater mass at fledging after brood reduction has occurred (Nilsson and Svensson, 1996; Boland *et al.*, 1997). Nestlings destined to die did so early and the remaining nestlings grew normally. However, this is not always the case; reduced broods may still have smaller nestlings (Stouffer and Power, 1991; Stoleson and Beissinger, 1997; Forbes and Glassey, 2000; Forbes *et al.*, 2002).

With synchronous broods, parents may have to work harder to keep all the offspring alive in broods without a behaviorally-induced hierarchy potentially leading to whole-brood loss in some years (Lack, 1954 but see Stoleson and Beissinger, 1997). In many studies, brood synchronization lead to increased fledging success but at a cost of offspring quality, as nestling mass is usually less than that in asynchronously-hatching broods (Amundsen and Slagsvold, 1991). Brood synchrony does not preclude brood reduction, but brood reduction is often delayed relative to asynchronous broods. Although hatching asynchrony may not be necessary for brood reduction, synchrony renders the process of brood reduction to be less efficient (Magrath, 1990; Amundsen and Slagsvold, 1991; Forbes and Glassey, 2000; Forbes *et al.*, 2002). Asynchronous hatching prevents wastage of energy on nestlings that may not survive anyway. It ensures that at

least some nestlings will survive; early-hatched nestlings are buffered while the later-hatched nestlings act as insurance against hatching failure and death of the earlier-hatched nestlings. In short, hatching asynchrony allows for the production of at least some good quality young regardless of the prevailing conditions (Offspring Quality Assurance Hypothesis, Slagsvold: 1986).

Often, the idea that hatching asynchrony is not required for brood reduction or that the hierarchies created do not allow all offspring to survive even when conditions would allow is used as an argument against adaptive brood reduction (Amundsen and Stokland, 1988; Stoleson and Beissinger, 1997). As such, many alternatives have been advanced to explain the adaptive significance to Lack's brood reduction hypothesis of hatching asynchrony.

Protecting the developing embryos from exposure to ambient temperatures ensures proper incubation and an early onset of incubation protects the developing embryos from temperature extremes. Within a clutch, smaller eggs occupying non-intermediate positions in larger clutches may be more susceptible to reduced hatchability (Potti and Merino, 1996). Hatching failure is common in many species (Fautin, 1941), and variable or discontinuous incubation can expose the developing nestlings to ambient temperatures leading to inadequate development (Stoleson and Beissinger, 1999). For example, in tropical ecosystems, high ambient temperatures may allow incubation to begin before the female initiates incubation. Uneven warming of eggs could lead to hatching failure. To protect against hatching failure the female begins incubation early -- as in some parrots -- moderating the inimical effects of the variable environmental conditions (Stoleson and Beissinger, 1999). However, if hatching failure is common, a

larger clutch size may be favoured as a hedge against unpredictable offspring loss (Lundberg, 1985; Forbes, 1990).

Others suggest that early incubation allows for a shorter time between first laying and first fledging, essentially reducing the amount of time with only eggs in the nest and thus the time exposed to predators (Nest Failure Hypothesis: Clark and Wilson, 1982; but see Richter, 1982). By initiating incubation prior to clutch completion, the timing of hatching and ultimately fledging is advanced for a portion of the clutch/brood. Asynchronous hatching increases the chance that at least a portion of the brood survives to fledging age.

A further explanation for hatching asynchrony is the Hurry-up Hypothesis, which suggests that early eggs and thus, early hatchlings, are exposed to different conditions than later-hatched offspring (Slagsvold, 1986). Food supply may peak at certain times during the breeding season, followed by a steep decline and asynchronous hatching ensures that at least some of the nestlings are present when food is at a maximum.

Synchronous hatching ensures that all nestlings will reach their peak food demands simultaneously, resulting in a heavy workload for parents. Asynchronous hatching may spread out nestling food demands and thus reduce the peak workload for parents (Hussell, 1972). Other explanations involve the amount of noise that nestlings make while in the nest (Noisy Nestling Hypothesis) – i.e., synchronous broods might be noisier due to greater competition between similarly sized nestlings (Perrins, 1965). Nestlings vocally beg for food and more frequent or more intense begging would be more detectable by predators. Thus, more asynchronous broods may benefit with decreased competition and yield quieter nests (Sibling Rivalry Hypothesis; Hahn, 1981). As well,

asynchronous hatching lessens the impact of predation on success of the brood (Clark and Wilson, 1981; Konarzewski, 1993).

Core and marginal offspring

Whatever its cause, hatching asynchrony leads to the creation of two types of nestlings. Nestlings hatching on the first day are termed "core" progeny while their later-hatched siblings are "marginal" progeny (Mock and Forbes, 1995).

Core nestlings, because they hatch earlier, are larger and will often outcompete their later-hatched marginal siblings (Mock and Forbes, 1995). Due to the rapid rates of growth seen in many altricial birds, large hierarchies can be created among nestlings, in some cases the older hatched nestlings can be many times the size of their later-hatched nest mates (Richter, 1984; Haydock and Ligon, 1986). Poor rearing conditions such as low ambient temperature as well as inclement weather and low food supply, affect survivorship within a brood. However, core nestlings still almost always survive in many species as they are buffered from the prevailing conditions with enough food from their parents(s) (Forbes and Glassey, 2000). Core nestlings have superior competitive abilities due to their more advanced developmental stage over later-hatched nestlings (Heg and van der Velde, 2001). As well, larger nestlings within the brood are frequently fed first and more often by the parents (Parker *et al.*, 1989; Boland *et al.*, 1997; Stoleson and Beissinger, 1997). The hierarchies that arise at hatching can be maintained for the majority of the nestling period, even in cases when all young survive (Ohlsson and Smith, 1994). Core nestlings may initiate the onset of fledging because they have reached their asymptotic mass, however, the younger nestlings may not be fully-grown in birds that

fledge synchronously (Nilsson and Svensson, 1996). Thus, another potential setback for marginal nestlings in some species is a shorter growing period within the nest than for core nestlings.

While the growth and survival of core nestlings is often assured, that of their marginal broodmates is not (Forbes et al., 1997; Krebs, 1999; Forbes and Glassey, 2000). Younger nestlings often succumb to starvation and/or neglect in fatal sibling competitions with older siblings (Mock, 1984, Haydock and Ligon, 1986; Stouffer and Power, 1991; Nilsson and Svensson, 1996; Stoleson and Beissinger, 1997). Brood reduction is more common in asynchronous and larger broods (Askenmo, 1977, Ohlsson and Smith, 1994).

The number of surviving marginal nestlings varies from year to year. In good years, food and weather conditions may allow the entire brood to be raised and the marginal brood will survive; in bad years, these nestlings are culled efficiently (Boland et al., 1997; Forbes et al., 2001). During periods of inclement weather, marginal offspring are often usually the first to perish. The hierarchy that is created at hatching can be overcome if conditions allow (Boland et al., 1997 but see Forbes et al., 2001). In some species, last-hatched young are fed preferentially and there may be differential allocation of resources to last-laid eggs (increased egg weight with later laying, Howe, 1976; preferential feeding, Krebs, 1999). For those species that seek out younger nestlings this could affect parental condition as they struggle to keep the entire brood alive and this behaviour may occur only when conditions allow (Boland et al., 1997). These behaviours may prolong the death of marginal young essentially allowing a parent a longer time to "decide" if the entire brood can be raised. Even when marginal offspring

survive they may still be smaller at fledging affecting future success. As well, delays in growth have been shown to increase the length of the nestling period (Richter, 1983). The rank of the nestling affects future fecundity in little egrets (*Egretta garzetta*). Lower ranked nestlings (i.e. the marginal nestlings) had significantly smaller broods when they bred (Thomas *et al.*, 1999). Additionally, the inferior lower ranked nestlings may be excluded to poorer quality territories.

