Breeding Biology and Parental Care of the Crimson Rosella

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Declaration

The research presented in this thesis is my original and independent work. Chapter 4 is co-authored with Ross Cunningham and Christine Donnelly who assisted with the statistical modelling.

No part of this thesis has been submitted for any previous degree.

Signed

Elizabeth A. Krebs

Elizabeth A. Krebs

Acknowledgments

I don't think its overstating events to say that at the end of my PhD I find myself a rather different person than when I began (and not only because of the ravages of time). True a journey starts with a single step, but if I'm not sure that I knew there would be 10,000 on the way!. My Phd has been full of many surprises both of an intellectual and personal nature, I would like to thank everyone who has contributed in equal measure.

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When I first arrived in Australia I was captivated by the amazing 'gaudy' red rosellas all around, and after years of scrutinising their behaviour I still am.

General Abstract

I studied the breeding biology and parental care of crimson rosellas (*Platycercus elegans*) breeding in nestboxes on Black Mountain, Canberra, Australia between 1993-1996. Crimson rosellas are broad-tailed parrots weighing about 140g which breed commonly in south-eastern Australia. Females initiated clutches in late September or early October, and laid clutches of 5.3±0.1 eggs. Eggs were laid at 1 to 4 day intervals. The breeding success of rosellas was highest during in the wettest year (1995), when they bred earlier, laid larger clutches and fledged more young. Many pairs appeared to defer breeding when conditions were very dry (1994). Pairs breeding early had larger clutch sizes but higher hatching failure than pairs breeding later in the season. Clutches hatched over 0.5 to 7 days and hatching asynchrony increased over the breeding season. Hatching asynchrony was not strongly correlated with clutch or brood size, suggesting that females varied the onset of incubation.

Asynchronous hatching reduces the growth and survival of last-hatched nestlings in most species. I examined the consequences of hatching asynchrony on the growth, size at fledging and survival of male and female rosella nestlings. Rosella broods had large and variable mass hierarchies at hatching: first-hatched chicks in some broods were seven times larger than last-hatched chicks. Despite large initial size differences, chicks of all hatching ranks grew at equal rates and fledged at similar sizes. Chick growth parameters were not related to the degree of hatching asynchrony, brood size, laying date or year and chicks of all hatching ranks had equal post-fledging survival. Asynchronous hatching, in rosellas, does not result in poor growth of last-hatched chicks, suggesting that parents may engage in behaviours which increase the growth and survival of last-hatched chicks and thereby reduce the costs of hatching asynchrony.

To determine how parents were able to maintain equal growth rates within broods with large size hierarchies, I examined how food was distributed to chicks of

differing hatching ranks. Fathers provisioned the brood at a higher rate and fed first-hatched chicks within the brood more than last-hatched chicks. Mothers distributed food equally to all chicks in the brood, but took longer to feed nestlings and spent more time in the box. Parents also distributed food differently to male and female chicks. Large males were fed more than all other nestlings, while female nestlings were fed equally irrespective of size. Thus, although food is allocated equally within rosella broods, this distribution is achieved through complex patterns of food allocation by mothers and fathers.

Although equal allocation of food can minimise competition between nestlings and maximise the growth of all young, it can be risky when food is scarce because it prevents efficient brood reduction . I used temporary chick removals to manipulate hunger of individual chicks and the whole brood in order to assess how mothers and fathers responded to different levels of nestling hunger. Overall parents fed individually hungry chicks more, but mothers and fathers responded differently to changes in nestling hunger. Fathers responded only to increased hunger of last-hatched chicks. Mothers did not respond strongly to changes in chick hunger and engaged in behaviours which reduced the ability of more competitive chicks to monopolise food. In contrast, when the whole brood was hungry, and feeding rates appeared inadequate for the whole brood, food was redistributed to first-hatched chicks. This was because mothers preferentially fed first-hatched chicks when all chicks were hungry. Fathers fed all chicks equally in the control and brood removal treatments. In crimson rosellas, mothers primarily regulate the distribution of food within the brood, and skew the allocation of food in a way consistent with a strategy of adaptive brood reduction when food is scarce.

The complex responses of rosella parents to changes in chick and brood hunger could also arise because of changes in chick behaviours. I examined interactions between nestlings and parents to assess how hunger affected chick begging and how parents responded to changes in begging. Hungry chicks only increased the intensity of their begging when the whole brood was hungry, suggesting the competition increases begging independently of chick hunger in crimson rosellas. Parents did not distribute

more food to all nestlings who begged more; mothers fed first-hatched chicks in proportion to their begging intensity, whereas fathers fed last-hatched chicks in proportion to their begging. Thus parents only used begging rates to adjust food allocation to some chicks within the brood. Since chicks did not differ in their begging towards either parent, and parents did not respond in a straightforward way to changes in begging, rosella parents appear to have control over the distribution of food to nestlings.

Table of Contents

Chapter 1

Introduction

Introduction

Theoretical overview

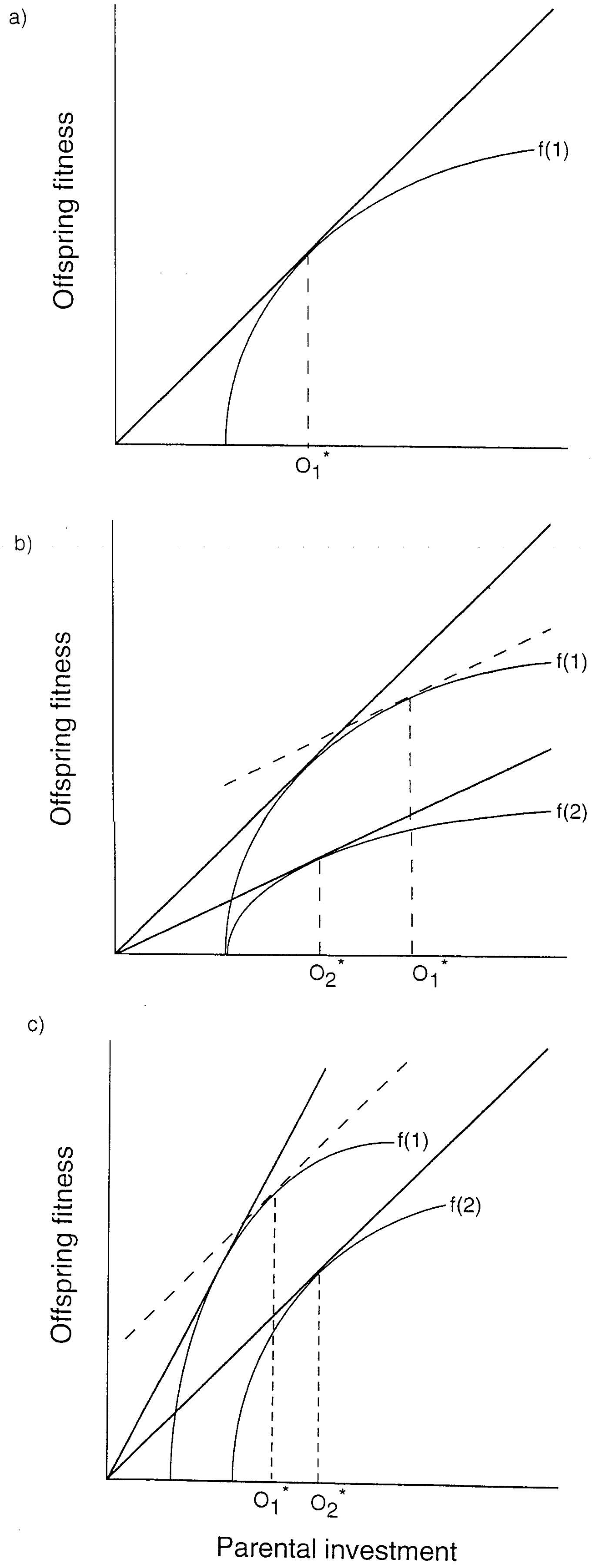
PARENTAL INVESTMENT

Parents care for young in a variety of ways, such as by providing nutrients and protection from predators. Parental care increases offspring survival and fecundity but is costly to parents (Winkler and Wilkinson 1988). Investing in an offspring reduces a parent's ability to invest in other offspring and is termed parental investment (Trivers 1972). The benefits of increased parental investment for an offspring are assumed to increase initially, and then reach an asymptote where further parental investment will not lead to increases in offspring fitness (e.g. Figure 1a). However the precise shape of the curve relating parental investment to offspring fitness is unknown.

If parents gain diminishing returns from investing in offspring, how much should parents invest in each offspring? Parents are predicted to invest in offspring so as to maximise their return per unit of investment (Clutton-Brock 1991). Smith and Fretwell (1974) used a simple graphical model to demonstrate that if all offspring benefit equally from a unit of parental investment, parents should invest equally in offspring (Figure 1a).

Optimal allocation of parental investment becomes more complex if young differ in their quality or ability to use parental resources. For example, Temme (1986) modelled the effect of differing seed quality on optimal parental allocation in plants. If offspring differed in the maximum fitness they could obtain, parents did best by investing more in the offspring with higher maximum fitness (Figure 1b). Counter intuitively, if offspring had the same maximum fitness but differed in the efficiency with which they utilised parental investment, parents optimised their marginal returns by investing more in the less efficient offspring (Figure 1c). Thus differences in the quality of offspring can alter the optimal pattern of parental allocation.

Figure 1. Graphical representation of optimal patterns of parental investment, a) when all offspring have the same fitness curve, b) when offspring 1 has higher maximum fitness than offspring 2, and c) where offspring 1 uses parental investment more efficiently than offspring 2. Fitness curves for offspring are labelled f(1) and f(2), and the dotted lines present optimal parental investment. Optimal investment in offspring is indicated by O^*. If all offspring benefit equally, from parental investment, parents maximise their fitness returns by investing equally in all offspring (a; Smith and Fretwell 1974). If offspring differ in their fitness, parents should provision offspring so that the rate of gain is equal for both offspring (parallel dotted and solid lines. In graph b, parents maximise their marginal returns by investing more in O_1. In graph c, parents maximise their returns by investing more in the less efficient offspring (O_2). (Redrawn from Temme 1986)


a)
Offspring fitness
f(1)
O_1^*
b)
Offspring fitness
f(1)
f(2)
O_2^*
O_1^*
c)
Offspring fitness
f(1)
f(2)
O_1^*
O_2^*
Parental investment

One difficulty with these models of optimal parental allocation is that they assume that the level of investment in current reproduction will not affect investment in future reproduction. However if parents have a fixed energy budget, they must trade off investment in an offspring against investment in all current and future offspring (Stearns 1992). This tradeoff can lead to conflict between parents and offspring over the allocation of parental resources. Parents and offspring are potentially in conflict over the distribution of resources because of genetic asymmetries in relatedness (Hamilton 1964; Trivers 1974). Parents are equally related to all offspring, whereas offspring are less related to their parents or siblings than they are to themselves. Since offspring are related to their parents by 0.5, they will weigh the costs of parental investment by half as much as their parents, leading to offspring favouring a higher level of investment than is optimal for parents (Figure 2). Similarly, offspring will favour a higher level of parental investment in themselves compared with their siblings, generating sibling rivalry between offspring. Genetic and kin selection models both show that the divergent genetic interests of parents and young can lead to phenotypic conflict (McNair and Parker 1979; Parker and Macnair 1978; 1979; Harper 1986; Godfray 1991; 1995).

FOOD ALLOCATION IN ALTRICIAL BIRDS

Parents feeding altricial nestlings birds are an ideal system in which to examine consequences of differing patterns of parental resource allocation. The nestling period in altricial birds is a period of intense parental care: nestlings grow rapidly and are entirely dependent on parents for food. Provisioning nestlings is costly for parents and parents who increase feeding rates can suffer reduced brood sizes or parental survival in the following year (see Bryant and Tatner 1988; Nur 1984). Thus changes in the levels of provisioning by parents are likely to have fitness costs and correlate to parental investment. Parents also frequently care for several young within a nest making interactions between parents and young conspicuous and easy to quantify.

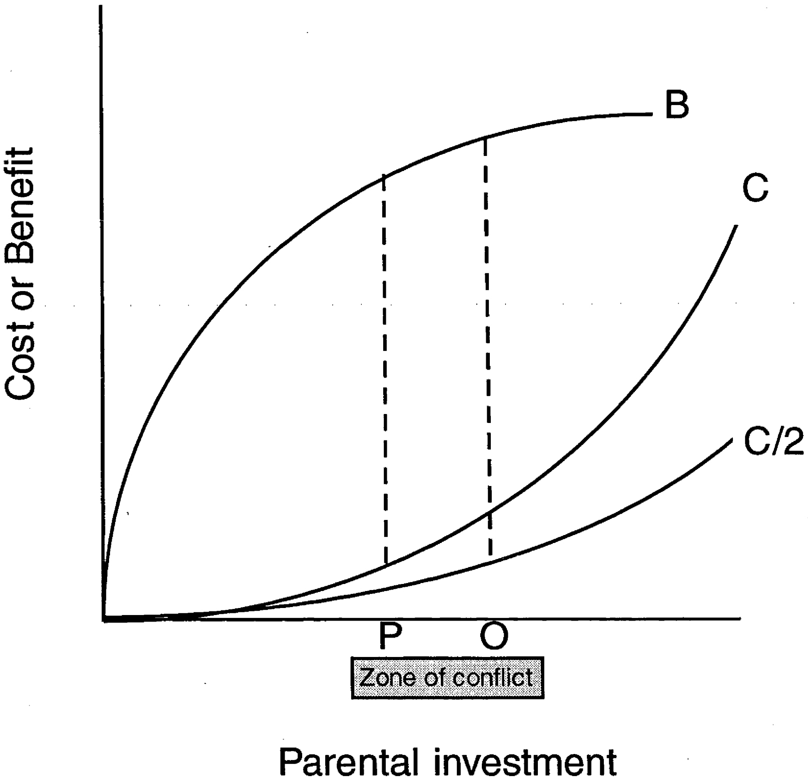


Figure 2. Graphical representation of parent-offspring conflict. The top curve (B) represents the benefit to parents or offspring of a given level of parental investment. Parental costs are plotted in the curve labelled C, and offspring costs in the curve labelled C/2. The dotted lines indicate the point at which parent or offspring maximise their net benefits. Two optimal levels of parental investment, exist, one for the parent (P), and another for the offspring (O). Parents and offspring will disagree over the distribution of resources because offspring weigh parental costs by their relatedness (0.5). The hatched area (zone of conflict) indicates where offspring will try to obtain more resources than is optimal for parents (Redrawn from Clutton-Brock 1991).

Passive and active food allocation

Food can be allocated within broods in two general ways, passively or actively. Parents allocate food passively by distributing food based on nestling behaviours, for example, by feeding the first chick to beg or the closest chick. Distributing food in this way allows parents to feed efficiently since the time spent choosing which nestling to feed is low. However, if competitive differences within the brood are large, allowing chick interactions to determine access to food can result in larger chicks monopolising food at the expense of smaller chicks. Thus passive food allocation is costly to parents if parents and chicks disagree over the appropriate distribution of food within the brood.