Environmental factors

The amount of food brought to the nest ultimately determines the number and quality of offspring. In good years, when food is abundant more offspring are often able to survive. Food supplementation experiments have often shown that more young can be fed and the amount of brood reduction is less (Boland *et al.*, 1997).

Weather can differ greatly from day to day, month to month and year to year, thus growth rates can often vary accordingly. The ambient temperature during breeding often affects growth and survival of nestlings (Fautin, 1941; Richter, 1984; Forbes *et al.*, 2001; McCarty, 2001). Variable insect abundance between years also will affect the survival (Blondel *et al.*, 1998; McCarty, 2001). Consequently, foraging success of parents will vary from year to year (Tinbergen and Verhulst, 2000). Unpredictable environmental conditions (weather conditions, rainfall and ambient temperatures, nutrient abundance are often correlated) will affect the fledging success (Fautin, 1941; Haydock and Ligon, 1986). Weather conditions also affect the number of young surviving, partial or whole brood loss is common during rainy or cool weather (Richter, 1984). Additionally, the amount of precipitation can have effects on the growth of older nestlings when food

demand is the highest (Siikimaki, 1996). Inclement weather can reduce the foraging ability of the parents, affect the activity of insects, and increase the energy required for thermoregulation. Variation in the number of nestlings differs between years due to environmental conditions (Orell and Koivula, 1988; Forbes *et al.*, 2001).

Offspring quality and recruitment

It is axiomatic that recruitment affects population health. Many factors play a role in the probability of a fledging surviving winter to the next breeding season. Low quality young will often have a reduced probability of recruitment (Orell and Koivula, 1988). The mass of the nestling will affect its ability to survive winter, requiring adequate lipid stores (Tinbergen and Boerlijst, 1990). The lightest broods of blue tits had a reduced recapture rate, however the largest nestlings did not have the highest recapture rate suggesting that larger size may in fact be maladaptive (Nur, 1984b). Nur also found that nestling mass and survival were not correlated except for the very lightest nestlings. In an insular blue tit population, fledging mass was correlated with recruitment, probably due to the range of environmental variability encountered (Blondel *et al.*, 1998). In blue tits environmental conditions affected the relationship between brood size and recruitment (Nur, 1984). Additionally, structural size may be affected, though structural development seems to be maintained unless conditions are extreme (Nilsson and Svensson, 1996; tarsus length, Saino *et al.*, 1997).

Survival once adulthood has been reached may also be affected by the growth conditions experienced during the nestling period (de Kogel, 1997). Delays in growth during the nestling period may not allow the nestling to recover even after conditions

improve and can have long-term effects beyond the nestling life also resulting in increased mortality. Nestling zebra finches (*Taeniopygia guttata*), for example, experiencing below average conditions did not "catch-up" in some areas of body condition up to twelve months post-fledge (de Kogel, 1997).

The mass of the fledgling will affect the prospect of obtaining mates. Larger individuals are often the more dominant (Garnett, 1981). Larger body size is often beneficial. Further, female blue tits raised in enlarged broods had a smaller average body mass and as adults began breeding later and laid smaller clutches (Blondel *et al.*, 1998).

Conditions experienced during nestling life may also affect sexually selected traits. For example, the number of nestlings in the nest affects the development and redness of beak colour in zebra finches, males developed their mature beak colour later (de Kogel and Prijs, 1996; de Kogel, 1996, 1997). Additionally, their beaks were not as red as those individuals from smaller broods were. The more intense beak colour of males raised in smaller broods carried through to adulthood. Males of this species raised in smaller broods also sang more for females during courtship. As a result, females found males from smaller broods more attractive.

Parental care

Parental care is important in the survival and success of the brood and some parents are better than others. Due to factors such as brood size, nutrient availability, and weather conditions, parents may incur a cost of reproduction. The clutch size that a female produces is constrained by the cost of reproduction. The process of feeding and brooding are time-consuming activities for parents; effort put towards breeding cannot be

directed towards themselves . Incubating and brooding can be costly for females as these activities may prevent the female from feeding herself. However, parents may determine the reproductive value of the brood they are raising and "decide" whether or not to incur a cost of reproduction, both offspring number and quality can determine reproductive value. Females will only pay the cost of reproduction when the brood is "worth" it. Larger broods may have a lower reproductive value as they would be smaller than nestlings in smaller broods, females would decide not to invest further in broods that she perceived to have a low reproductive value (Horak, 2003).

In some species, survival and/or subsequent breeding attempts may not be affected by the current reproductive effort (Young, 1996; Blondel et al., 1998). Variation between parents of the same species in terms of clutch size laid as well as brood size raised is common even within the same territories. In some species males help the female to raise the brood and may compensate for a larger brood size. Females may not lose more weight with larger brood sizes because males help feed the young (Dijkstra et al., 1990; Moreno et al., 1995). In polygynous species like the red-winged blackbird, broods that are fed by males fledge more young than female-only fed broods however, it has been shown that only 10 percent of males will feed young in this species (Beletsky and Orians, 1990).

Sexual dimorphism

In many altricial birds, females are smaller than males, and the brood sex ratio is female-biased. The greater demands of males appear to leave them vulnerable to food shortfalls. Males can beg more often and receive a greater proportion of the food due to

their large size; they are able to reach higher (Teather, 1992). Redwing males grow faster and reach a higher mass than females, while females leave the nest earlier than males, reaching adult mass sooner as well as have faster rates of feather growth (Holcomb and Twiest, 1970).

The Trivers-Willard Hypothesis states that natural selection will favour producing more of the cheaper sex when food is short (Trivers and Willard, 1973). When resources allow the more costly sex, usually the male in altricial species is favoured (Weatherhead, 1983, results are slight). Additionally, males may occupy the last laid eggs, making up the marginal brood (Howe, 1976; see also Forbes *et al.*, 2002). This could have an adaptive benefit; males will only be raised when conditions allow. Males can be efficiently reduced from the brood when needed and are more susceptible to brood reduction than females (Howe, 1976). Females also develop feathers earlier and reach endothermy sooner than their male siblings (Teather, 1993). Thus, females could aid in the endothermic properties of the brood. Additionally, females that have primary harem status in the great reed warbler (*Acrocephalus arundinaceus*) produce more sons, i.e. a high quality female will produce high quality offspring (Westerdahl *et al.*, 2000, but see Weatherhead, 1983). Male quality is especially important, as females are often the choosier sex. Competitive differences between sexes may affect the number of eggs laid and ultimately the number of nestlings surviving.

Conclusions

The "need" to maximize the quantity and quality of offspring results in behaviours to do just that. The prevalence of hatching asynchrony, although the reasons and significance behind these behaviours are disputed, often results in brood reduction of one or more of usually the last-hatched young. Variability among individuals renders some more suitable than others under fluctuating environmental conditions.

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Chapter 3: Brood engineering as a conservation strategy for altricial birds.

Abstract

Brood reduction associated with asynchronous hatching is ubiquitous in altricial birds. Its occurrence, however, varies widely according to family structure, defined as the number of core and marginal offspring. Brood reduction is infrequent in small broods composed of core progeny, and common in large broods with at least one marginal nestling. These differences present an opportunity to engineer brood structure to enhance the reproductive success of threatened or endangered species. The technique – described as brood engineering – is based upon using knowledge of the relationship between family structure and reproductive success to transfer nestlings with low prospects of survival (e.g., a last-hatched nestling in a brood of five), into nests where they have a high chance of survival (e.g., a brood of two core progeny). This technique of brood engineering was field-tested in a two-year experimental study of marsh-nesting red-winged blackbirds (*Agelaius phoeniceus*). On average, each nestling transfer resulted in an increased reproductive success of approximately four-tenths of a nestling. This work suggests that nestling transfers based upon a priori knowledge of individual survival prospects in relation to family structure may be an effective management tool for conservation biologists.

Introduction

Declining bird populations have become more common with increased rates of habitat loss, brood parasitism, and competition with exotic species. As a result, wildlife managers have had to increasingly implement management protocols in order to arrest these population declines. Captive breeding, removal of brood parasites, habitat protection and translocation of birds to areas better suited to survival have all been used to help enhance the success of avian populations (Franzreb, 1990; Elliot, 1999; Kus, 2002).

Egg or nestling transfers have also been used for the conservation and management of birds. Whooping cranes (*Grus americanus*) provide a useful model. This species is an obligate brood reducer, laying two eggs but rarely raising two nestlings to independence (Kuyt, 1995). The second egg serves chiefly as insurance against the failure of the first egg to hatch. Wildlife biologists have noted this 'surplus' reproductive capacity, and have used egg transfers to enhance reproductive success. Eggs are removed from nests with two viable eggs, and either moved into nests with inviable eggs, or used in captive breeding programs. This management tool has played an important role in the recovery of whooping cranes from near extinction in the 1940's (Kuyt 1995).

Might similar methods be used to enhance populations of other birds that do not practice obligate brood reduction? Though not as dramatic, many altricial birds practice facultative brood reduction, where the full brood sometimes but not always survives. When brood reduction does occur, later-hatched 'marginal' progeny are the customary victims (Lack 1947; Mock 1984; Magrath 1990; Mock and Forbes, 1995). Though marginal nestlings do not always survive alongside their first-hatched nestmates (the

'core' brood), they may play an important insurance role for parents, often replacing failed or feeble core nestlings (Mock and Parker, 1986, Forbes, 1990; Mock and Forbes 1995; Forbes et al., 1997; 2001) They also create surplus progeny that are used by parents for a variety of purposes, including insurance (Mock and Forbes 1995). Most altricial species hatch their eggs asynchronously by initiating incubation before clutch completion (Clark and Wilson, 1981; Magrath, 1990). Due to rapid rates of growth, hierarchies among the nestlings are common (Howe, 1976; Mock, 1984; Haydock and Ligon, 1986; Magrath, 1990; Forbes and Glassey, 2000). The core brood – the nestlings that hatch first – enjoy an advantage in nestling competitions, as they are better able to compete for food with their small, younger, and developmentally delayed marginal nestmates (Richter, 1984; Haydock and Ligon, 1986; Nilsson and Svensson, 1996). As a consequence, core nestlings enjoy secure prospects for growth and survival as they are effectively buffered from the effects of environmental variability (Forbes et al., 2001). The survival of the marginal progeny, however, is on average lower and more variable. Marginal offspring may serve an insurance function when eggs fail to hatch or core progeny die early (Mock and Parker, 1986; Forbes et al., 1997, 2001; Krebs, 1999)

The environmental conditions encountered during breeding often affects the number of surviving nestlings, with more surviving in benign (e.g., warm, food rich) conditions (Richter, 1984; Blondel et al., 1998; Forbes et al., 2001; McCarty, 2001; Rytkonen and Orell, 2001). Due to unpredictable food or weather conditions, the initial clutch or brood size may prove to be overly optimistic, rendering brood reduction necessary. The behaviourally-induced size hierarchy facilitate this process. Marginal nestlings are customarily the first to perish when food is short (Lack, 1954; Magrath,

1990; Amundsen and Slagsvold, 1991). In some years, brood reduction is the norm, whereas in others it may be unnecessary. As such, the most productive brood size can vary from year-to-year (Nur, 1984). The ability to tailor the brood to prevailing conditions allows for the production of high quality progeny, which is important as the probability of survival, future fecundity, as well as the initiation of breeding can be affected by mass at fledging (Tinbergen and Boerlijst, 1990; Blondel *et al.*, 1998; Thomas *et al.*, 1999).

Just as in the whooping crane, the differential survival and insurance value of marginal offspring in variable environments can be used to increase the survival of both an individual nestling as well as the entire brood. By improving growth conditions for marginal nestlings either by decreasing brood size or making the composition of the brood more conducive to survival, management protocols can potentially be established for many altricial birds. The transfer of marginal nestlings, where they are placed into nests where their chance of survival is much greater is one possibility. As well, core nestlings exert a strong effect on the survival of the marginal nestlings and their removal also has the potential to improve the survival prospects for the remaining brood.

The red-winged blackbird (*Agelaius phoeniceus*) is a good model system for a pilot study of nestling transfers to enhance reproductive success. It is abundant, widespread and the nests are easily accessible. Moreover, it is tolerant of human disturbance, and parental recognition of their offspring does not begin until just before fledging, making them ideal for manipulation (Edwards *et al.*, 1999). A further advantage is that the behaviour and ecology of this species is well known. Indeed, it may be the best-studied non-game bird in North America. Redwings hatch their eggs

asynchronously and brood reduction is frequent. Its clutch size (two to six) falls within the range of most passerine birds and its breeding habits are more representative of the majority of altricial birds unlike the relatively rare obligate brood-reducing species such as certain cranes and pelicans.

The logic of the proposed protocol is straightforward: to improve the survival prospects of individual offspring, increasing the likelihood of recruitment to the future breeding population. In this study a long-term (11-year) study of the population ecology of red-winged blackbirds provided the demographic foundation for this work. Understanding the sizes and brood compositions that historically have proven to be the most successful allows for the manipulation of brood size and structure to maximize the probability of nestling survival.

Methods

Study Species and Natural History

Red-winged blackbirds are colonial, polygynous breeders belonging to the family Icteridae. Females provide most parental care including all incubation and brooding of eggs/nestlings. Males sometimes assist in feeding older and larger broods (Beletsky and Orians, 1990). For the population studied between 1993 and 2003 the average clutch size was 3.94 (sd = 0.086, n = 11 years) and the average brood size was 3.51 (sd = 0.137, n = 11). The average number of nestlings surviving to fledging (defined as 8 days post-hatch) was just under three nestlings ($\bar{x}$ = 2.72, sd = 0.96). Incubation typically lasts 11 or 12 days and the nestling period varies between 10 and 12 days (Jaramillo and Burke,

1999). Asynchronous hatching is normal and incubation typically begins with the second or third egg and creates a wide array of brood (or sibship) structures (Table 1).

Field Methods

The experimental component of this study was conducted on populations of red-winged blackbirds breeding in wetlands near Winnipeg, Manitoba in the spring and early summer of 2002 and 2003. Nests were located either during nest construction or during egg laying. Once located, nests were censused daily to determine clutch size and laying order of eggs. Eggs were marked numerically when laying order was known; otherwise they were marked alphabetically. As well, hatching order, hatching failure, brood composition (i.e. the number of core and marginal chicks), presence and absence of nestlings and thus nestling survival/fledging success were also determined from the daily census. After hatching, nestlings were marked for individual identification and weighed daily using electronic balances. To prevent premature fledging, nestlings were not handled after day 10 of the nestling period (day of hatch = day 1). Nests were visually inspected on days 11 and 12 for the presence or absence of nestlings. Fledging success was determined as the number of nestlings surviving to day 8, which is a reliable index of recruitment to the breeding population (Weatherhead and Dufour, 2000). Along with nest success, causes of nesting failure were also determined. These causes included depredation of entire nests, disappearance of all eggs and/or nestlings from one day to the next, or whole brood loss, usually caused by death of the female, determined by the death of all nestlings on one day preceded by normal nestling growth.

Experimental nestling manipulations 2002 and 2003

After the daily nest census, appropriate nestling manipulations were determined during the hatching period, using historical demographic information on expected nestling survival in relation to brood size and structure as a guide (see below for further details). Each nestling was handled gently and quickly transported between nests (time of transfer was normally 1-5 min) to reduce the amount of potential stress on manipulated nestlings. Nestlings were normally transferred on the day of hatching to avert any potential problems with nestling recognition by the parents and thus any possible nestling discrimination among manipulated and non-manipulated nestlings (Edwards *et al.*, 1999). As well, this allowed the transfers to be completed before the age at which most brood reduction occurred, maximizing the potential benefit of the manipulation (averaged around day five, Whittingham and Robertson, 1994).