Parents can overcome the costs associated with passive food allocation by actively allocating food to chicks. Parents could feed chicks selectively based on their size, age, sex or condition, or parents could distribute food in a fixed way, such as equally to all chicks. Active allocation of food allows parents to precisely control the distribution of food within the brood and to alter it if conditions change.

Controlling the distribution of food can also benefit parents by reducing competition between nestlings and preventing individual chicks from monopolising food. Selective feeding will increase the time required to distribute food within the brood because parents must identify and choose which chick to feed (Stamps et al. 1985; Gottlander 1987). Thus actively allocating food to nestlings will increase the energy and possibly, predation costs of feeding compared to passive allocation of food.

In practice, it can be difficult to separate passive from active patterns of food allocation because parents may actively allocate food to the nestlings that are also favoured by competitive interactions. For example, in black-legged kittiwakes (*Rissa tridactyla*), unsolicited feeds by parents are always directed towards large chicks in the brood, suggesting parents selectively feed large chicks. However in most studies active allocation can only be inferred if parents preferentially feed chicks who would not be favoured in competitive interactions.

Hatching asynchrony and competitive differences between young

Regardless of the patterns of food allocation parents ultimately engage in, females often create underlying competitive differences between young through their behaviour prior to hatching. For example females can affect the size of nestlings by laying eggs of different sizes (Cassidy St. Clair 1996), or increase their competitive ability by increasing the relative testosterone concentration within the egg (Schwabl 1993; 1997). However, females create the most pronounced differences in the competitive ability of young by initiating incubation during egglaying, which results in the asynchronous hatching of nestlings. By producing a clutch which hatches asynchronously, females generate an age and size hierarchy within broods, where the competitive abilities of chicks will differ in a predictable way.

The function of hatching asynchrony varies between species, and can reflect selection on incubation or hatching patterns (see Clark and Wilson 1981; Magrath 1990; Stoleson and Beissinger 1995, for reviews). For example initiating incubation during egglaying may increase the viability of early laid eggs (Arnold et al. 1987). Alternatively, asynchronous hatching patterns can allow efficient brood reduction (Lack 1947). Regardless of its specific function, asynchronous hatching leads to reduced food allocation to later-hatched chicks in most species (Greig-Smith 1984; Bryant and Tatner 1990; Stouffer and Power 1990; Price and Ydenberg 1995; Ostreiher 1997). If asynchronous hatching is the result of selection on the incubation period, the consequences to food allocation may represent a cost to parents. Alternatively, if hatching asynchrony has evolved because of selection on hatching patterns, a skewed distribution of food can benefit parents. In addition, although a skewed distribution of food may be advantageous to parents when food is scarce, several studies have found reduced survival of later hatched chicks even when food was abundant suggesting that hatching asynchrony may have general costs (Amundsen and Slagsvold 1991; Bryant 1978; Werschkul 1979; Stoleson and Beissinger 1997).

The costs and benefits of patterns of food allocation

Passive food allocation is far more frequently observed than active allocation (Table 1). In many species, parents allocate food passively by feeding chicks who are closest (Teather 1992; MacRae et al. 1993; Leonard and Horn 1996) or who beg most vigorously (Bengtsson and Ryden 1983; Price and Ydenberg 1995; Leonard and Horn 1996). In contrast, active allocation of food to last-hatched chicks has only been described in four species in the wild (Table 1).

Passive allocation of food may be more commonly observed because the costs frequently outweigh the benefits of an active parental strategy, such as equal allocation. If parents allocate food in a way counter to chick interests, active allocation can be costly because it increases the levels of conflict between parents and offspring (Forbes 1993). Active food allocation, should therefore be observed in species where the relative costs are low, or the benefits of feeding in this way are high.

The costs of active allocation are likely to be lower in species where the extra time involved in selectively distributing food to young is small relative to the frequency of feeding. Selective feeding is also likely to be less costly where the chance of predation at the nest is low, such as in hole nestling and some colonial species. Long nestling periods may reduce the costs of selective feeding because they minimise the costs associated with deviations in brood growth rates, allowing nestling growth to be more variable. Asynchronous fledging may increase the benefits of active allocation by increasing fitness returns per unit of investment for later-hatched chicks. In species with asynchronous fledging, later hatched nestlings only have to grow at the same rate as other chicks to fledge at the same size as their earlier-hatched siblings. By contrast, in species where young fledge synchronously, if later-hatched chicks are to survive they need higher growth rates to catch up with their older siblings.

Active allocation is infrequently observed and rarely studied, partly because researchers have focused on how chick behaviours affect food distribution rather than the nuances of parental behaviour. However, an intriguing study by Stamps and colleagues examined parent-offspring interactions in a captive parrot (budgerigars, *Melopsittacus undulatus)* and revealed that parents allocated food in a complex way. Although

Table 1. Examples of the patterns of food allocation observed in altricial birds which hatch asynchronously. Parental feeding strategies are categorised as passive (P), active (A) or both (P/A) based on the author's assessment of whether chicks or parents control the distribution of food within the brood. If active patterns of allocation were observed, I have indicated the sex of parent engaging in active allocation, where known. All active allocation was in favour of small or later-hatched chicks, except where indicated with a #.

Species	**How fed?**	**Which sex?**	**Reference**
American robins *Turdus migratorius*	P		Smith and Montgomerie (1991)
Arabian babblers *Turdoides squamiceps*	P		Ostreiher (1997)
Black-legged kittiwakes *Rissa tridactyla*	A#	unknown	Braun and Hunt (1983)
Blue throats *Luscinia s. svecica*	P		Smiseth et al. (1998)
Budgerigars *Melopsittacus undulatus*	A	Female	Stamps et al. (1985)
Canaries *Serinus canarius*	P		Kilner (1995)
Cattle egrets *Bubulcus ibis*	P		Mock and Ploger (1987)
European bee-eaters *Merops apiaster*	P		Lessells and Avery (1988)
Great tits *Parus major*	A#	unknown	Bengtsson and Ryden (1983)
Pied flycatchers *Ficedula hypoleuca*	P/A	Female	Gottlander (1987)
Red-winged blackbirds *Agelaius phoeniceus*	A	Male	Westneat et al. (1995)
Starlings *Sturnus vulgaris*	P		Kacelnik et al. (1995) Cotton et al. (1996)
Stonechats *Saxicola torquata*	P		Grieg-Smith 1980
Tree Swallows *Tachycineta bicolor*	A	Female	Leonard and Horn (1996)
White-winged choughs *Corcorax melanorhamphos*	P/A	unknown	Boland et al. (1997)
Yellow-headed blackbirds *Xanthocephalus xanthocephalus*	P		Price and Ydenberg (1995)

selective feeding of large chicks

budgerigars hatch highly asynchronously, parents did not simply distribute food to the first chicks they encountered, but fed chicks based on their condition, hatching rank and sex (Stamps et al. 1985; 1987; 1989). In addition, mothers and fathers did not use the same rules of allocation. Mothers selectively fed small and undersized offspring, whereas fathers distributed food to large offspring. Mothers distributed food much slower rate than males, suggesting that selective feeding was costly, and Stamps et al. (1985) suggested this pattern should only occur when food is plentiful.

The work by Stamps and colleagues describes the most complex patterns of parental food allocation studied to date. Budgerigars, and parrots in general, share many life history characteristics which differ from the commonly studied passerine species and which may make parents more likely to engage in complex patterns of food allocation Parrots are long lived and breed monogamously, probably with the same partner (Forshaw 1981). Most species are secondary hole nesters and consequently have relatively low rates of nest predation and long nestling periods (Saunders et al. 1984). Many parrot hatch extremely asynchronously, and in some species, young fledge asynchronously (Forshaw 1981; Stoleson and Beissinger 1995).

Structure of thesis

In this thesis, I investigate the growth of nestlings and patterns of parental allocation of food in a population of crimson rosellas (*Platycercus elegans elegans* Gmelin) and ask the following questions:

What affects the breeding success of rosellas?

In Chapter 2 I describe the breeding biology of crimson rosellas. Although rosellas are a common species, their breeding biology has not been well described in the wild. I examine the breeding success of pairs and assess the effect of annual and seasonal changes on clutch size, incubation and hatching asynchrony. In addition I examine the role of social interactions in determining breeding success.

How does asynchronous hatching affect the growth and survival of nestlings?

In Chapter 3, I examine in detail the patterns of nestling growth and survival. Broods hatch with variable asynchrony, and I assess the consequences of hatching asynchrony for the growth and survival of nestlings of different hatching ranks and sexes.

Do parents reduce the costs of hatching asynchrony through food distribution?

In Chapter 4, I describe the feeding rates and distribution of food within rosella broods by mothers and fathers. Since the growth and survival of nestlings was not affected by the degree of hatching asynchrony, I examine how the patterns of food allocation within the brood produced equal growth of all nestlings. Male rosella chicks are larger at fledging than females, so I also examined how food was allocated to different sexes.

Do parents actively alter the distribution of food based on nestling hunger?

In Chapter 5, I manipulate the hunger of rosella nestlings to understand how different levels of hunger within the brood affect food allocation for chicks of different hatching ranks. I examine whether mothers and fathers differ in how they distribute food to young when hunger in the brood is low and compare it to when hunger in the brood is high.

Do parents or young regulate the distribution of food within broods?

In Chapter 6, I examine the responses of rosella nestlings to changes in nestling and brood hunger. If begging signals chick hunger, hungry nestlings should beg more, irrespective of the level of competition within the brood. However, if parents control of the allocation of food within the brood, they may ignore nestling begging and distribute food in other ways.

Finally, in Chapter 7, I summarise the results to date and speculate on future directions.

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Chapter 2

The breeding biology of crimson rosellas (*Platycercus elegans*) on Black Mountain, A.C.T.

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Running head: Crimson rosella breeding biology

The breeding biology of crimson rosellas (*Platycercus elegans*) on Black Mountain, A.C.T.

Abstract

I studied the breeding behaviour of crimson rosellas (*Platycercus elegans*) in Canberra, Australia between 1993-1996. Females rosellas initiated breeding in late September or early October, laying a mean of 5.3±0.1 eggs at 1 to 4 day intervals. Fifty percent of all eggs laid, fledged successfully. Rosellas had the highest breeding success in the wettest year (1995), when they bred earlier, laid larger clutches and fledged more young. Unexpectedly, breeding success was not lowest in the driest year (1994), although fewer birds attempted breeding and hatching success was low. In this study, poor environmental conditions for breeding were counterbalanced by decreased levels of conspecific interference through egg destruction. Overall, 55.8% of all clutches initiated were destroyed during laying, and more than half of this was attributed to rosellas. The reasons for egg destruction by rosellas were not clear. Boxes where clutches were destroyed were not quickly reoccupied and egg destruction was not highest when competition for nesting hollows was most intense. Clutch size and egglaying intervals decreased over the breeding season, but the length of incubation did not. Large clutches did not produce more fledglings because more eggs failed to hatch, especially early in the season. Eggs in a clutch hatched over a period of 0.5 to 7 days. Total hatching asynchrony increased over the breeding season and was not strongly correlated with clutch or brood size. This suggests that females rosellas initiated incubation at different times during laying. Clutches with longer hatching intervals took longer to incubate. If females in poor condition are inefficient incubators, female condition may effect the degree of hatching asynchrony.

Introduction

Parrots are a highly distinct morphological group (Smith 1975) having evolved from an ancient lineage of birds with no close living relatives (Sibley and Alhquist 1990). Despite their superficial homogeneity parrots have adapted to a wide variety of habitats and are found in tropical, desert, temperate and even alpine habitats (Forshaw 1989; Collar and Juniper 1987). Their social organisation also varies, and species can be sedentary, nomadic or seasonal migrants (Forshaw 1981).

The majority of parrots are socially monogamous, and appear to have long term pair bonds (Forshaw 1989). Most species are secondary hole nesters and are dependent on the availability of hollows to breed. Both sexes engage in parental care, although females often incubate alone. The clutch sizes of parrots are extremely variable and range from a single egg in Macaws (*Ara* spp.; Munn *et al.* 1992) and Cockatoos (subfamily: Cacatuinae; Forshaw 1981), up to 10 eggs in green-rumped parrotlets (*Forpus passerinus;* Waltman and Beissinger 1992) and budgerigars (*Melopsittacus undulatus*; Wyndham 1981). All parrots hatch their eggs asynchronously, and several species initiate incubation on the first egg, producing extreme hatching spreads of up to 2 weeks (Saunders 1982; Stoleson and Beissinger 1995).

Australia has approximately one-fifth of the world's parrot species and the greatest diversity of forms (Forshaw 1981). Nevertheless, many species of Australian parrots have suffered serious population declines since European settlement and currently 13 species are listed as vulnerable or endangered (Commonwealth Endangered Species Protection Act 1992). Others species, such as galahs (*Cacatua roseicapillus*) and sulphur-crested cockatoos (*Cacatua galerita*) have adapted readily to agricultural and urban development and have increased in population and range (Forshaw 1981).

The reasons for declining populations vary between species, and include degradation and loss of feeding or breeding habitat, predation and disease (Forshaw 1981; Saunders 1982). However, the factors affecting the breeding success of parrots can be complex and it is often difficult to identify the causes of low breeding success, particularly in declining populations (e.g. Snyder *et al.* 1987). Therefore, detailed studies of parrots in the wild are necessary in order to understand what limits breeding success.

Rosellas (*Platycercus spp.*) are a widely distributed and abundant genus of broad-tailed parrots consisting of 14 closely related races of 4 separate species (Ovenden *et al.* 1987). Crimson rosellas (*Platycercus elegans elegans*) belong to the blue-cheeked race and are a common breeding resident of south-eastern Australia. Despite their abundance, the breeding biology of rosellas in the wild is poorly understood. I studied the breeding behaviour of crimson rosellas breeding in nestboxes over four years. In this paper, I report on the patterns of breeding success, and assess which factors determine breeding success in rosellas

Methods

Species and study area

Crimson rosellas are a medium sized parrot weighing between 120-170g. The sexes have similar plumage, but males are about 15% larger than females. Fledglings have a predominantly green plumage with a red cap on their head, although juvenile plumage varies from completely red to mostly green (unpublished data). This plumage becomes increasingly mottled with red, until birds acquire red adult plumage during their second year (Forshaw 1981). Rosellas breed in pairs. The female is responsible for all incubation and brooding but both parents feed the young during the 35 day nestling period (Forshaw 1981).

I studied rosellas in dry sclerophyll eucalypt forest (*Eucalyptus rossi; E. macrorhyncha*) in Black Mountain Nature Reserve, Canberra, Australia. Pairs bred in nestboxes set out in a grid 50 metres apart and mounted on trees between 4 and 6 metres above the ground. Nestboxes were constructed out of 16 mm plywood and measured 25x25x40 cm (length x width x height). In 1993, boxes had a 7.5 cm entrance hole cut into the front panel of the box. Unfortunately high levels of predation resulted from this design (see Table 2). I believe that currawongs were responsible for most of this predation for the following reasons; i) chicks disappeared from the box without a trace (dead chicks are typically not removed), ii) only middle sized chicks disappeared (small chicks could not be reached and large chicks were too large to remove), and iii) currawongs were observed sticking their heads into entrance holes on several occasions. I modified entrance holes in 1994 with a 10 cm length of 7.35 mm diameter PVC pipe leading into the centre of the box. This design completely alleviated "currawong" type predation. Rosellas readily occupied most boxes. In late August of each year, I cleared all boxes and added 10 cm of wood chips to the bottom.