Manipulations resulted in three types of nests: donor nests, foster nests and reciprocal swap nests. For donor nests, core or marginal nestlings were removed and placed into foster nests. The position of the new experimental nestling within the foster brood was noted as well as the change in the brood composition of both the donor and foster broods. To control for the potential effects of the experimental transfer, I reciprocally exchanged nestlings of the same age and caste (core and marginal).

Non-experimental Nests

Unmanipulated nests were used for comparison with experimental nests. Fledging success in this population varies across years (Forbes *et al.*, 2001). I classified years as above or below average by comparing mean fledging success within a year to the

11-year arithmetic mean ($\bar{x}$ = 2.73 fledglings per successful nest). Demographic data from 1993 to 2003 was used to determine the relationship between brood structure and the incidence of brood reduction.

Methods of analysis

Expected survival

The average expected survival for a given brood composition was determined from demographic records of red-winged blackbirds from 1993 to 2003 (for the experimental work records from 1993 to 2001 were used. These files were updated with the 2002 and 2003 data for this thesis, Table 2). Further, using data from 1993 to 2003, the expected survival for a given brood composition (number of core and marginal nestlings) was determined using a multiple regression model to determine the chief antecedents of nestling survival.

Additions and removals

The expected survival was determined for each brood composition pre-manipulation and compared to the observed survival post-manipulation (See Figure 1; Table 4).

The cost of removal was estimated as:

$$\text{Cost (C)} = E\left(X_{bef}\right) - X_{aft} \tag{1}$$

where X_{aft} is the observed fledging success in donor broods , and E (X_{bef}) is the expected

fledging success from a brood of the same structure as that in the donor nest before the

nestling transfer.

The benefit of an addition was estimated as:

$$\text{Benefit (B)} = Y_{aft} - E(Y_{bef}) \qquad\qquad (2)$$

where Y_{aft} is the observed fledging success in foster broods, and $E(Y_{bef})$ is the expected

fledging success from a brood of the same structure as that in the foster nest before the

transfer.

The expected benefit or cost of a manipulation was estimated as:

$$\text{Net benefit (or cost)} = B - C \qquad\qquad (3)$$

Statistical analysis

Due to a polytochomous distribution of data an approximate randomization was

used to determine the statistical significance of the overall cost/benefit of the

manipulations (the difference between the benefit of addition and the cost of removal, D).

For similar reasons bootstrap confidence intervals were computed.

Additionally, I compared the observed survival in a manipulated brood to the

expected for a brood of the same structure after the manipulation had taken place. This

was done to determine if manipulated broods yielded the same number of nestlings as

unmanipulated broods of the same structure. Using the estimated cost and benefits, the

mean difference was calculated and again an approximate randomization was used for computation of P values. As well, a paired Student's t-test was used to determine whether the fledging success that resulted following the nestling transfer differed from the expected for the same initial brood structure.

Hatching failure

Whether the incidence of hatching failure within a brood conformed to a uniform random distribution was examined with a chi-square test of goodness of fit. Whether failure rate varied with clutch size was also tested with a chi-square test of goodness of fit, using binomial random frequencies for the expected distributions.

Rationale behind nestling transfers

The modal brood size at fledging was three nestlings (Table 2). Intuitively it makes sense to try to create broods of three nestlings. As well, the caste (core or marginal) of nestling affects overall fledging success (Table 3). Removing a marginal nestling with a low expected survival results may in fact have little negative effect on fledging success in a given nest. But if that same nestling is placed in a nest where it has a higher expected survival, a substantial gain in overall reproductive success, when the donor and foster nests are considered together, may be realized. The lowest survival is for last-hatched marginal nestlings.

Another route to increasing reproductive success may occur via a 'trickle down' effect. Marginal nestling survival rises as core brood size falls (Forbes et al. 1997, 2001,

Forbes and Glassey, 2000), and thus reducing the size of the core brood may realize a net

benefit, if the removed nestling can be placed into an equally favourable situation.

Table1. Frequency of different brood structures at hatching observed in red-winged blackbirds from 1993 to 2003. Brood structure is defined as the number of core and marginal nestlings at hatching.

| | Marginal nestlings at hatching | | | |
Core nestlings at hatching	0	1	2	3
1	13	45	92	81
2	43	133	179	19
3	48	190	29	
4	14	6		

Table 2. The expected survival for a given brood structure (number of core and marginal progeny) estimated from field data gathered from 1993 to 2003. The arithmetic mean, samples size (n) and standard error of the mean (se) are shown.

Number of core nestlings at hatching	Number of marginal nestlings at hatching				
	0	**1**	**2**	**3**	**4**
1	1.00 n = 5 se = 0	1.85 n = 34 se = 0.062	2.36 n = 55 se = 0.120	3.04 n = 50 se = 0.106	4.50 n = 2 se = 0
2	2.00 n = 27 se = 0	2.53 n = 77 sd = 0.077	2.79 n = 130 se = 0.083	3.47 n = 17 se = 0.211	
3	2.65 n=26 se = 0.110	2.74 n = 106 se = 0.194	3.41 n = 22 se = 0.194		
4	3.10 n =10 se = 0.348	4.00 n = 4 se = 0.410			

Table 3. The probability of core and marginal survival due to brood structure as well as survival of the last-hatched marginal nestlings based on field data collected from 1993 – 2004, n is the number of broods.

Core Brood Size at Hatching	Marginal Brood Size at Hatching	Proportion of core offspring surviving to fledging	Proportion of marginal offspring surviving to fledging	n	Survival of Last Hatched Marginal Nestlings	n
1	0	0.682		22		
1	1	0.955	0.864	66	0.864	66
1	2	0.869	0.789	107	0.740	102
1	3	0.940	0.707	83	0.357	83
1	4	1.000	0.786	7	0.214	7
2	0	0.952		42		
2	1	0.866	0.608	161	0.614	158
2	2	0.847	0.486	183	0.366	183
2	3	0.952	0.533	21	0.150	20
2	4	1.000	0.000	1		
3	0	0.840		52		
3	1	0.800	0.363	162	0.363	157
3	2	0.959	0.256	41	0.134	41
4	0	0.750		12		
4	1	0.778	0.333	9	0.333	9

Table 4. Definitions of variables used to determine cost and benefit of removal and addition.

	Donor Brood	Foster Brood
Before Transfer	X_{bef}	Y_{bef}
After Transfer	X_{aft}	Y_{aft}

Figure 1. Schematic view of nestling transfers used in experiments.

BEFORE

Donor   Foster

X_{before} Y_{before}

AFTER

X_{after} Y_{after}
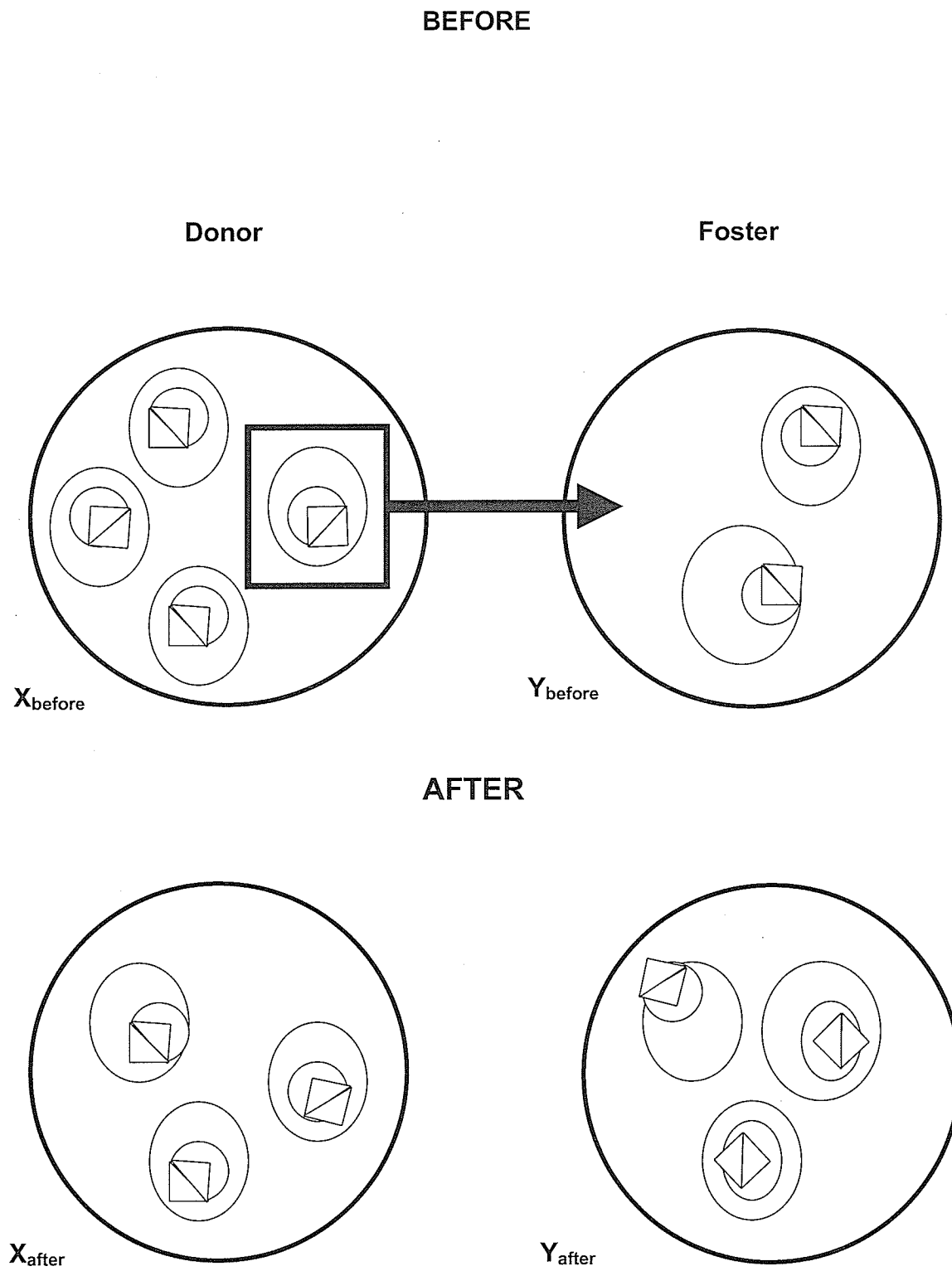
Results

Overall fledging success

The average number of fledglings surviving to day 8 was below average in both the 2002 ($\bar{x} = 2.41$, se = 0.115, n = 78) and 2003 ($\bar{x} = 2.58$, sd = 0.110, n = 93) field seasons compared to the long-term (1993-2003) average for this population ($\bar{x} = 2.73$). Data from the two seasons were pooled to increase the sample size for donor and foster nests.

Factors affecting the number of fledglings

The average survival for each brood composition in each year type (above or below average) from 1993 to 2003 was used to determine the principle factors affecting nestling survival (Table 5). A multiple regression model accounted for 83.5% of the variation in fledgling success (F = 23.32, df = 5, 28; P < 0.0001). The number of core and marginal nestlings as well as the interaction between core and marginal nestlings, the year type (modelled as a dummy variable, good or bad, based on whether the average day-8 brood size in a given year was above or below the 11-year mean) as well as the interaction between the number of core offspring and year type account for almost all of the variation in the number of nestlings surviving to fledging. The interaction between the number of marginal nestlings and year type was removed, as it did not significantly explain any additional variation in the number of fledglings surviving to fledging.

Nestling transfers

Sixty-two nests were manipulated in 2002 of which 41 survived until the nestlings fledged. The remaining nests failed due to predation or flooding and included 17 donor nests, 13 foster nests, and 11 reciprocal swap nests. In 2003, 42 nests were manipulated of which 33 were successful and included 10 donor nests, 13 foster nests and 10 reciprocal swap nests.

A comparison of the observed survival of nestlings in donor and foster nests with the expected survival from their pre-manipulation brood composition indicated a net benefit of approximately four-tenths of a nestling per manipulation ($D = 0.389$, P = 0.011, approximate randomization).

I also examined the accuracy of the method of estimating brood success by comparing observed survival in these experimentally manipulated broods to the expected survival of broods of the same composition. The productivity of manipulated broods was very close to expectation ($D = -0.020$ nestlings/brood, two-tailed P = 0.902, approximate randomization). Thus, my demographic records from unmanipulated broods provided a good predictor of the reproductive success of manipulated broods.

Foster vs. donor nests

Overall, adding one nestling increased the average number of fledglings over the expected number by nearly three fourths of a nestling (Table 5). There was no difference between adding a core or marginal nestling (Multiple Regression: $F = 7.12$, df = 3,6, $P = 0.021$).

Removing nestlings should logically, decrease the number of surviving nestlings in the experimental nest. But because I removed nestlings from situations where their survival prospects were poor, this cost was modest averaging about one third of a nestling ($\bar{x} = 0.352$). Nests in which marginal nestlings were removed performed better than those with core nestlings removed. The cost of removing marginal nestlings was much lower than the cost of removing core nestlings (Multiple Regression: $F = 20.926$, df = 3,8, $P < 0.0004$).

Reciprocal swap nests

The effect, if any, of nestling transfers would be demonstrated in a negative difference between expected and observed survival after the swap had taken place. In both years there was not a negative effect on survival.

Hatching failure

The success of this experiment may lie with exploiting nests that had experienced hatching failure. The overall probability of hatching failure per egg was 10.4% and was independent of clutch size (Chi-square test of independence: $\chi^2 = 0.26$, df = 4, $P = 0.99$). As well, hatching failure was independent of laying order (Chi-Square test of goodness of fit: $\chi^2 = 4.26$, df = 10, $P = 0.93$). Using a binomial random model, hatching failure conformed to a random distribution, i.e. for a clutch of three, hatching failure should occur 33.3% of the time for each egg in the clutch ($\chi^2 = 11.81$, df = 6, $P = 0.07$). Thus, for red-winged blackbirds in this population, the rate of hatching failure is constant and random with respect to laying order and clutch size.

Table 5. Multiple regression analysis of the factors affecting nestling survival to day 8 ($R^2 = 0.835$, $F = 23.30$; df = 5, 28; $P = 0.0001$). The regression coefficient (β) and associated P value are shown.

Independent variate	β	P-value
Intercept	0.348	0.326
Year type	-0.166	0.669
Core brood size at hatching	0.617	0.000
Marginal brood size at hatching	0.960	0.000
Core brood size x Year	0.244	0.134
Core brood size x Marginal brood size	-0.176	0.028

Table 6. Summary results of brood manipulations in 2003 and 2003. Costs and benefits are in units of offspring survival per transfer.

	Mean (+/- 95% CI)	n
Cost	0.352	26
Benefit	0.741	27
Net Result (Benefit)	0.389	53

Discussion

Overall nestling transfers yielded a substantial net benefit to recruitment. Individual nestlings were removed from broods where demographic records predicted poor survival prospects and transferred to broods with considerably better prospects for survival. The results are not surprising. Other studies have shown that by placing last-hatched nestlings into first-hatched positions in the nest the probability of survival climbs to 100% (Haydock and Ligon, 1976). However, the goal was to increase the success of an entire brood, not solely the manipulated nestling.

Donor broods

The results suggest that the removal of nestlings from donor broods resulted in only modest costs. The obvious question is "why?" A reduction in the number of nestlings in donor broods could potentially alleviate food stress for those remaining. A reduction in brood size reduces the food limitations present in some years and can reduce the hierarchy imposed on the nestlings at hatching (Westerterp *et al.*, 1982). Improving growth conditions results in larger body mass for the nestlings (Rytkonen and Orell, 2001; Ohlsson and Smith, 1994). However, on average, three nestlings fledge more often than not in this population, creating nests smaller than three would demonstrate a cost of removal if the brood was reduced below that number.