In the ACT, rosella pairs began "prospecting" for hollows in early August, although they did not lay eggs until early October. I checked nestboxes for activity every 2 to 7 days starting in mid-September. The use of a nestbox by rosellas was easy to infer from chew marks, feathers, removal of wood chips, and the presence of birds calling and perching on the boxes. A pair was considered to have occupied a box when, after signs of activity, a female was observed inside a box on two consecutive occasions.

Egg-laying, incubation and hatching

The date of clutch initiation was determined either directly, or if the clutch was partly laid by back dating, assuming a 2 day laying interval (mean for all known inter-egg intervals = 2.1 ± 0.1, n = 37). Boxes were checked every 2 to 7 days during laying. I was able to determine the interval between consecutive eggs to within one day in boxes checked every 2 days. Recently laid eggs were easily recognisable by the presence of translucent blotches. Thus, the most recent egg detected in a clutch could either be assigned as having been laid that day, or the day before. The interval from first laid to last laid (total laying interval) was known to within 1 day for the majority of the clutches initiated. Clutches were considered to be complete if eggs were incubated and the last egg had been laid more than 4 days previously. Incomplete clutches occurred when eggs were destroyed (see below), or abandoned. In 1995, I marked eggs as laid with indelible ink to examine laying and hatching sequences.

I have defined incubation as the interval from when the last egg was laid to when the last chick hatched as it is difficult to determine precisely when full incubation is initiated. This measure should provide the best minimum estimate of incubation interval, although incubation may take longer for early laid eggs (average interval from last laid to first hatched is only 3 days less than last laid to last hatch, although the laying period averages 8 days). To ensure that high levels of hatching failure did not bias my estimate of incubation, I have only included clutches where 2 eggs or less failed to hatch. This estimate should not be biased by high levels of hatching failure for the last laid egg, since hatching failure was evenly distributed throughout the laying sequence (see Results).

Boxes were checked daily for hatching and in most cases chick hatching order was observed directly. Where more than one chick hatched on the same day, hatch time was assigned based on the fullness of the crop (newly hatched chicks are not fed immediately), the dryness of the down. If it was unclear which chick had hatched first and chicks were identical in size, I assigned tied hatching ranks. If first measurements of a brood were not made until several chicks had hatched, chicks were ranked by wing chord length. Wing chord length correlated very strongly to chick age, especially during the first week (Spearman rank correlation, all known age chicks, $r_S = 0.97$, $n = 175$) These broods were never more than 4 days old, and size hierarchies in broods are most pronounced early in the nestling period. All newly hatched chicks were marked by trimming the down on different parts of the body.

Egg and chick mortality

Rosella eggs were subject to mortality both during egg laying and after incubation had begun. Eggs that were destroyed during laying ("egg destruction") were assigned to one of two causes. Eggs were assumed to have been destroyed by other rosellas if found destroyed with distinctive parrot bill shaped cuts in the shell, egg contents still on the bottom of the nest, and no other sign consistent with a mammalian presence were in the box. Mammalian predation was inferred if faeces were observed on or in the nestbox, if the egg was found whole or carefully cleaned out (sometimes below the nestbox), or if remains of a leaf nest (sign of possums) were also found in the box. Nestboxes were occasionally occupied by ring-tailed possums (*Pseudocheirus peregrinus*) and sugar gliders (*Petaurus breviceps*) and although the extent to which they eat eggs is not known (Strachan 1983), they appear to be the most likely mammalian egg predators on Black Mountain. I was able to assign a likely cause of mortality to eggs only if they were recently destroyed. In many cases only small pieces of shell were found in the box. If an egg failed to hatch, I categorised the timing of mortality as follows: (i) undeveloped, unfertilised or addled egg; (ii) partially developed embryo; or (iii) well developed embryo with down that died just before or during hatching

Chick mortality during the nestling period was assigned to one of 4 categories: (i) predation, (ii) starvation, (iii) physical defect, and (iv) unknown. Predation was attributed either to currawongs, as observed in 1993, or to mammalian predators based on tooth marks, faeces and other signs in the box. Death due to starvation was also subdivided into situations where chicks hatched and died within the first 3 days without being fed (or fed very little) and older chicks, often small underweight chicks close to fledging age, who died after their siblings had fledged. Rosellas engage in no nest sanitation and bodies of starved chicks remained in the box.

Analyses

For overall patterns of breeding success, I have reported data from 1993 to 1996. Measures of breeding success only include completed clutches. Only eight clutches were laid in 1996, therefore, I have only used this year's data in the describing the overall patterns of breeding success. I have also not included any nestboxes from 1993 where currawong predation occurred in my estimates of fledging success. Currawong depredation would be very unlikely in natural rosella hollows on Black Mountain, since they generally have narrower entrance holes and are deeper than nestboxes. Since the population of rosellas on Black Mountain was large and many natural nesting hollows occurred in my study area, I was unable to distinguish between initial nesting attempts and re-nesting attempts after egg predation or destruction. I have measured the length of the breeding season as the dates on which the first and last clutch were initiated.

Breeding success was examined in two ways. Firstly I calculated the percent of eggs laid that hatched successfully and the percent of all chicks hatched that fledged. The former is a measure of egg hatchability and the latter a measure of chick survival.

Secondly, I analysed the number of chicks hatched or fledged for each breeding attempt as a measure of productivity. Fledging success per breeding attempt was only calculated when there was no currawong predation and at least one chick hatched.

Where the data had a normal distribution and constant variance, I used an analysis of covariance to simultaneously examine the effect of categorical and continuous variables on a particular response variable. A full model was fitted, including 2-way interactions, but interaction terms and variables were dropped if they did not contribute significantly to the model. The results of a final fitted model including all significant effects are reported. In the case of non-significant effects, the statistics refer to the results of the final model plus the non-significant variable. Non-parametric tests were used where standard transformations failed to produce a normal data distribution. Means are reported followed by standard errors. All analysis was done using SPSS 6.1 statistical software (Norusis 1994a; 1994b).

Results

Components of breeding success

Egglaying and clutch size

Rosellas laid eggs at 2.1 ± 0.1 day intervals (n = 37) ranging from 1 to 4 days. Although the mean interval between eggs laid early in a clutch (eggs 1 to 3) appeared to be less than between last laid eggs (last 3 eggs), the difference was not statistically significant (interval between first eggs laid, x= 2.1 ± 0.1 days; last eggs x = 2.5 ± 0.3; Mann-Whitney U = 42.5, p = 0.14, n = 23). As expected, the total laying interval between first and last eggs increased significantly with clutch size and tended to vary with year (ANOVA, clutch size effect : $F_{3,30} = 6.33$, p = 0.002; year effect: $F_{2,30} = 3.53$, p = 0.07). Total laying interval also declined significantly over the breeding season, after controlling for clutch size (ANCOVA; $F_{1,29} = 7.89$, p = 0.009; Fig. 1). Thus, a given size clutch took longer to lay early in the season compared to late in the season.

Overall, crimson rosellas laid 5.3 ± 0.1 eggs/clutch (n = 71) ranging from 3 to 8 eggs. Clutch size varied significantly between years (ANCOVA, controlling for laying

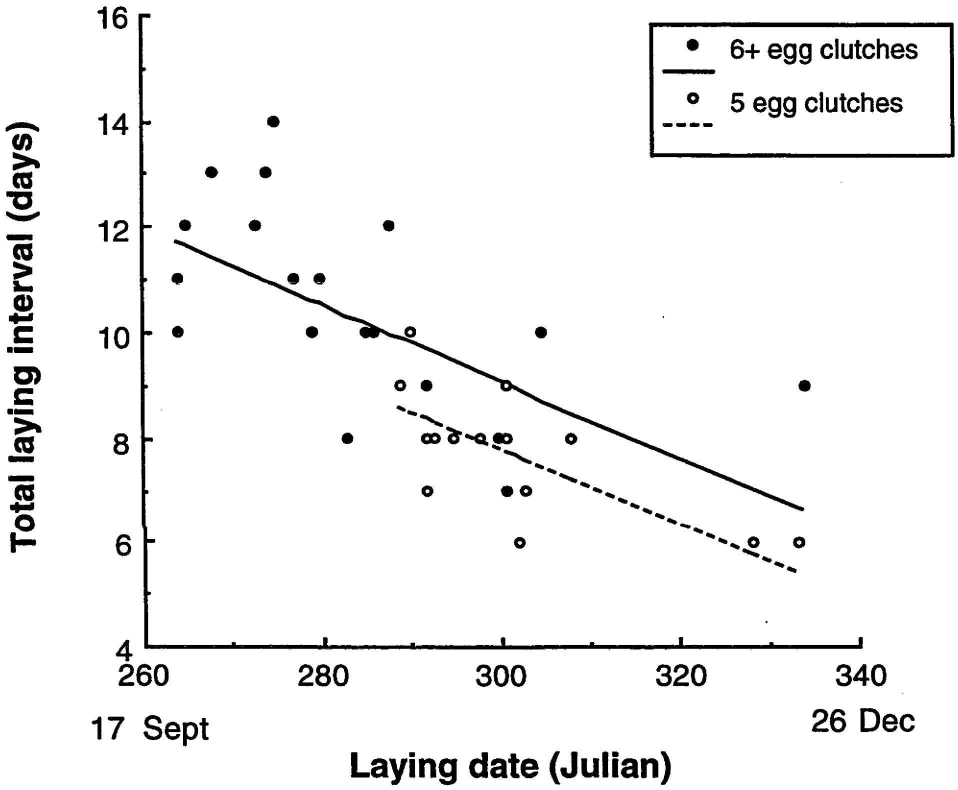


Fig. 1. The relationship between the total laying interval of a brood and laying date fitted separately for 5-egg and 6 eggs and greater clutches. Regression lines for each group are presented (5-eggs: laying interval = 30.0 - (0.073) * laying date; 6^+-eggs: laying interval = 31.0 - (0.073) * laying date)

date; $F_{2,56} = 5.93$, $p = 0.005$; Fig. 2), with larger clutches being laid in the wettest year (1995; Fig. 1). Clutch sizes declined over the breeding season, and this pattern was apparent in each year of the study (Regression analysis; 1993: $F_{1,15} = 6.35$, $p = 0.02$; 1994: $F_{1,21} = 9.35$, $p = 0.006$; 1995: $F_{1,18} = 7.94$, $p = 0.01$; Fig. 3). Seasonal declines were most apparent for the largest clutch sizes, 7 and 8 eggs, which were only laid within the first 20 days of the breeding season (Fig. 3).

Incubation

Incubation periods (last laid to last hatched) varied considerably between broods (mean = 19.7 ± 0.4 days, range 16 - 28 days, n = 28 broods). None of the measured variables explained variation in the incubation period. Incubation period was not related to clutch size year or laying date (ANCOVA; clutch size effect: $F_{3,21} = 0.28$, $p = 0.84$; year effect: $F_{2,21} = 0.41$, $p = 0.67$; laying date covariate: $F_{1,21} = -1.85$, $p = 0.19$).

Hatching patterns

Clutches hatched 3.6 ± 0.2 eggs (n = 71), ranging from 0 to 7 chicks. The number of chicks hatched / clutch did not vary between years after controlling for differences in clutch size (ANCOVA; $F_{4,56} = 1.9$, $p = 0.16$; Fig. 2), and did not change over the breeding season (ANCOVA controlling for clutch size;: $F_{2,56} = 0.8$, $p = 0.38$).

Hatching success for all completed clutches was 68.5 ± 4% (n = 71) in the nestboxes, and ranged from 0 to 100% . Overall levels of hatching success varied significantly between years (Kruskal Wallis Test: H = 12.63, p = 0.02, n = 63), and were lowest in the driest year and highest in the wettest year (Table 1).

Hatching failure did not appear to differentially affect first or last hatched eggs. Rates of egg mortality did not differ significantly with laying order (% eggs failing to hatch: First or second eggs = 10.7%; middle eggs = 6.7%; last or penultimate eggs = 12.5%, $X^2 = 0.58$, df = 2, $p > 0.95$, n = 14 broods). More than half the eggs that failed to hatch were completely undeveloped (Table 2).

Table 1. Summary of the breeding success of crimson rosellas breeding in Black Mountain nestboxes between 1993 -1996.

The number of clutches / broods in each category is indicated in brackets. The percentage of clutches completed was calculated from all clutches initiated and is a measure of egg loss during laying. The percentage of eggs hatched is a measure of hatching success for all completed clutches. The percentage of chicks fledged is a measure of fledging success and was calculated only for all broods that hatched at least one egg. The percentage of eggs which produced fledgings is an overall measure of productivity.

Year	Annual rainfall (mm)$^{\Delta}$	# of nestboxes available	First egg	occupied (%)	clutches initiated per box	% clutches completed (n)	% eggs hatched (n)	% chicks fledged (n)	% eggs producing fledglings (n)
1993	692	22	6 October	100	1.09	75.0 (24)	78.3 (19)	50† (10)	36.0† (10)
1994	383	46	12 October	60.9	0.76	68.6 (35)	50.4 (24)	88.1 (18)	46.1 (24)
1995	801	44*	21 September	84.1	1.27	50.0 (56)	80.0 (20)	76.0 (20)	60.8 (20)
1996	672	36*	4 October	80.5	0.94	29.4 (34)	56.1 (8)	87.0 (7)	50.0 (8)
Mean	637			81.4	1.02	55.8	66.3	75.3	50.0

$^{\Delta}$as reported for Canberra by the Australian Bureau of Meteorology
* number of useable boxes, the remainder were occupied by bees
† figure does not include mortality due to currawongs (see Methods)

Table 2. Sources of mortality for eggs and chicks.