Removing marginal nestlings from donor broods resulted in lower costs than removing core nestlings. The low cost of removing marginal nestlings results from their already low probability of survival. This is especially apparent in below average years when their chance of survival falls further. However, even in good years, it is possible in

some species that the smallest nestlings may still not be able to overcome the competitive disadvantage becoming buried under its older siblings, especially with large brood sizes (Haydock and Ligon, 1986; Stouffer and Power, 1991; Forbes *et al.*, 1997). Since the conditions that marginal nestlings experience during their nestling life may have long-ranging effects beyond the range of the current breeding season, increasing their growth would prove beneficial (Thomas et al., *1999*). The removal of marginal nestlings had a minimal impact on the survivorship of the brood. Later-hatched nestlings often exert little, if any, any effect on the brood, thus, when they perish or are removed experimentally the brood may not even benefit from increased growth (Forbes *et al.*, 1997; Stoleson and Beissinger, 1997; Forbes and Glassey, 2000). However, the early removal of nestlings could benefit the entire brood, food that may potentially be "wasted" on nestlings that would not survive anyway may be redirected to the remaining nestlings. As well, removing nestlings within the first couple of days of the nestling period is most beneficial potentially averting delays in growth for the entire brood. Nests that experience natural brood reduction can have smaller masses than those that do not (Forbes and Glassey, 2000). Further, some species seek out the smallest nestlings and may expend energy to keep them alive; by removing these nestlings, the parent(s) may benefit as well (Krebs, 1999).

Foster broods

The greatest benefits of nestling additions were observed in the smallest foster broods. In fact, on average there was a benefit of almost three quarters of a nestling. When a manipulation increased donor brood size from three to four nestlings the benefit

of addition was often minimal. The modal brood size averaged three nestlings in this population, and increasing the brood size beyond that number would more often than not fail to increase in the number of fledglings. Thus, it may be better to play the odds and produce broods that have proven to be the most successful. The unpredictability of conditions during the breeding season does not allow determination of the type of year until after it has occurred. However, basing manipulations on a large data set allowed for educated decisions to be made regardless of year type.

There was no obvious difference between adding nestlings that were originally core and marginal progeny. However, the survival of transferred nestlings does depend upon their position in the foster brood. Creating new marginal nestlings may not be the best choice as the same level of hatching asynchrony is maintained or a hierarchy could be created. Marginal additions may not be able to compete though this may depend on brood size as well as the size hierarchy (Haydock and Ligon, 1986). However, common sense often prevailed when deciding on manipulation type. In this experiment, the transfers from donor to recipient broods were designed to increase survival. Some transfers were deliberately avoided knowing that a marginal nestling would not survive in a large brood. The variable survival of marginal nestlings makes them logical candidates for transfer. Often the probability of survival can only increase, especially if they become core nestlings in the foster brood.

A few considerations to keep in mind to prevent over-taxing the brood: manipulations should be kept in the natural range of brood sizes for the species. A decline in mass is a common trend as brood size becomes larger however, effects on survival most often occur in the largest manipulated brood sizes and are intensified in

poor years (Nur, 1984b; Neuenschwander *et al.*, 2003). Nestlings of smaller mass may not survive as well as larger nestlings after fledging and can have smaller broods when they begin breeding (Nur, 1984; Thomas *et al.*, 1999). A summary of brood enlargement experiments showed that an increase in brood size resulted in an increase in the number of fledglings. However, the body mass usually declined which in some instances had survival effects to the next breeding season (Dijkstra *et al.*, 1990). There is limited evidence that suggesting that fledging mass is correlated with post-fledging survival in redwings (Hengeveld, 1989).

Hatching failure

Nests that experienced hatching failure are ideal candidates for foster nests. In redwings in my study population, hatching failure occurs randomly in roughly 10% of eggs: the rate of egg failure is independent of clutch size and laying order (unpubl. data). Other populations appear to experience different rates of hatching failure (Whittingham and Robertson, 1994). As would be expected with a binomial random variable, multiple eggs failed to hatch in some clutches. Redwings, presumably unable to predict hatching failure appear to lay clutches larger than they can normally be expected to rear, and rely upon a combination of hatching failure and brood reduction to trim the brood to a manageable size. In other species, the female "counts on" producing a brood size of four from a clutch of four and the clutch size she produces may be in line with what she is capable of raising. The extra eggs serve as insurance and the brood is reduced as needed (Barber and Evans, 1995; Krebs, 1999; Forbes *et al.*, 2001). Targeting nests with hatching failure as foster nests may yield the greatest benefit. Females with larger

original clutch sizes may be better able to raise a larger brood in some instances (Barber and Evans, 1995; Pettifor *et al.*, 2001).

Threatened and endangered species may even be more susceptible to hatching failure due to small population sizes. Inbreeding occurs at a higher rate in small populations, which in turn results in an increase in deleterious alleles matching up at a consequence of inviable offspring. Individuals that are more closely related may produce a lower number of offspring due to increased hatching failure (Bensch *et al.*, 1994). This would lend to the creation of more opportunities for engineering brood size.

Hatching failure may also stem from another extrinsic cause. Brood parasites such as cowbirds frequently remove host eggs or prevent efficient incubation of host eggs resulting in hatching failure – e.g., 12% fewer host eggs hatched following shiny cowbird (*Molothrus bonariensis*) parasitism (Wiley, 1985; Hauber, 2003). These naturally reduced broods could also be used for accepting nestlings. Management programs often involve removing cowbird eggs from parasitised nests (Franzreb, 1990). In some species where host nestlings are larger than the cowbird, the effect of the cowbird on host nestling survival is small or non-existent (Hauber, 2003). But in nests where the cowbird hatches before the host and/or is larger than the host, the host nestlings suffer with impaired growth and survival (Kilner, 2003). Short incubation time may allow for cowbirds to hatch before their hosts (McMaster and Sealy, 1998). Cowbird nestlings could also be manipulated and placed into positions in nests where they exert very little effect on survivorship of the host nestlings.

Brood engineering and the critical brood size

Interestingly, increasing brood size in some cases may improve growth conditions. Adding nestlings to singleton and pairs of nestlings may be especially beneficial. Ectothermic altricial nestlings prevail early in the nestling period. The onset of endothermy occurs about halfway through the nestling period (Olson, 1992). Up until that point the nestlings rely on parental brooding and during parental absences huddling with their nest mates in order to maintain their body temperatures, they are effectively endothermic (Clark and Balda, 1981). As well, larger broods reach this endothermic stage before broods that are smaller (Clark, 1982; Sullivan and Weathers, 1992). And once endothermy has been reached, larger brood sizes may still have reduced thermal energy costs: huddling continues to be beneficial. The maintenance of body temperature above ambient is particularly important early on as body temperature essentially dictates metabolic rate and thus, growth rate. Delays in growth result in smaller body masses of fledglings and can extend the nestling period. However, a critical brood size for huddling with nest mates may be required. As well, smaller broods may require more food in order to maintain the same growth as larger broods that have the benefit of more efficient huddling. Energy is shunted away in order to fuel the metabolic requirements of thermoregulation (Westerterp *et al.*, 1982). A larger brood exposes less body surface to the ambient conditions resulting in greater thermal inertia. Huddling reduces heat loss during parental absences, keeping body temperatures, metabolic rates and growth high (Olson, 1992). The critical surface area to volume ratio has been shown in a variety of altricial species to affect when brood or effective endothermy begins (O'Connor, 1975; Yarbough, 1978; Clark and Balda, 1981). Maintaining body temperature during parental

absences often requires a minimum number of nestlings; smaller brood sizes may lose more heat during parental absences and could potentially experience reduced growth and even death (Yarbough, 1978; Pereyra and Morton, 2001). Another benefit of a larger brood size comes with an earlier decrease in brooding in large broods and females need to spend less time brooding larger broods (Westerterp et al., 1982; Sanz and Tinbergen, 1999). For asynchronously hatching species where the brood hatches over several days, the onset of effective endothermy can potentially be delayed because it may take longer for the critical mass to be reached. Increasing brood sizes in nests with one or two nestlings may be beneficial in terms of optimal growth for the red-winged blackbird as well as other altricial species.