Egg mortality were only assessed during 1995 and 1996. Only mortality from incubated eggs is considered (see also Table 3). Chick mortality was broken down into predation by currawongs (1993; see methods) and unknown predation. Currawong predation was not included in the total breakdown of chick mortality since it was an artefact of nestbox design in 1993 and was subsequently altered. Starvation was categorised as occurring close to hatch (within 3 days), or later in the nestling period. The number of chicks in each category is indicated and percentages are given in brackets

Source of mortality	1993	1994	1995	1996	Totals
Eggs					
Failed to develop	-	-	12 (44.4)	13 (81.2)	25 (58.1)
Partially developed	-	-	13 (48.1)	2 (12.5)	15 (34.9)
Died hatching	-	-	2 (7.4)	1 (6.2)	3 (7.0)
Chicks					
Predation: a) currawongs	31 (66)	-	-	-	-
b) other	2 (4.3)	0	4 (18.2)	1 (25)	7 (13.5)
Starvation: a) at hatch	3 (6.4)	5 (55.5)	10 (45.5)	4 (75)	22 (42.3)
b) older chicks	4 (8.5)	1 (11.1)	4 (18.2)	0	9 (17.3)
Physically deformed	4 (8.5)	2 (22.2)	2 (9.1)	0	8 (15.4)
Unknown	3 (6.4)	1 (11.1)	2 (9.1)	0	6 (11.5)

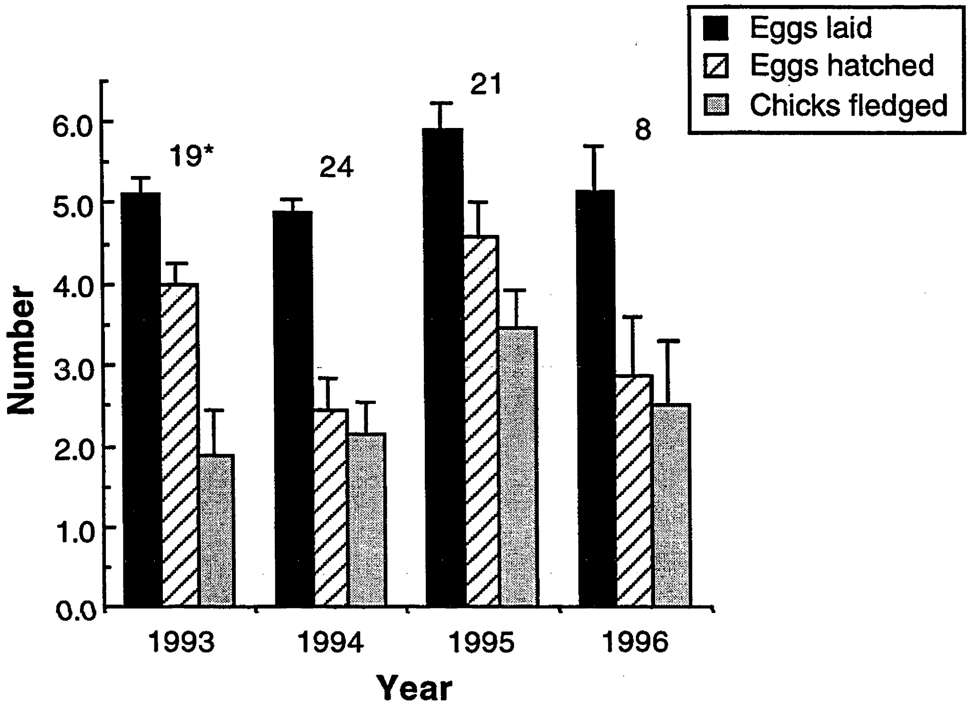


Fig. 2. Breeding success per attempt presented separately for each year of the study (mean ± se). The bars represent the number of eggs laid, chicks hatched per completed clutch, and the number of chicks fledged for all nests where at least one chick hatched. Sample sizes are indicated over each group of bars. (*The number fledged in 1993 only includes boxes where currawong predation did not occur).

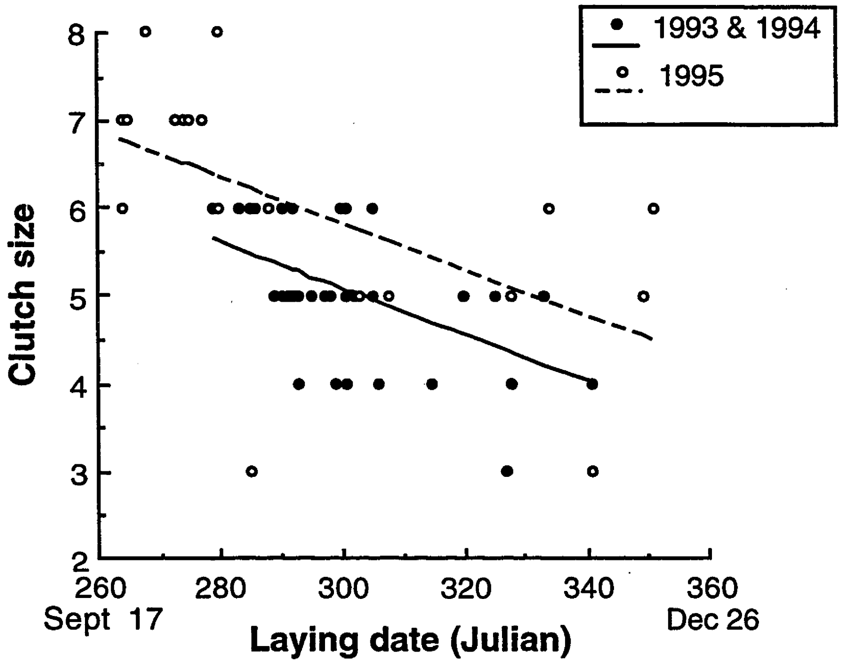


Fig. 3. The relationship between clutch size and laying date for 1993 and 1994 combined, and 1995. Regression lines are presented for each group (1993/94: clutch size = 12.96 - 0.026 * (laying date); 1995: clutch size = 13.70 - 0.026 * (laying date)).

All rosella broods hatched over a shorter interval than they were laid in (Wilcoxon paired-signed rank test; $Z = -4.54$, $p < 0.0001$, $n = 28$), suggesting that incubation began midway through laying. The total hatching interval in broods was 3.6 ± 0.2 days ($n = 46$) ranging from 0.5 to 7 days. Total hatching intervals did not vary between years (ANCOVA, controlling for laying date; $F_{2,38} = 1.42$, $p = 0.25$) but increased significantly over the season (ANCOVA controlling for brood size; $F_{1,36} = 7.94$, $p = 0.008$; Fig. 4). Total hatching interval did not increase with initial clutch size (ANCOVA, controlling for laying date ; $F_{5,36} = 1.67$, $p = 0.21$; Fig. 5a), although it increased significantly with the number of chicks hatched (ANCOVA, controlling for laying date; $F_{5,36} = 5.89$, $p < 0.001$; Fig. 5b).

One reason total hatching interval may correlate with brood but not clutch size is due to hatching failure. However, total hatching intervals were not significantly correlated to brood size in broods where all eggs hatched ($F_{1,17} = 0.48$, $p = 0.50$). Furthermore, hatching intervals did not increase monotonically with brood size and only broods of three differed significantly in hatching interval from larger broods (Duncan's multiple range test: brood size 3 vs. 4, 5 and 6, $p < 0.05$; Fig. 5b). The lack of a strong relationship between brood size and hatching intervals suggests that the onset of incubation is variable in rosellas.

Clutches with longer hatching intervals also had longer incubation periods (clutches that had 2 or less eggs failing to hatch: Regression analysis: $F_{1,25} = 12.4$, $p = 0.002$; Fig. 6; for clutches where all eggs hatched: $F_{1,8} = 4.81$, $p = 0.06$). This was not due to increased incubation time in large clutches (ANCOVA - incubation by clutch size interaction: $F_{3,24} = 0.53$, $p = 0.59$). Thus birds who spent a smaller proportion of the day incubating may also have initiated incubation sooner, increasing the total hatching interval.

Chick mortality and fledging success

Starvation soon after hatching was the major source of nestling mortality in three out of four years, and overall, constituted nearly half observed mortality (Table 2). Mortality due to predation, starvation of older nestlings and physical deformities occurred

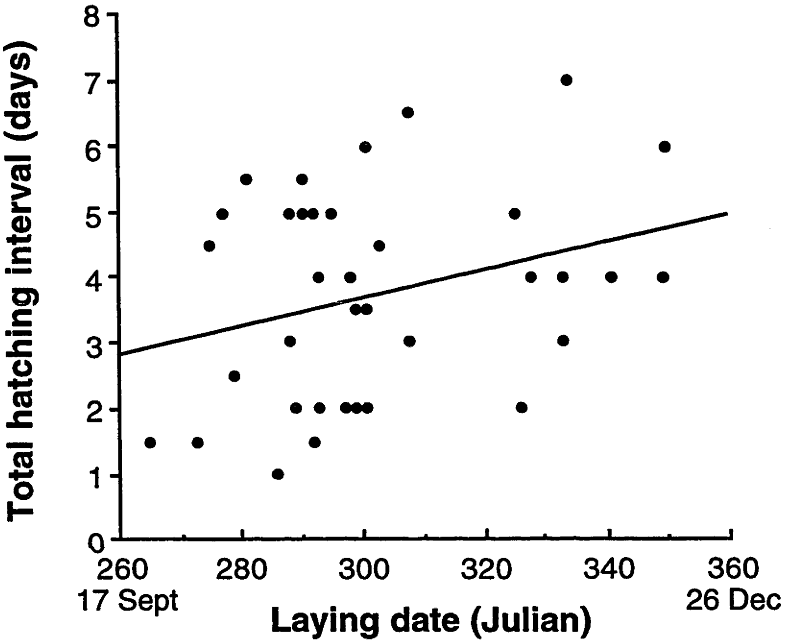


Fig. 4. The relationship between total hatching interval and laying date for all years combined (Total hatching interval = -3.0 + 0.022 * (laying date)).

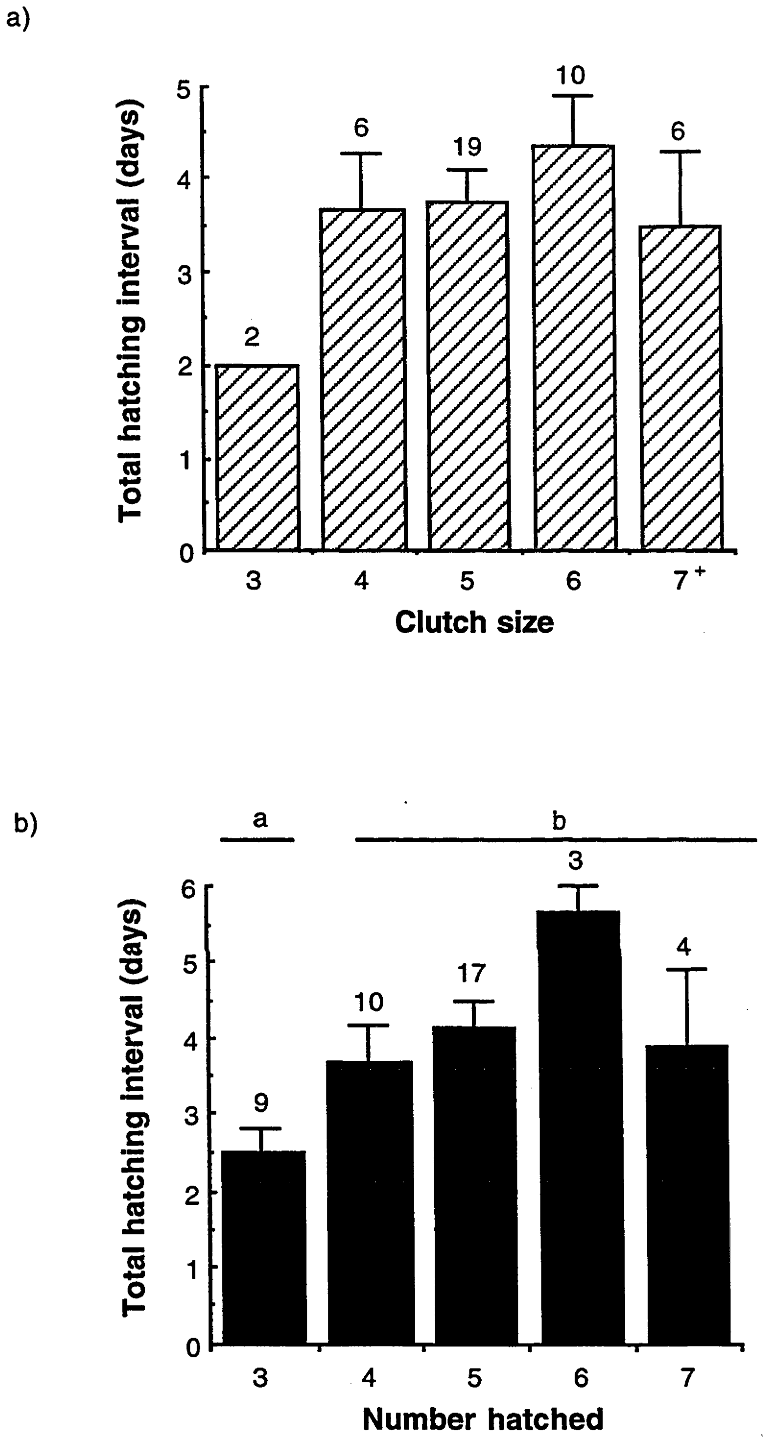


Fig. 5. a) Total hatching interval plotted by clutch size (mean ± se). All years are combined and sample sizes are indicated over each bar. None of the clutch sizes differed in their total hatching interval (see text). b) Total hatching intervals plotted by brood size (mean ± se). Total hatching interval varied between brood sizes and significant differences as detected by post hoc comparisons are indicated by letters over each bar. Different letters represent significantly different means (see text)

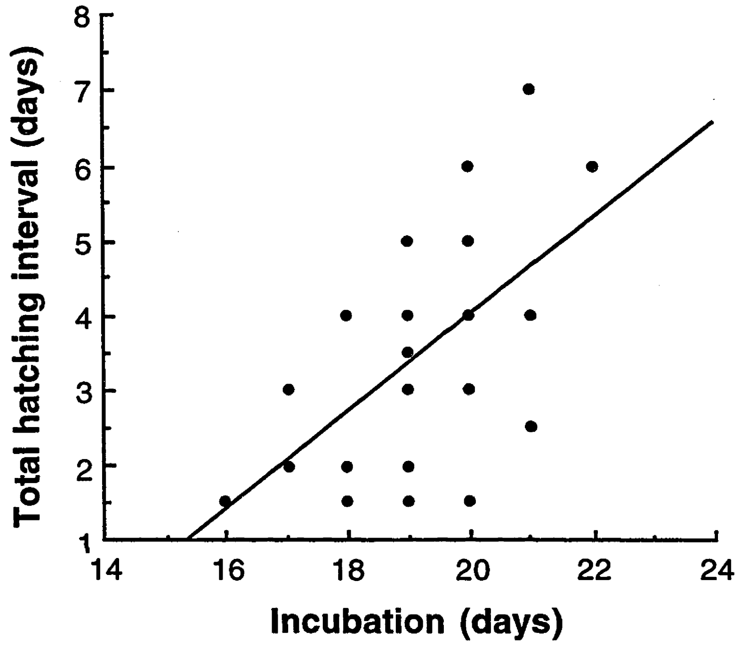


Fig. 6. Total hatching interval plotted against the length of incubation for a brood (Total hatching interval = -8.96 + 0.65 * (incubation)). Incubation length for each brood was measured as the interval from laying of the last egg to hatching of the last egg. The data are for all years combined, and include only clutches where 2 eggs or less failed to hatch. A single extreme value, where incubation took 28 days was removed, although its inclusion did not alter the relationship (see text).

at about equal rates in each year (Table 2). Currawong predation due to inadequate nestbox design was the main source of mortality in 1993, but was not observed in subsequent years following modifications to nestboxes.

The proportion of chicks hatched surviving to fledge, did not vary significantly between years (Kruskal Wallis Test: $H = 4.6$, $p = 0.10$, $n = 47$), and was neither lowest or highest in the most extreme years. Pairs who hatched at least one nestling, fledged 3.0 ± 0.3 chicks ($n = 56$) ranging from 0 to 7 chicks. The number of chicks fledged per attempt varied significantly between years (ANOVA; $F_{2,42} = 3.87$, $p < 0.03$; Fig. 2) although only the lowest (1993) and highest (1995) years differed significantly (1993 vs. 1995; Duncan's multiple range test, $p < 0.05$). Since the clutch size of rosellas declines over the breeding season, the number of chicks fledged would be expected to decrease over the season. However, the number fledged per attempt did not change over the breeding season (ANCOVA controlling for year; $F_{1,42} = 0.09$, $p = 0.77$). This appeared to be due to high levels of hatching failure, particularly early in the breeding season, since initial clutch sizes did not correlate with the number of chicks fledged (Spearmans rank correlation: $r_s = 0.15$, $p = 0.25$, $n = 49$), whereas the number hatched was significantly positively correlated with the number fledged ($r_s = 0.80$, $p < 0.001$, $n = 49$).

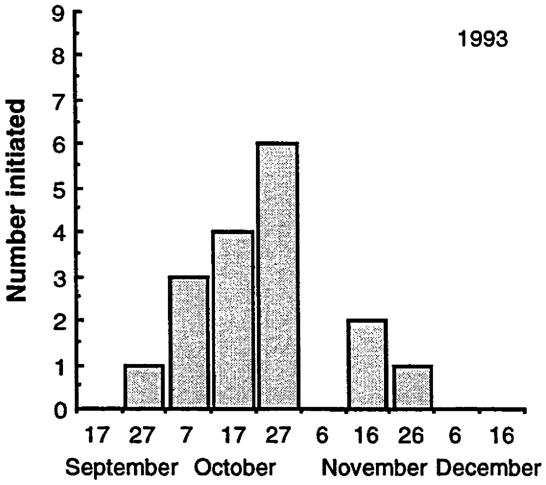
Determinants of breeding success

Interannual variation

Female crimson rosellas initiated breeding in late September and early October and the date of the first egg varied by 3 weeks over the study (Table 1; Fig. 7). The duration of egglaying also differed between years and ranged between 7.5 to 12.5 weeks. Climatic conditions varied considerably over the four years of my study (Table 1). The driest year (1994) had half the rainfall of the other years, and was particularly dry in the 3 months preceding breeding (July-September total rainfall; 1993 = 214 mm; 1994 = 41 mm; 1995 = 101; 1996 = 207 mm, Australian Meteorological Bureau). Rainfall appeared to affect the date breeding was initiated in rosellas. Crimson rosellas initiated breeding earliest in the wettest year (1995) and latest in the driest year (1994). Rainfall also correlated to the length of the breeding season. Clutches were initiated over the longest

Fig. 7. The temporal distribution of clutch initiations over the breeding season presented separately for each year. Clutch initiations were summed for each 10 day interval of the season beginning with the date indicated under each bar.

a)


1993
Number initiated
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7
17
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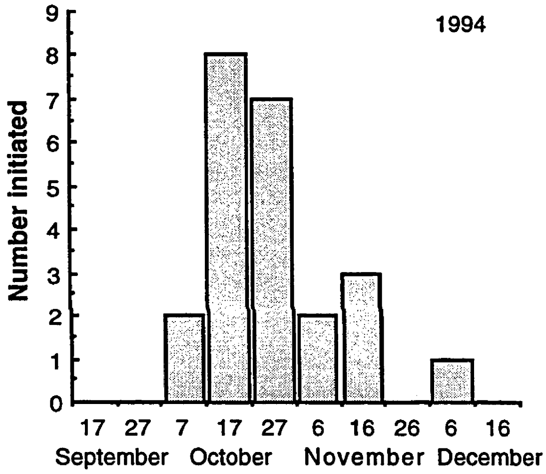
16
September
October
November
December

b)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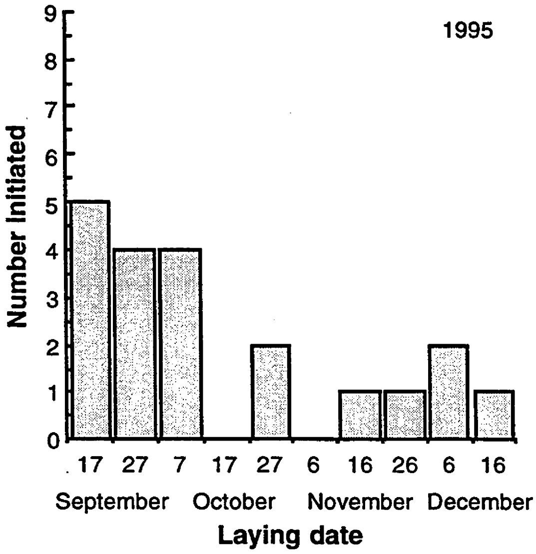
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period in the wettest year (1995). Interestingly, 1995 was also the only year in which I observed 3 known pairs attempt a second brood.

Rainfall also appeared to influence the number of pairs attempting to breed. The proportion of boxes occupied varied significantly between years ($X^2 = 11.59$, df = 3, $p < 0.01$, n = 148) with the lowest number occupied in the driest year (1994). The number of clutches initiated per available nestbox followed the same pattern and 40% fewer clutches were initiated during the driest year compared to the wettest (0.76 clutches/nestbox vs. 1.27; Table 1).

Female age and experience

Although I do not know the ages of most of the breeding pairs in this study, 14% of all breeding females (n = 71) had partially green subadult plumage. Since female crimson rosellas are capable of breeding in their first year (Forshaw 1981; Vogels 1996), these birds were young, relatively inexperienced birds breeding for the first or possibly second time. Females breeding in subadult plumage did not initiate clutches later in the breeding season than females breeding in red plumage: 11 (20.8% of pairs) subadult females bred in the first half of the season, and 8 (30.8% of pairs) bred in the second ($X^2 = 0.91$, df = 1, $p>0.5$). Nor did females in subadult plumage lay smaller clutches than birds in adult plumage (adult birds: x = 5.2 ± 0.2 eggs, n = 61; vs. young birds: x = 5.8 ± 0.2, n = 10; t-test = -1.51, p=0.14). Over the whole study, subadult females fledged the same number of chicks as adult females (subadult females: x = 3.0 ± 0.8, n = 8; adult females: x = 2.6 ± 0.3, n = 54; t-statistic = -0.18, p = 0.86)

Social interactions- egg destruction

Variability in interannual breeding success was not only caused by the numbers of pairs attempting to breed, or the clutch size of breeders. In every year, consistently more pairs of rosellas initiated breeding in boxes than successfully bred. The major factor affecting whether birds were successful at breeding was whether the clutch survived to completion. Clutches frequently were destroyed during laying, typically at the 1 to 2 egg stage. Pairs always abandoned the nestbox when eggs were destroyed, potentially renesting elsewhere (1 banded pair was observed to renest after its clutch was destroyed).

Rates of clutch destruction varied significantly between years ($X^2 = 15.9$, df = 3, $p < 0.005$, n = 149) with 1996 having the highest rate and 1993 having the lowest (Table 1). Clutch destruction appears to be primarily perpetrated by other crimson rosellas, although direct observation of this behaviour is difficult. On two occasions, male crimson rosellas were observed leaving a box where a recently destroyed egg was subsequently found, and in one case the bird was identified as a banded male from a nearby box. The patterns of egg destruction were consistent with attack by crimson rosellas in over 50% of cases in each year, whereas only 10% of cases could be attributed to mammals (Table 3). If egg destruction reflects intense competition for breeding vacancies, the proportion of nests subject to egg destruction should peak early in breeding season when competition should be most intense. This does not appear to be the case in crimson rosellas, a relatively constant proportion of eggs are destroyed over the season, suggesting individuals opportunistically destroy clutches they encounter (Fig. 8).

Table 3. Causes of egg destruction.
Cases of egg destruction broken down by cause for 1995, 1996 and overall. Percentage of total destruction ascribed to each cause is given in brackets.

Cause	1995	1996	Total
Rosella	18 (64.3%)	13 (54.2%)	31 (59.6%)
Mammal	3 (10.7%)	3 (12.5%)	6 (11.5%)
Unknown	7 (25%)	8 (33.3%)	15 (28.8%)
Totals	28	24	52

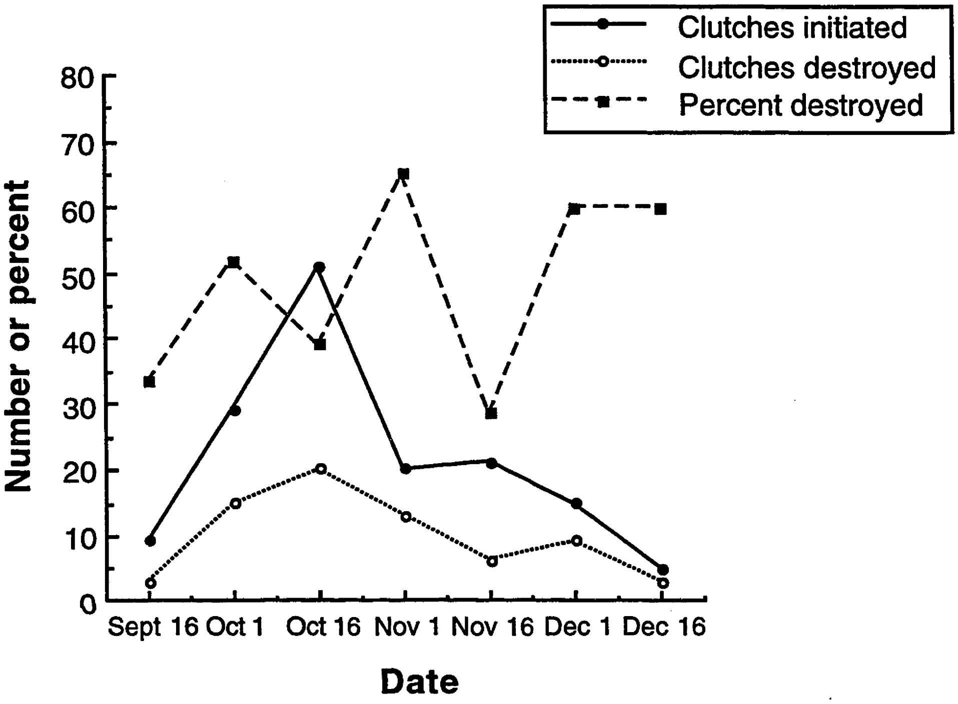

Fig. 8. The number of clutches initiated and the number and percentage destroyed over the breeding season. Data from all years are combined.

Discussion

Egglaying and clutch size

The egglaying interval was variable in rosellas, particularly towards the end of laying, although a two day interval between eggs was most common. This is similar to the egglaying intervals reported for galahs (Rowley 1990) and long billed corellas (*Cacatua pastinator*) (Smith 1991). Egglaying intervals can vary considerably between parrot species from as little as one day between eggs in green-rumped parrotlets (Beissinger and Waltman 1991) to as long as 16 days in white-tailed black cockatoos (*Calyptorhynchus funereus*) (Saunders 1982). Egglaying intervals are also reported to vary within species of parrots, although the patterns and reasons for this variation have not been well investigated (Snyder et al. 1987; Rowley 1990; Beissinger and Waltman 1994).

Variation in egglaying intervals within species has been argued to reflect variation in food availability for the female (Astheimer 1985). In European kestrels (*Falco tinnunculus*), females who received food supplements had larger clutch sizes and smaller inter-egg intervals than control females (Aparicio 1994). Crimson rosellas in this study showed significant seasonal declines in laying interval even after controlling for differences in clutch size. This suggests that late breeding females are less energetically constrained during laying than early females. Seasonal patterns of food availability were not known in this study, but the breadth of rosellas diet suggests that food availability is unlikely to increase substantially over the breeding season (Magrath and Lill 1983). Even if food availability does not change over the breeding season, pairs breeding late in the season would have decreased metabolic costs due to increasing ambient temperatures and increased foraging time due to increases in daylength. In this study, daylength increased by 2.75 hours or 11.5% between early and late laying birds.

Crimson rosellas most frequently laid a clutch of five eggs. This pattern is probably common to the tribe Platycercini, and five egg clutches have been reported as typical in all species where breeding patterns have been documented in the wild (Forshaw 1981). Rosella clutch sizes declined over the breeding season in all years. Seasonal clutch size declines are common in single-brooded Northern hemisphere birds (Klomp

1970; Crick *et al.* 1993) but have not been well described for Australian birds (Ford 1989). However, clutch size declines seem to be common in parrots and decreases have been reported between early and late-breeding individuals in long-billed corellas (Smith 1991); galahs, (Rowley 1990); green-rumped parrotlets, (Waltman and Beissinger 1992) and white-tailed black cockatoos (Saunders 1982).

If clutch sizes have evolved to maximise the number of surviving young (Lack 1947), it may be adaptive for an individual to reduce its clutch size later in the breeding season. Clutch size may be reduced if the amount of food available to feed chicks decreased over the season (Perrins 1970), or if young hatched later in the season have a lower probability of recruitment (Daan *et al.* 1990). Seasonal decreases in clutch sizes in crimson rosellas are unlikely to be a proximate constraint of poor food availability since laying intervals decreased over the breeding season. I do not know the recruitment patterns of young in this population, but patterns of chicks survival do not suggest that the probability of recruitment is dependent on hatching date. In this study, the mean hatching date of chicks surviving at least 4 months did not differ from that of all breeding attempts (hatch date of surviving chicks = October 26th ± 6 days, n =16; hatch date of all clutches = October 26th ± 3 days, n = 63).

Alternately, if young birds or birds in poor condition have a lower optimal clutch size than older more experienced birds, clutch sizes may decline over the breeding season if older birds are able to initiate breeding sooner than younger birds (Poole 1989). Dominance interactions between dominant and subordinate birds may also lead to a negative correlation between laying date and clutch size. In crimson rosellas, breeding pairs are highly aggressive towards prospecting new pairs and possibly destroy subordinates eggs (Vogels 1996). Inexperienced or subordinate individuals may be unable to breed until later in the season when dominant pairs become less aggressive. However, there was no indication in this study that young female rosellas breeding in subadult plumage bred later in the season.

Incubation and hatching patterns

The causes of intraspecific variation in incubation are not well understood, but are likely to be related to parental attentiveness and external temperatures (Drent 1975). In rosellas, incubation period did not decrease over the breeding season, suggesting that increasing ambient temperatures did not effect incubation. Incubation period was also not related to clutch size, suggesting that females can incubate large clutches as effectively as small clutches. The length of incubation was only found to be correlated with the total hatching spread in a brood. It is not clear if inefficient incubation somehow produced larger hatching intervals or if females in poor condition choose to begin incubation sooner and benefited in some way from a larger hatching spread.