Another potential benefit of adding nestlings could be to prevent nestlings in small broods from growing too large. In one careful study, the greatest survival after fledging was never the largest nestlings (Nur, 1984b). By feeding a nestling indefinitely, a nestling can only get so large and be fed so much before they either benefit no further or decline in survival probabilities (Diminishing Returns Hypothesis - Slagsvold et al., 1995). Thus, adding additional nestlings to small broods may prevent wasting parental effort and potentially preventing producing nestlings that are too large.

Egg manipulations vs. nestling transfers

Here, I examine the potential of nestling transfers to enhance reproductive success. Egg transfers are a possible alternative method of manipulation. Moving eggs could potentially avoid any problems associated with handling nestlings. However, we did not see any affect of the manipulations on survival. Potential difficulties with

manipulating eggs rather than nestlings include the unpredictability of hatching failure. In redwings, hatching failure is a random variable. The predicted brood size may not be the same as what is observed, but in which nest and what egg? First, with foster nests, potentially adding more eggs could affect incubation efficiency by increasing hatching failure or increasing the incubation period (Engstrand and Bryant, 2002). The female's brood patch typically can accommodate a certain number of eggs. Differences in egg sizes of different females of the same species are common as well (Muma and Ankney, 1987; Christians, 2002). Egg size can affect contact with the female's brood patch. Additionally, hatching failure occurs often in some species and the number of eggs hatching cannot be predicted. This may not cause any difficulty for foster nests. However, for donor nests, reduction in the number of eggs, in addition to hatching failure, particularly multiple failures, can potentially cause a large reduction in brood size (removing one egg from a four-egg clutch with one or two eggs failing). With nestling transfers, the hatching brood size is determined before manipulations take place. As well, determining the onset of incubation is not always certain and the level of hatching asynchrony can only be forecast imprecisely. Thus, waiting until nestlings hatch allows for better-designed transfers. As well, by waiting for nestlings to hatch, the abilities of the parents may become apparent. Some will experience early brood reduction, indicating a poor prognosis for fostered nestlings in such nests, or sickly nestlings may be found indicating poor food quality being brought to the nest.

The role of environmental variability

Environmental variability is inescapable for natural populations of birds and can have lasting effects on survival. For example, ambient temperature affects the growth and number of offspring surviving in broods of red-winged blackbirds (Forbes *et al.*, 2001). In most species, food availability and weather conditions are unpredictable varying both within and between breeding seasons (Siikimaki, 1996). Some species do experience relatively regular cycles of prey abundance and can adjust their brood size depending on the yearly cycle (Korpimaki and Rita, 1996). Additionally, food abundance can vary over a given year, with nutrient availability peaking at certain times of the year – it is important for the nestling period to be well-timed (Rytkonen and Orell, 2001). Year after year, temperatures increase throughout the spring towards summer. Conditions such as those are predictable: it will be on average warmer in the summer than it is in the spring. However, below or even above normal temperatures, storm systems, and other peculiarities in the normal course of the breeding season cannot be accurately predicted more than a few days in advance. Inclement weather can have strong effects on the brood, resulting in nestling death, reduced growth, longer nestling periods, and can effect future survival (McCarty, 2001). Reports of stormy weather reducing offspring survival are frequent (Richter, 1984).

In my field study in 2002 and 2003, nest failure was often due to unpredictable weather conditions, especially early in the breeding season. Extended periods of rain in 2002 reduced offspring numbers substantially, and manipulations of redwings that took place during this time were less successful than those after.

The success of nestling transfers may also rest upon year quality that can only be evaluated retrospectively. In particular, little benefit may occur in above average (good) years. In good years, food may not be limiting. With sufficient provisioning for all, the entire brood could have been raised with high quality fledglings being produced (Nur, 1984b; Orell and Koivula, 1988). When conditions are favourable, differences in the growth and survival of core and marginal offspring may narrow or vanish entirely (Forbes et al. 2001), whereas in poor years starvation may affect primarily the marginal offspring (Orell and Koivula, 1988). Thus, in above average years, for example, instead of improving overall survival by removing nestlings, the quality of the nestlings may be maximized. In poor years, nestling transfers could reduce food stress in donor nests. Thus, there are potential benefits to nestling transfers in either year type, with little obvious cost.

In addition, differences in food availability between populations of birds can potentially be taken in to account when manipulating nestlings. Nestling transfers with threatened species could occur over a larger geographic scale, to take advantage of local differences in breeding conditions. Even breeding areas in relatively close proximity can have a wide variation in resources. Again red-winged blackbirds provide an example: populations in woodland marshes are more productive than agricultural marshes and consequently the nestlings are fed more and have a higher probability of survival (Whittingham and Robertson, 1994). In addition some areas are more susceptible to predation. Moving nestlings to areas where predation is lower could yield benefits to threatened species as the population could have higher potential as a source of recruits (Vierling, 2000).

The role of predation

There may be further benefits to reducing brood size and hence sibling competition. More synchronous nests have been reported to be noisier as there is greater competition among the nestlings (Perrins, 1965). Removing core nestlings may improve the condition of the marginal nestlings resulting in less time spent begging (Haydock and Ligon, 1986). Larger, noisier broods may also be more susceptible to predation (Perrins, 1965). A reduced brood size may also result in less foraging trips for the female, thus making the nest less conspicuous to predators. However, with the small-scale of brood manipulations (one nestling) the differences between broods may not be sufficiently great to have any noticeable difference. And any benefits from alterations of brood size or structure may be offset by the increased investigator disturbance around the nesting area that may make nests more susceptible to predation. However, quick and deliberate nest surveys can reduce the likelihood of predation.

The role of parental quality

Increasing brood size can negatively affect the parents raising the brood; females can lose more weight as brood size increases, affecting future survival (Nur, 1984). A cost of reproduction may be associated with increased brood size, where the parents body condition, future fecundity and potentially survival may be affected if they invest (feeding, brooding) too much in the current breeding attempt (Nur, 1984; Young, 1996). In many cases, there seems to be a ceiling effect to how much an individual will invest (i.e. will increase feeding up until a certain point) so as to not negatively affect future

reproductive prospects (Saino *et al.*, 2000). Due to some females not increasing their provisioning rate as brood size increases, the amount of food per chick can decline (Martins and Wright, 1993). Conservative manipulations may decrease the probability of negatively affecting both the parents and the brood, avoiding a cost of reproduction. However, many studies have demonstrated the ability of parents to successfully fledge more offspring than the clutch size produced, thus increasing brood size may not be detrimental with small increases such as was completed (Dijkstra *et al.*, 1990). Rather, constraints on clutch size may be present during egg laying (Nur, 1984b).

In red-winged blackbirds and other polygynous species females are responsible for all or most of the feeding and brooding of nestlings. Only 10% of males fed nestlings in one study and 71% in another (Beletsky and Orians, 1990; Yasukawa *et al.*, 1993). In some species, males also may compensate for an increase in brood size, preventing overworking the female (Moreno *et al.*, 1995). Male-fed nests fledged more young than nests where males did not feed. Males that fed had better quality nestlings and in redwings, nests that have both parents feeding fledge more young (Amundsen and Slagsvold, 1991; Patterson, 1991). In addition, redwing males tend to feed the first nest on their territory (Patterson, 1991; Yasukawa et al., 1993). Male feeding may be more important in bad years or in areas that have lower productivity to increase survival prospects for the brood (Whittingham and Robertson, 1994). Moving nestlings into nests where male feeding has been observed may result in increased survival and growth.