Although I did not examine the onset of incubation directly, several lines of evidence suggest that female rosellas varied their incubation patterns. Firstly, total hatching interval for broods showed the opposite pattern to laying intervals and increased significantly over the breeding season. If birds were beginning incubation after laying a specific egg, decreased laying intervals later in the season should lead to a reduced, not increased hatching asynchrony. Secondly, the total hatching interval in broods did not correlate strongly with initial clutch size or brood size as would be expected if females used similar incubation patterns. Interestingly, the largest brood sizes (7 chicks) had a smaller mean hatching asynchrony than expected, suggesting that high quality females might choose to begin incubation later. Several other studies have shown that females are capable of facultative manipulation of hatching asynchrony in response to food availability (Nilsson 1993; Wiebe and Bortolotti 1994) or male foraging ability (Green and Krebs 1995).

Long hatching intervals are common to most species of parrots (Stoleson and Beissinger 1995), although the function of asynchronous hatching in this group is unclear. In crimson rosellas hatching asynchrony also increased over the breeding season. This means that early breeding females initiated incubation later in the laying sequence than late laying females, consistent with the hypothesis that early laying females were energetically constrained. Energetic constraints have been shown to alter the incubation patterns in great tits (*Parus major*) and food supplemented females initiated incubation earlier, and produced more asynchronously hatching broods (Nilsson 1993). Hatching asynchrony in crimson rosellas is unlikely to be due to proximate constraints on the timing of incubation since females spend considerable time in the hollow prior to incubation and hatching intervals were not closely correlated with clutch or brood sizes.

Asynchronous hatching can also be a mechanism to facilitate brood reduction when food is insufficient for the whole brood (Lack 1947). Female American kestrels (*Falco sparverius*) for example, decreased the degree of hatching asynchrony when food was abundant, probably to minimise the risk of brood reduction (Wiebe and Bortolotti 1994). Patterns of chick mortality in crimson rosellas suggest hatching asynchrony may also be tied to the probability of brood reduction. Nearly half of chick mortality observed in this study was due to chicks starving soon after hatching. Chicks at this point are helpless and dependent on parental stimulation to elicit feeding behaviour, suggesting that parents failed to feed some newly hatched chicks. Consistent with this hypothesis, the degree of hatching asynchrony was higher in broods where early mortality occurred (hatching interval: broods with early mortality = 4.6 ± 0.5 days, n = 9; brood with no early mortality = 3.3 ± 0.3, n = 25; t-value = 2.03, p = 0.05)

Fledging success

Despite the strong seasonal decline in clutch size, the number of rosella chicks hatched and subsequently fledged did not decline over the breeding season. Thus, large, early laid clutches were not necessarily more productive than smaller late ones. Interestingly, green-rumped parrotlets also showed no association between clutch size and breeding success over clutches ranging from 5 to 10 eggs (Beissinger and Waltman 1991). Why then did female rosellas lay large clutches? One possibility is that longer laying intervals early in the season lead to decreased egg viability (Stoleson and Beissinger 1995), and females laid extra eggs as “insurance” against the hatching failure of early laid eggs . The overall proportion of rosella eggs failing to hatch did not differ according to laying sequence or laying date, and it would be interesting to determine whether the hatchability of first laid eggs declined with long laying intervals. A second possibility is that if females are occasionally able to fledge all chicks, large clutches may still be advantageous overall. Breeding success in rosellas is consistent with this pattern. Although the proportion of eggs hatching was highly variable early in the breeding season, some rosellas were able to lay, hatch and fledge all chicks from large clutches. Consistent with this idea, the coefficient of variation for the number of chicks hatched was twice as large in the largest clutches compared to the smallest (7 - 8 eggs: cv = 1.99; 3 eggs: cv = 0.99) .

Determinants of breeding success

Interannual variation in breeding success

Weather conditions appeared to effect the number of crimson rosella pairs attempting to breed. In the driest year, 1994, fewer nestboxes were occupied, fewer clutches were initiated and hatching success of eggs was low, whereas in the wettest year nestbox occupancy, clutch initiation and hatching success were high. Rainfall patterns have been shown to correlate to breeding success in galahs (Rowley 1990), long-billed corellas (Smith 1991) and regent parrots (*Polytelis anthopeplus*), western rosellas (*Platycercus icterotis*), Port Lincoln parrots (*Barnardius zonarius*) and red-capped parrots (*Purpureicephalus spurius*) (Long 1990) in Western Australia. The effect of rainfall on breeding success varied between studies. For galahs and corellas, high levels of rainfall and storms were associated with lowered breeding success, mostly due to damage to hollows and exposure of nestlings. For western rosellas and regent, Port Lincoln and red-capped parrots, above average rainfall prior to the breeding season lead to increased food availability and consequently higher breeding success.

Higher levels of rainfall may have increased food availability for crimson rosellas since the wettest year produced the highest number of fledglings per breeding attempt. However it is unclear whether low levels of rainfall decreased food availability for rosellas. Hatching success was lowest in the driest year, which could have been due to reduced nest attendance owing to poor food availability. Starvation of nestlings was not higher in the driest year, fledging success was high, and the number of chicks fledged per attempt was intermediate, suggesting that food was not limiting. Low hatching success could also have been the result of high temperature or low humidity (Drent 1975).

Differences in food availability, however, are not necessarily reflected in measures of breeding success. Rowley (1990) found in his seven-year study of galahs, that the year of lowest food availability, smallest clutches and shortest breeding season had the second highest number of chicks fledged per nest. Only two-thirds of breeders in the study area even attempted to breed, and although most of his banded birds were of unknown ages, his data suggested that only older, more experienced galahs were able to breed in poor environmental conditions. Forgoing breeding would be expected to be a common strategy in relatively long lived birds such as parrots and could explain the similar patterns of breeding success observed in crimson rosellas.

In this study, I have also found that rosellas did not have the lowest breeding success during the driest year. Whether it was due to more experienced birds breeding is less clear. The number of females breeding in sub-adult plumage was equal in each year and I have no data to suggest that younger females had lower breeding success than adult females. Young females did not differ from adult females in their clutch initiation dates, clutch sizes, or fledging success. Possibly these results were confounded by male breeding experience, since males were never observed to breed in subadult plumage, or perhaps some females breeding in adult plumage were also inexperienced breeders. Interestingly the driest year also had the lowest levels of egg destruction were observed, suggesting that low densities of breeding birds may reduce interference competition between pairs, potentially increasing overall breeding success.

Egg destruction

The component of breeding success that varied most between years was the proportion of clutches destroyed during laying. In order to breed, crimson rosellas need to successfully obtain and defend a nesting hollow against conspecifics. Breeding pairs of rosellas clearly defended a buffer zone around the hollow which included nearby trees, and actively tried to prevent other pairs from settling within this area. Fights and agonistic interactions were most frequently observed during prospecting and egglaying and nestboxes situated close to another breeding pair seemed to be especially vulnerable to egg destruction.

I do not have precise measures of the density of breeding birds in my study site since rosellas spend up to 2 months inspecting different hollows, making it difficult to assess whether a pair observed at a hollow is breeding. However, I do not think that the levels of egg destruction observed were simply an artefact of nestboxes increasing the density of nesting hollows. Nestboxes placed in an area with an apparently lower density of breeding rosellas had similar levels of egg destruction. Pairs on Black Mountain frequently defended more than one hollow and many trees had several apparently suitable hollows (sometimes including nestboxes). Despite the opportunity, I never observed more than one pair of rosellas breeding in a single tree (see also Vogels 1996).

High levels of aggression towards conspecifics, especially early in the nestling cycle, is common in parrots and has been described in budgerigars (Wyndham 1981); white-tailed black cockatoos (Saunders 1982); Puerto Rican parrots (*Amazona vittata*) (Snyder *et al.* 1987); galahs (Rowley 1990); and green-rumped parrotlets (Waltman and Beissinger 1992). In this study, crimson rosellas attempt to prevent new pairs from settling and occupying new hollows through aggression and egg destruction. In an aviary experiment, Vogels (1990) found that dominant female eastern rosellas (*Platycercus eximius*) destroyed the eggs of subordinate females preventing them from breeding. Egg destruction has also been documented in a wild nestbox breeding population of crimson rosellas near Armidale, NSW (Vogels, 1996). I was not able to observe which individuals engaged in egg destruction in this study, but two opportunistic sightings were of males apparently destroying eggs.

It is not clear what benefit resident pairs obtain by preventing new birds from settling nearby. Pairs leaving the hollow flew away from their territory, apparently to feed, so competition for food is unlikely. If predation was correlated to the density of breeding birds, a pair might benefit by reducing the density of neighbouring breeding pairs. However, predation rates were not high on adults or chicks. Egg destruction could result from short term competition for hollows. However, in this study, boxes subject to egg destruction were abandoned and never quickly reoccupied. Egg destruction was also not highest early in the breeding season when competition for breeding hollows is most intense.

Egg destruction might reflect long term competition for suitable hollows, since pairs of rosellas are present in the breeding area year round and have been observed to use a different hollow in the same area to breed in subsequent years. Rendell and Robertson (1989) also found that breeding tree swallows (*Tachycineta bicolor*) often attempted to defend more than one hollow, although this may have been an attempt by males to become polygynous. Interestingly, aggression towards prospecting pairs of rosellas appeared to decrease once the resident female was incubating as found in white-tailed black cockatoos (Saunders 1982). Thus close breeding neighbours may be most costly early in breeding or when breeding is closely synchronised.

Egg destruction has been described in several other monogamous species. Starlings (*Sturnus vulgaris*) removed eggs from other pairs nests, however, these clutches were not deserted, and this behaviour may have been associated with brood parasitism (Lombardo *et al.* 1989). Brood parasitism is unlikely to explain egg destruction in rosellas because clutches were abandoned and boxes remained unoccupied after eggs were destroyed. Male and female house wrens (*Troglodytes aedon*) destroy all surrounding clutches and nests of conspecifics and others early in the breeding cycle (Belles-Isles and Picman 1986). Belles-Isles and Picman (1986) argue that it reduces competition for hollows and possibly for food, although they show no evidence to suggest that either is limited.

Egg destruction has not been described in other parrot species although circumstantial evidence suggests that it may occur. This is not surprising given the difficulties of detecting of egg destruction in deep, dark natural hollows. Most studies of parrots in natural hollows have also avoided frequent checks to minimise disturbance during laying, but several studies refer to unspecified predation and desertion at the egg-laying stage (Rowley 1990; Waltman and Beissinger 1992; Wyndham 1981). In budgerigars, 25% clutches were deserted for unknown reasons before hatching (Wyndham 1981). Waltman and Beissinger (1992) do not report on sources of egg mortality, but 3 pairs of green-rumped parrotlets deserted their chicks due to harassment by breeding neighbours. Female white-tailed black cockatoos aggressively repel other females from the nesting area before egg laying. Saunders (1982) reports that females readily deserted eggs and that eggs were destroyed in early incubation, although this was attributed to competition with galahs in some cases.

It is often assumed that parrots and secondary cavity nesters are limited by the availability of suitable nesting hollows (e.g. Forshaw 1981; Martin and Li 1992). This is likely to be true where habitats have been extensively cleared or degraded (e.g. thick-billed parrots *Rhynchopsitta pachyrhyncha*; Lanning and Shiflett 1983), or where a species is dependant on a single type of nesting tree (Puerto Rican parrots; Snyder *et al.* 1987). In many species, however, hollows appear to be abundant. Long (1990) found that only 36% of suitable hollows were occupied by Port Lincoln parrots. Budgerigars did not consistently use many apparently suitable and previously used hollows, suggesting that hollows also did not limit breeding opportunities (Wyndham 1981). In this study only 81% of available nestboxes were occupied.

Waltman and Beissinger (1992) argue that high nestbox occupancy and agonistic interactions in green-rumped parrotlets are the result of limited nest sites, although they do not quantify the density or availability of hollows. High levels of competition for breeding vacancies however, does not necessarily imply that suitable hollows are limiting. In rosellas, many more birds initiated breeding than appeared to be successful, and many apparently suitable "hollows" were abandoned due to egg destruction. Similarly, Saunders (1982) argued that high levels of agonistic interactions between pairs produced an even spacing of breeding pairs of white-tailed black cockatoos that was not predicted by the spacing of suitable hollows.

Although parrots frequently do not appear to be limited by the availability of breeding hollows, species differ dramatically in their tolerance for conspecifics when breeding. Galahs and long-billed corellas are relatively gregarious and will occasionally nest in the same tree (Rowley 1990; Smith 1991). Breeding pairs of Port Lincoln parrots typically are spaced, but will breed in adjacent trees when suitable hollows are clumped. The distribution of breeding thick-billed parrots in pine woodlands reflected hollow availability when the habitat was seriously fragmented and degraded by selective logging

(Lanning and Shiflett 1983). In contrast, white-tailed black cockatoos (Saunders 1982), even in degraded habitat, did not tolerate pairs breeding in close proximity prior to incubation. Breeding pairs of Major Mitchell cockatoos (*Cacatua leadbeaterii*) were regularly spaced throughout their habitat, and although they frequently nested in the same tree as other parrots, they were always at least one kilometre away from breeding conspecifics (Rowley and Chapman 1991).

The breeding success of crimson rosellas depends on a complex interaction of ecological and social factors that can make it difficult to predict. Interannual and seasonal differences clearly affect the breeding success and probably the breeding strategies of rosellas. However, both the number of birds initiating clutches and initial clutch size were found to be poor predictors of breeding success in this study, and the factors influencing egg destruction and hatching success obscure. Breeding pairs of rosellas were observed to remain in the area they bred in for several years, suggesting that there may be complex social hierarchies between older resident birds and young pairs seeking breeding vacancies. Like all secondary hole nesting birds, it is a prerequisite for crimson rosellas to have suitable hollows to breed in. However, in long-lived relatively sedentary birds, like many parrots, we must understand the interactions between social organisation and breeding biology to understand reproductive success.

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Chapter 3

Last but not least: nestling growth and survival in asynchronously hatching crimson rosellas

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Running head: Growth in asynchronously hatching rosellas

Last but not least: nestling growth and survival in asynchronously hatching crimson rosellas

Summary

1. Many species of altricial birds hatch their young asynchronously within broods. Although there are many potential benefits to parents, hatching asynchrony reduces the growth and often survival of last-hatched nestlings. I examined the consequences of hatching asynchrony on the growth, size at fledging and survival of male and female nestlings of an Australian parrot, the crimson rosella *Platycercus elegans*.

2. Crimson rosellas broods hatched over 1.5 to 7 days creating mass hierarchies where first-hatched chicks were up to seven times larger than last hatched chicks. Hatching asynchrony and mass hierarchies increased over the breeding season, but were not strongly correlated with brood size.

3. Male chicks grew faster and were larger at fledging than females. Growth rates did not differ between hatching ranks. Chicks of all ranks were of equal sizes at fledging, but last-hatched male chicks had lower fledging mass in pairwise analyses. Female mass at fledging did not decrease with hatching rank. Chick growth rates and size or mass at fledging were not related to hatching asynchrony, mass or size hierarchies in broods, brood size, laying date or year in mixed model analyses.

4. Last-hatched chicks had equal post-fledging survival as other chicks, however, they were more likely to die during the nestling period. Increased mortality of last-hatched nestlings occurred only at hatching and chicks had equal mortality rates over the remainder of the nestling period. Early brood reduction was not associated with brood size or hatching asynchrony but increased over the breeding season, and in broods with high hatching success.

5. Hatching asynchrony in rosellas, unlike in most previous studies, did not lead to poor growth and subsequent survival of last-hatched chicks. This suggests that the costs of

hatching asynchrony are low in this species and that selective feeding by parents may increase the growth and survival of last-hatched chicks.

6. Reduced growth and survival of later hatched chicks is not an inevitable consequence of asynchronous hatching, however, the costs to parents of overcoming competitive interactions between chicks may be higher than the benefits in most species.

Introduction

Young hatch sequentially in many species of birds, producing an age and size hierarchy within the brood. Hatching asynchrony within a brood varies from several hours in many passerines (Clark & Wilson 1981), to several weeks in some owls and parrots (Wilson et al. 1986; Saunders 1982; Waltman & Beissinger 1992). The function of hatching asynchrony has been the subject of many studies and continues to be hotly debated (reviews by Amundsen & Slagsvold 1991; Magrath 1990; Stoleson & Beissinger 1995). Producing a size and age hierarchy within the brood via asynchronous hatching could promote parental feeding efficiency (e.g. Hussell 1972; Hahn 1981), facilitate efficient brood reduction when resources are limited (Lack 1947; 1968), or be the non-selected consequence of constraints on incubation patterns (Clark & Wilson 1981).

Despite the variety of explanations for asynchronous hatching, the consequences are remarkably similar across species. Hatching asynchrony is associated with reduced growth and survival of last-hatched nestlings (e.g. Bryant & Tatner 1990; Veiga 1990; Wiebe 1996; Ostreiher 1997), even in species with small hatching spreads (Greig-Smith 1984; Stouffer & Power 1990). Hatching patterns are clearly controlled by parents through the timing of the onset of incubation (Bryant 1978; Magrath 1992). However, size hierarchies within a brood are often reinforced by processes controlling the distribution of food after hatching. In most species access to food is determined by a dominance hierarchy among chicks, or through scramble competition in the nest, both of which favour larger chicks (e.g. Bengtson & Ryden 1983; Poole 1989; Kacelnik et al.

1995). Thus reduced growth of last-hatched chicks is probably a consequence of their poor competitive ability in interactions over food.

Whether poor growth and survival of last-hatched chicks is congruent with parental interests is less clear. Increased mortality of last-hatched nestlings may benefit parents and surviving chicks when food is limited. On the other hand, if reduced nestling growth results in low fledging weights post-fledging survival of chicks can be reduced (Perrins 1965; Nur 1984; Magrath 1991). Reduced growth and survival of last-hatched chicks may occur in asynchronous broods regardless of food availability (e.g. Bryant 1978; Werschkul 1979; Amundsen & Stokland 1988; Wiebe & Bortolotti 1995; Nilsson & Svensson 1996; Stoleson & Beissinger 1997). For example, in little blue herons (*Egretta caerulea*), broods of even-aged nestlings grew at the same rate as early-hatched nestlings in asynchronous broods suggesting that parental ability to distribute food was more important than the amount of food delivered (Werschkul 1979). Similarly, last-hatched chicks in house martin (*Delichon urbica*) broods with large size hierarchies were ten times more likely to die than in broods with subtle hierarchies even when food was abundant (Bryant 1978). Consequently, parents may be forced to trade-off the benefits of asynchronous hatching against reduced ability to control the distribution of food within the broods.

The majority of studies of hatching asynchrony have focussed on passerines which have relatively low levels of hatching asynchrony. In contrast, non-passerines show extreme variability in hatching patterns (Ricklefs 1993; Stoleson & Beissinger 1995). For example, parrots (Aves: Psittaciformes) have predominantly asynchronous hatching patterns (Stoleson & Beissinger 1995), and considerable variation in the degree of hatching asynchrony both within and between species. Some parrots initiate incubation on the first egg; examples include green-rumped parrotlets (*Forpus passerinus;* Waltman & Beissinger 1992) and white-tailed black cockatoos (*Calyptorhynchus funereus;* Saunders 1982). In others, incubation can begin on the last egg (e.g. Major Mitchell's cockatoo*Cacatua leadbeaterii*, Rowley & Chapman 1991). Detailed studies on groups such as parrots are necessary to determine if poor growth and subsequent survival of last-hatched chicks is a general cost of hatching asynchrony, or if species with extreme hatching asynchrony have evolved mechanisms to reduce the costs of a large size hierarchy.

In this study, I quantified variation in hatching asynchrony in a medium-sized parrot, the crimson rosella (*Platycercus elegans* Gmelin). I examined the consequences of hatching asynchrony for chick growth, size at fledging and survival of chicks, both in the nest and after fledging. Male rosellas are larger than female rosellas and I used molecular sexing of nestlings to evaluate growth and size at fledging for each sex independently. If hatching asynchrony disadvantages last-hatched chicks, it may be more costly for last-hatched males and I assessed whether the costs of hatching asynchrony differed between the sexes.

Methods

STUDY AREA AND METHODS

I studied crimson rosellas breeding in nestboxes in Black Mountain Nature Reserve, Canberra, Australia between August 1993 and January 1997. Fifty nestboxes were placed in a grid 50 metres apart in dry sclerophyll Eucalypt forest (*Eucalyptus rossii, E. mannifera and E. macrorhyncha*) during August 1993. Up to three pairs of rosellas attempted to breed in a particular nestbox over a breeding season, but high levels of egg destruction and hatching failure resulted in many pairs failing or having very poor breeding success. In total I monitored the breeding success of 64 pairs incubating clutches.

In this study, females rosellas initiated breeding in late September or early October, laying a mean ± se of 5.3 ± 0.1 eggs (range = 3 - 8; n = 64 broods) at 2 to 4 day intervals. Rosellas hatched 4.0 ± 0.2 chicks (range = 1 - 7; n = 64), and fledged 2.7 ± 0.2 chicks (range = 0 - 7; n = 64). Hatching success in some broods was very low, averaging 75 ± 3% (range = 13 - 100%; n = 64) for the entire study.

Nestboxes were inspected at least weekly during the laying period. In most cases, I visited boxes daily during the predicted hatching period until all nestlings had hatched. Where the order of hatching was observed directly I assigned a hatching order to each chick and a hatching time to the nearest half day, based on the dryness of a chick's down and whether it had been fed (chicks are not fed until 6 hours after hatching). Where more than one chick hatched on the same day, hatching time was assigned based on a combination of wing chord length and dryness of the down. If chicks were so similar in size that it was unclear which chick had hatched first, I assigned tied hatching ranks. In broods where several chicks had already hatched, I assigned each chick an age retrospectively using a regression of wing chord on age for all chicks of known hatching times. These broods were never more than 4 days old, and I never noted rank reversals early in the nestling period.

All newly hatched chicks were marked by trimming the down on different parts of the body, and 7 day old chicks were marked with a single colour band to allow individual recognition. Nestlings were weighed to the nearest 0.1 g at hatching and subsequently to the nearest 1 g, using Pesola spring balances. Wing chord length was measured to the nearest 0.5 mm using a stainless steel ruler. Tibia length (outer edges of joints) was measured to the nearest 0.1 mm using dial callipers. All chicks in a brood were measured each time a new chick hatched to obtain a measure of the size hierarchy at the completion of hatching. After hatching was complete, the brood was measured at least weekly until the oldest chick was 30-33 days of age. Broods were not measured after this age, since disturbance was likely to cause the premature fledging of older chicks. Consequently, last hatched chicks in broods with large hatching spreads may have been measured for a final time when only 23 days old. All chicks were banded with a numbered Australian Bird and Bat Banding Scheme stainless steel band and a unique combination of anodised aluminium colour bands prior to fledging.

SEXING INDIVIDUALS

Adult male crimson rosellas are 10% - 20% larger than females, and differ in bill morphology. Nestlings, however, can be difficult to sex because size differences are small at hatching and because weight and size measurements overlap between the sexes. Therefore, to determine the sex of all nestlings, I used a sex specific genetic marker. A blood sample (100 μL) was taken from each chick at least 15 days after hatching for use in sexing and other genetic work. Two PCR primers (P2 and P8; Griffith et al. 1998) were used to amplify a gene (CHD) on the W-chromosome. The heterogametic sex, females, were identified by the presence of two distinct bands on an agarose gel, and males by the presence of only one band (see Griffiths et al. 1998 for details of the method).

HATCHING HIERARCHIES

I quantified the hatching hierarchy within a brood in two ways: (i) the total hatching asynchrony (first hatched to last hatched) within a brood to the nearest 0.5 day, as outlined above, and (ii) the relative difference in nestling size for chick mass ('mass hierarchy'), and for tibia length ('size hierarchy'). The relative difference in nestling size was calculated as: ((size of first hatched chick) - (size of last hatched chick)) / (mean size of all nestlings) (Wiebe & Bortolotti 1994a; Bryant & Tatner 1990). Since measures of the size or mass hierarchy within a brood could be biased by the age at which the last hatched chick was first measured, I have only calculated it for broods where the last hatched chick was measured within 24 hours of hatching.

I excluded all broods where more than two eggs or chicks failed to hatch or died. In total, I examined the growth of 130 individual chicks in brood sizes ranging from three to seven. In addition, I included 13 broods from 1993 which were depredated during the nestling period, in order to maximise the number of broods with known hatching asynchrony and size or mass hierarchies.

GROWTH

I calculated growth curves for tibia length and mass for each chick. Tibia length provides a measure of overall skeletal size. Chick mass is a more variable measure due to crop and stomach contents; however, it provides a composite measure of chick size and condition. I did not fit growth curves to wing length because primaries continued to grow after fledging.

The logistic form of a growth curve (Ricklefs 1971) described changes in chick mass and tibia length well. Variance in chick mass increased with age, therefore, I transformed the data and fitted $\log_e$(mass) to a $\log_e$(logistic curve). Three parameters describe the shape of a logistic curve: the asymptote, the rate constant (k) and the point of inflection. I used the estimate of asymptote from the curve as a measure of chick mass or size at fledging. However, the point of inflection and the rate constant (k), in logistic curves, are both dependent on the value of the asymptote (Ricklefs 1971). This makes these measures difficult to interpret for chicks of differing sizes and of limited biological meaning. I have therefore not included estimates of inflection points or rate constants in analyses. Instead, I calculated the average growth rate over the linear portion of a growth curve, a measure not dependent on the final mass or size of a chick.

Two difficulties were encountered fitting logistic growth curves to mass. First, many rosella nestlings peaked in mass about ten days prior to fledging and subsequently decreased in mass with large fluctuations until fledging. Thus estimates of asymptotic mass varied between chicks depending on the distribution of measurements during the plateau of the curve. Second, in some broods, chicks hatching last were only measured once during the plateau of the curve, making estimates of the asymptote less accurate. In general the logistic curve appeared to produce asymptotic estimates of mass that appeared unrealistically low for last-hatched chicks. I therefore calculated a second estimate of mass at fledging by using the mean mass for each chick for measures taken after the growth curve reached a plateau at 21 days post-hatch. Measures of mean maximum mass were highly correlated to predicted asymptotic mass ($r = 0.87$, $p < 0.001$, $n = 123$), especially for first hatched chicks ($r = 0.92$, $p < 0.001$, $n = 38$) but as suspected, less strongly for last hatched chicks ($r = 0.83$, $p < 0.001$, $n = 29$).

Tibia length reached a plateau earlier in the nestling period than mass and varied less between measurements. Consequently, estimates of asymptotic tibia length from the logistic growth curves were assumed to be unbiased and accurate for all individuals. I was unable to calculate adequate measures of linear growth rates for tibia length because the duration of the linear phase was short, lasting only from one to 10 days after hatching during which I took too few measures to give reliable estimates. The tibia of many chicks was only measured twice during this period, and the slope of some individuals were unrealistic, particularly if the measures were taken one or two days apart. I therefore used linear growth rates calculated from wing chord measurements. Wing chord growth is much slower than tibia length and remains approximately linear between 8 and 28 days after hatching.

If less than five measurements were taken for a chick, a growth curve was not calculated. Since mass, tibia and wing were not measured on all occasions, sample sizes vary depending on the measure used.

MORTALITY

Chicks which died during the nestling period either died soon after hatching without being fed, or later in the nestling period due to predation, physical defects or unknown causes (Krebs unpublished). I categorised mortality as occurring early in the nestling period, late in the nestling period or post-fledging for all nests that hatched at least 3 chicks (allowing a first, middle and last-hatched category, see below). I used the number of banded fledglings resighted at least 3 months after leaving the nest as a measure survivorship after fledging.

ANALYSES

I examined the effect on chick growth of six different explanatory variables: year, laying date, brood size, total hatching asynchrony (in days) or the brood size or mass hierarchy, sex, and hatching rank. Since hatching asynchrony and brood size and mass hierarchies were highly correlated and describe similar biological variables, I entered each separately as explanatory variables in alternate models in order to assess their independent impact on chick growth. I assigned hatching ranks to chicks by grouping them as first-hatched, middle-hatched or last-hatched within the brood. This resulted in large broods having more than one middle-hatched chick, however it allowed comparisons based on hatching order for broods of different sizes. If hatching ranks were tied for first or last chicks within a brood (see above), this resulted in the brood having more than one chick categorised as first or last. However, this only occurred in a few large broods, and never eliminated the middle-hatched category.

Analysing differences between chicks of different hatching ranks across broods requires a repeated measured design. However, least squares models do not allow for unbalanced data within a repeated measures design. Therefore, to analyse differences in growth across differing brood sizes, I have used a mixed model incorporating random and fixed effects (REML, Restricted Maximum Likelihood; GENSTAT 5 Committee 1993). Five variables describing chick growth and size at fledging were each used as response variables in separate models: asymptotic mass, mean maximum mass, the linear rate of mass increase, asymptotic tibia length, and linear rate of wing growth. Nestbox was included as a random term in all mixed models. I fitted a model by initially including all explanatory variables and two-way interactions. Terms were dropped from a model in a stepwise procedure by assessing the change in deviance between the full model and the submodel. Any significant terms were included in subsequent model fitting. A final model was selected by sequentially dropping non-significant interactions and then non-significant main effects, until only significant terms remained. I avoided any confounding effects due to the order of deletion by adding and dropping any term that was close to significant ($p<0.20$) from the final model. The results of model fitting for chick growth rates are presented for all main effects and four biologically important interactions (sex*rank, sex*hatching asynchrony, rank*hatching asynchrony and brood size*rank). For simplicity, interaction terms were not presented if non-significant.

For analyses where each brood was represented only once, I used least squares models for continuous response variables and logistic regression for dichotomous variables (SPSS software; Norusis 1994).

For all fitted models, I verified the normality of the data using residual and normal probability plots. Log transformations were used to produce a linear relationship between hatching asynchrony and laying date. Means and standard errors are reported throughout, except where otherwise indicated.