Limitations

One problem that was encountered was not having suitable nests on a given day. A suitable donor nest may have presented itself, however, there was not always a foster nest to place the nestling. Thus, manipulations have to be done as soon as possible and can be limited by the availability of foster nests. An undernourished or sickly nestling may not be able to recover even when placed into a more favourable position within the brood. This procedure would probably have to be limited to threatened species. Due to the very nature of endangered species, where the population size is very low, suitable donor and foster nests may not often be available, reducing the utility of the brood engineering technique.

Additionally, predation of nests can have a strong effect on survival and proliferation of a population. Manipulations can improve nest success, but if the nestlings are eaten, obviously, no improvement has been made. Thus, in many cases, other management techniques should also be in place to prevent losses due to predation. Additionally, species that are intensively managed would benefit the most from this procedure. Knowledge about nestling survival, the most productive brood size, hatching failure, and parental ability would improve the success of a brood engineering protocol. Most importantly, this procedure would be limited to the species that hatch their eggs asynchronously; competitive asymmetries must be present. The success of this procedure was based on moving nestlings that would probably not survive into nests where the chances of survival were much greater; a synchronous nest would not result in the same affect.

The possibility of unintentional selection from brood engineering may be a concern. In some captive bred fish, unintentional selection has occurred because captivity can select for traits that may not be beneficial in the wild. As an example, in fish, larger eggs are better able to survive after hatching however the female, in turn, produces fewer eggs. The smaller eggs have lower survival but the female is capable of producing more of them (Heath *et al.*, 2003). In captivity because the fish are being raised in a relatively mild environment (i.e. without predators and no food shortages), the selection for larger eggs is relaxed and smaller eggs become more common. Smaller eggs have a lower probability of survival in the wild (Einum and Fleming, 2000). In addition, wild populations of salmon that are supplemented with captive-bred individuals demonstrate a trend towards smaller egg size (Heath *et al.*, 2003). Removing selection pressures can result in genetic change fairly rapidly in fish in captivity. Captivity can lead to genetic fixation of alleles that cannot be removed once released into the wild (Lynch and O'Hely, 2001). Inbreeding and genetic drift may also result (Wang and Ryman, 2001).

Is the same effect possible as a result of brood engineering? By removing nestlings from large broods the selective pressures against large brood size may be reduced. The females producing large clutches do not have to raise a large brood. Once the manipulations end, the selective pressures against large clutches may return. Will the parents and offspring be negatively affected similar to that seen in fish?

The behaviour of many altricial birds prevents over-taxing the brood. Adaptive brood reduction prevents allocation of resources beyond the parent's capabilities in a given year (Lack, 1947, 1954). If not able to raise the entire brood the marginal nestlings

die. In the brood engineering protocol the most commonly removed nestlings would be the ones that are in fact reduced naturally. The survival of the last hatched nestlings depends on random weather and thus food conditions, therefore their survival is variable. Removing marginal nestlings simulates a good year. Once the manipulations end, the breeding season to follow would be similar to a bad year.

The very purpose of brood engineering is to prevent the population size from becoming too low, which can result in genetic bottlenecks. Because they are not being raised in captivity, the selection pressures are the same. Whereas captive breeding fish may result in an increase in deleterious alleles and inbreeding, the brood engineering protocol is designed to reduce the possibility of those problems in a wild population.

Future directions

Sex ratio manipulation

In this study, the sex of the nestlings was not determined before manipulation. In sexually dimorphic birds like the red-winged blackbird as well as many other species the amount invested to successfully rear males and females differs. Males are often larger, reach greater adult mass, and require a greater investment by parents during their nestling life. Whether the sex of the eggs differs with the order of laying is unknown for many species. In one study, the sex ratio varied greatly, favouring females, with males being reduced from the brood when conditions did not allow, suggesting that males make up the later-hatched eggs (Howe, 1976). This ensures females produce only good quality males. Females, being cheaper to produce may dominate in poor years (Weatherhead,

1983). Potentially brood manipulation experiments could place marginal males into core positions, where they may dominate due to their potential size advantage (Teather, 1992). A study of common grackles (*Quisculus quiscula*) showed that when two males were present, the entire brood suffered. Broods composed of all females or a male and a female enjoyed better growth and survival (Teather and Weatherhead, 1989). However, since most offspring do not become dimorphic until later in the nestling period manipulations would more often than not take place before dimorphism was reached. The potential to sex nestlings immediately after hatching using molecular markers may make sex ratio manipulations potentially more feasible.

Potential study species

Red-cockaded woodpeckers (*Picoides borealis*), a cooperatively breeding species have benefited from offspring manipulations (Richardson *et al.*, 1999). In the past orphaned nestlings have been placed into other nests as a management practice. It has been suggested that when the brood exceeds the abilities of the adult group, to move the extra nestlings into nests where there are more helpers available to feed the nestlings (Richardson *et al.*, 1999). As well, in order to prevent brood reduction, it has been suggested that small brood sizes should be used and nestlings that are manipulated should be close in age to the foster nest. Potential brood engineering strategies could be applied to this species to enhance efforts already in place. Additionally, juvenile males remain on the territory to help with future breeding attempts. Moving males to new areas may be beneficial as they will remain as helpers around the nest (Wallace and Buchholz, 2001). In cooperatively breeding species, nests that have helpers often will produce more young of better quality (Reid, 2003).

Endangered kakapos (*Strigops habroptilus*) in New Zealand are intensively managed (Elliott *et al.*, 2001). Currently, attempts at captive breeding have had poor success, and thus are now used only for sickly or low weight nestlings. In some instances, in areas where predation could not be prevented, eggs were removed from nests in anticipation of predation and incubated artificially. Additionally, the nests are heavily protected against predation using a system of baits and traps and monitored by video nocturnally. The potential to place eggs into natural predator-free breeding areas could use a brood engineering protocol established for this species. Since this species is already intensively managed, the potential for a brood engineering protocol is great. Placing eggs/nestlings into nests where they could survive and or improving survival of all nestlings through manipulations could potentially be used for this species. Chicks that are smaller than average could be placed into nests where their chance of survival is much greater reducing the need for hand raising. Indeed, it has been predicted that one third of nestlings will not be able to be raised by their mothers (Elliott *et al.*, 2001). Having nestlings develop in natural nests prevents any problems associated with captive breeding. Re-introductions, habituation to humans, and problems with proper feeding protocols often cannot be avoided when raising wild species in captivity (Elliott *et al.*, 2001). However, increasing the wild population without relying on hand rearing would be a positive step in the conservation of this and other species.

Improving survival and growth conditions of nestlings will prove beneficial to threatened species. Increasing the number of recruits into the population could potentially have great effects on small populations of birds. In this study, actual recruitment rate was not determined only assumed from survival until fledging. It can be

assumed that not all individuals will survive to breeding, but by improving nestling condition by reducing brood size, and reducing the competitive hierarchy, better quality individuals may be produced, and thus have improved survival. As the number of threatened species increase, novel methods of increasing reproductive success are needed. A brood engineering protocol can be used in order to increase the number and survival of nestlings avoiding the costs of captive breeding and subsequent reintroductions.

General conclusions

The translocation of nestlings can feasibly be used to increase the number of birds surviving in asynchronously hatching altricial birds by using well-planned manipulations. There are two elements that are important in order to create broods that have a high probability of survival:

1) The presence of marginal offspring. Marginal nestlings are key in improving survival prospects for broods using the technique of brood engineering. Their survival is both lower and more variable than that of core offspring. Because most core nestlings are likely to survive anyway, there is little room for their survival to increase following transfer to a new brood. In many cases, the opposite is true for marginal nestlings. In large broods (five-chick broods in red-winged blackbirds), the prospect of marginal offspring mortality is very high in unreduced broods. A transfer to almost any other brood is likely to yield some benefit.

2) Nests that experience hatching failure are ideal foster nests. Hatching failure reduces brood size and in red-winged blackbirds and likely other species, is a random event. By exploiting the surplus marginal offspring, nestlings that are often "wasted" in brood reduction, brood engineering can potentially increase the number and quality of nestlings that survive to independence.

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