Results

HATCHING ASYNCHRONY

Crimson rosella broods hatched over an interval of 1.5 to 7 days (mean ± sd = 3.6 ± 1.6, n = 48). Hatching asynchrony increased with laying date (Fig. 1) and brood size (Fig. 2a). However, total hatching asynchrony increased most between three chick

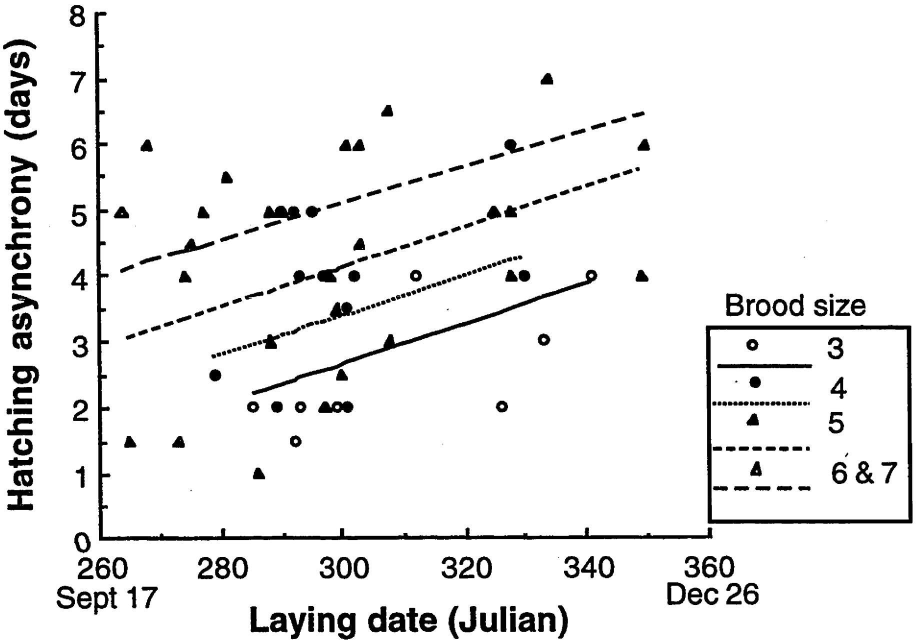

Fig. 1. The relationship between total hatching asynchrony and laying date in crimson rosellas. Hatching interval increased significantly over the breeding season and with increasing brood sizes (ANCOVA - laying date covariate: $F_{4,31} = 7.2$, $p = 0.01$; brood size effect - $F_{4,31} = 3.6$, $p = 0.02$). The predicted lines are shown for each brood size.

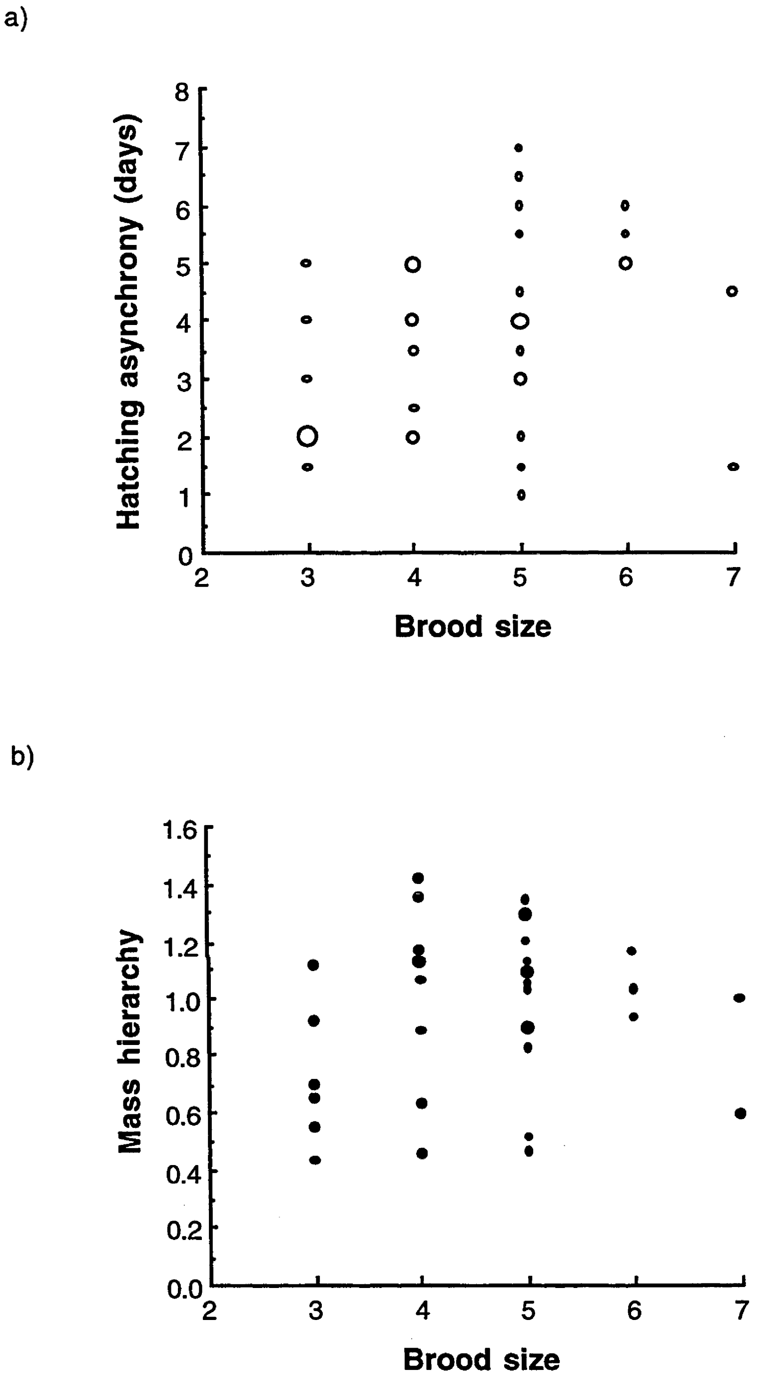

Fig. 2. a) Total hatching asynchrony and b) brood mass hierarchy versus brood size for all rosella broods measured in 1993-1996. Total hatching asynchrony increased significantly with brood size (see Fig. 1). Only broods measured within 24 hours of the last egg hatching were included. Small dots represent 1 data point; medium dots, 2 data points; large dots, 3 data points; and one very large dot, 4 data points.

broods and all other brood sizes (Fig. 2a), and when only clutches with no hatching failure were considered did not increase with brood size (ANCOVA controlling for laying date, $F_{4,17} = 0.48$, $p = 0.49$).

MASS AND SIZE HIERARCHIES

Mass hierarchies at the end of hatching ranged from 0.43 to 1.42 (mean ± sd = 0.96 ± 0.28, n = 34). Mass hierarchies larger than mean brood mass were common and first-hatched chicks could be 40 g or 700% heavier than last-hatched chicks. Mass hierarchies increased with hatching asynchrony (Fig. 3a) and laying date (Fig. 4), but not with brood size (ANCOVA, controlling for hatching asynchrony and laying date - $F_{4,33} = 0.3$, $p = 0.80$; Fig. 2b).

Mass and size hierarchies within a brood were highly intercorrelated ($r = 0.78$, $p = 0.0001$, $n = 29$). Overall, size hierarchies at hatching were smaller, and ranged from 0.14 to 0.70 (mean ± sd = 0.41 ± 0.16). Size hierarchies increased with hatching asynchrony (Fig. 3b), but did not increase with laying date or brood size (ANCOVA - controlling for hatching asynchrony: laying date covariate, $t = -0.7$, $p = 0.56$; brood size effect, $F_{4,30} = -0.7$, $p = 0.62$).

NESTLING GROWTH AND SIZE AT FLEDGING

Male rosella chicks grew faster and had higher asymptotic masses and tibia lengths at fledging than female chicks (Table 1 & 2; Fig. 5). No other variable consistently explained variation in chick growth or size at fledging (Table 1 & 2; Fig. 5).

Although hatching rank did not generally explain differences in chick size or growth in mixed models, last-hatched chicks had lower asymptotic masses than first-hatched chicks (Table 1 & 2). Mean maximum masses were not significantly smaller for last-hatched chicks, further suggesting that logistic growth curves may have underestimated the mass of last-hatched nestlings at fledging (see Methods). To further assess any impact of chick rank on growth or size at fledging, I also compared the differences for each sex in a pair-wise comparison. To maximise the number of useable broods, I have assigned chicks of either sex as "first-hatched" if they hatched first or

Table 1. Summary of REML model fitting for the following response variables: a) asymptotic mass (g), b) mean maximum mass (g), c) linear growth rate for mass (g), d) asymptotic tibia length (mm) and e) linear growth rate for wing chord (mm). Asymptotic estimates were derived by fitting a logistic curve to individual chick measurements (n=130; see Methods for further details). The order in which the variables are presented in the tables does not reflect the order with which they were dropped from the model (see Methods). The change in deviance is reported when each variable is removed from the model. Abbreviations are as follows: BS=brood size, HA=hatching asynchrony (in days), laydate=laying date, rank=hatching rank (first, middle, last). All possible 2-way interactions were tested, but I have presented results from those of biological interest. No other interactions were found to be signficant. All p-values less than or equal to 0.10 are reported, any greater than 0.10 are termed non-significant (ns).

a) Asymptotic mass

Explanatory Variable	**Model variable removed from**	**Change in deviance (χ^2)**	**d.f.**	**p**
laydate	sex+rank+BS+HA+year+laydate	0.24	1	ns
year	sex+rank+BS+HA+year	1.60	3	ns
HA	sex+rank+BS+HA	1.48	1	ns
BS	sex+rank+BS	3.36	4	ns
rank	sex+rank	6.24	2	<0.05
sex	sex+rank	63.9	1	<0.001
sex*rank	sex+rank+sex*rank	3.42	2	ns
sex*HA	sex+rank+HA+sex*HA	2.87	1	<0.10
rank*HA	sex+rank+HA+rank*HA	0.79	2	ns
rank*BS	sex+rank+BS+rank*BS	8.66	8	ns

b) Mean maximum mass

Explanatory Variable	Model variable removed from	change in deviance (χ^2)	d.f.	p
laydate	sex+rank+BS+HA+year+laydate	0.05	1	ns
year	sex+rank+BS+HA+year	3.59	3	ns
HA	sex+rank+BS+HA	0.48	1	ns
BS	sex+rank+BS	2.30	4	ns
rank	sex+rank	3.63	2	ns
sex	sex+rank	55.13	1	<0.0001
sex*rank	sex+rank+sex*rank	1.04	2	ns
sex*HA	sex+HA+sex*HA	3.23	1	<0.10
rank*HA	sex+rank+HA+rank*HA	0.55	2	ns
rank*BS	sex+rank+BS+rank*BS	6.94	8	ns

c) linear growth rate of mass

Explanatory Variable	Model variable removed from	change in deviance (χ^2)	d.f.	p
laydate	sex+rank+BS+HA+year+laydate	0.28	1	ns
year	sex+rank+BS+HA+year	1.11	3	ns
HA	sex+rank+BS+HA	0.00	1	ns
BS	sex+rank+BS	7.38	4	ns
rank	sex+rank	1.05	2	ns
sex	sex+rank	17.24	1	<0.0001
sex*rank	sex+rank+sex*rank	4.34	2	<0.10
sex*HA	sex+HA+sex*HA	0.69	1	ns
rank*HA	sex+rank+HA+rank*HA	2.26	2	ns
rank*BS	sex+rank+BS+rank*BS	6.22	8	8

d) Asymptotic tibia length

Explanatory Variable	Model variable removed from	change in deviance (χ^2)	d.f.	p
laydate	sex+rank+BS+HA+year+laydate	0.05	1	ns
year	sex+rank+BS+HA+year	14.86	3	<0.01
HA	sex+rank+BS+HA+year	0.00	1	ns
BS	sex+rank+BS+year	6.91	4	ns
rank	sex+rank+year	0.17	2	ns
sex	sex+year	46.11	1	<0.0001
sex*rank	sex+rank+year+sex*rank	3.19	2	ns
sex*HA	sex+HA+year+sex*HA	0.26	1	ns
rank*HA	sex+rank+HA+year+rank*HA	0.66	2	ns
rank*BS	sex+rank+BS+year+rank*BS	5.17	8	ns

e) Linear growth rate of wing chord

Explanatory Variable	Model variable removed from	change in deviance (χ^2)	d.f.	p
laydate	sex+rank+BS+HA+year+laydate	0.28	1	ns
year	sex+rank+BS+HA+year	0.76	3	ns
HA	sex+rank+BS+HA	0.74	1	ns
BS	sex+rank+BS	7.48	4	ns
rank	sex+rank	0.14	2	ns
sex	sex+rank	1.49	1	ns
sex*rank	sex+rank+sex*rank	0.62	2	ns
sex*HA	sex+HA+sex*HA	3.81	1	p<0.10
rank*HA	rank+HA+rank*HA	1.42	2	ns
rank*BS	rank+BS+rank*BS	10.12	7	ns

Table 2. Comparison of asymptotic mass, growth rates and asymptotic tibia length for crimson rosella chicks grouped by sex and hatching order (first middle and last hatched). Hatch order did not significantly affect any measure except asymptotic mass (Table 1).

a) Males

Growth variable	**First hatch** ($\bar{x}$ ± se)	**n**	**Mid hatch** ($\bar{x}$ ± se)	**n**	**Last hatch** ($\bar{x}$ ± se)	**n**	**overall** ($\bar{x}$ ± se)	**n**
asymptotic mass	138.2±3.0	15	139.2±1.8	28	136.8±4.0	10	138.5±1.5	53
mean mass	139.4±2.6	13	142.9±1.8	27	137.6±2.9	10	140.9±1.3	50
linear growth rate (mass)	7.94±0.38	15	7.49±0.20	25	7.33±0.27	8	7.61±0.17	48
tibia length	56.2±0.4	15	56.7±0.36	27	56.3±0.5	8	56.5±0.24	50
linear growth rate (wing)	5.75±0.09	15	5.54±0.09	25	5.56±0.13	8	5.61±0.06	48

b) Females

Growth variable	**First hatch** ($\bar{x}$ ± se)	**n**	**Mid hatch** ($\bar{x}$ ± se)	**n**	**Last hatch** ($\bar{x}$ ± se)	**n**	**Overall** ($\bar{x}$ ± se)	**n**
asymptotic mass	130.2±2.9	25	124.7±2.0	31	128.7+2.6	20	127.6±1.4	76
mean mass	132.1±2.2	25	127.2±2.0	29	127.8±2.3	19	129.0±1.3	73
linear growth rate (mass)	6.86±0.15	21	7.20±0.27	28	7.36±0.25	20	7.15±0.14	69
tibia length	55.0±0.3	25	54.2±0.3	31	54.4±0.5	19	54.5±0.2	75
linear growth rate (wing)	5.56±0.10	19	5.51±0.07	30	5.63±0.14	18	5.55±0.06	67

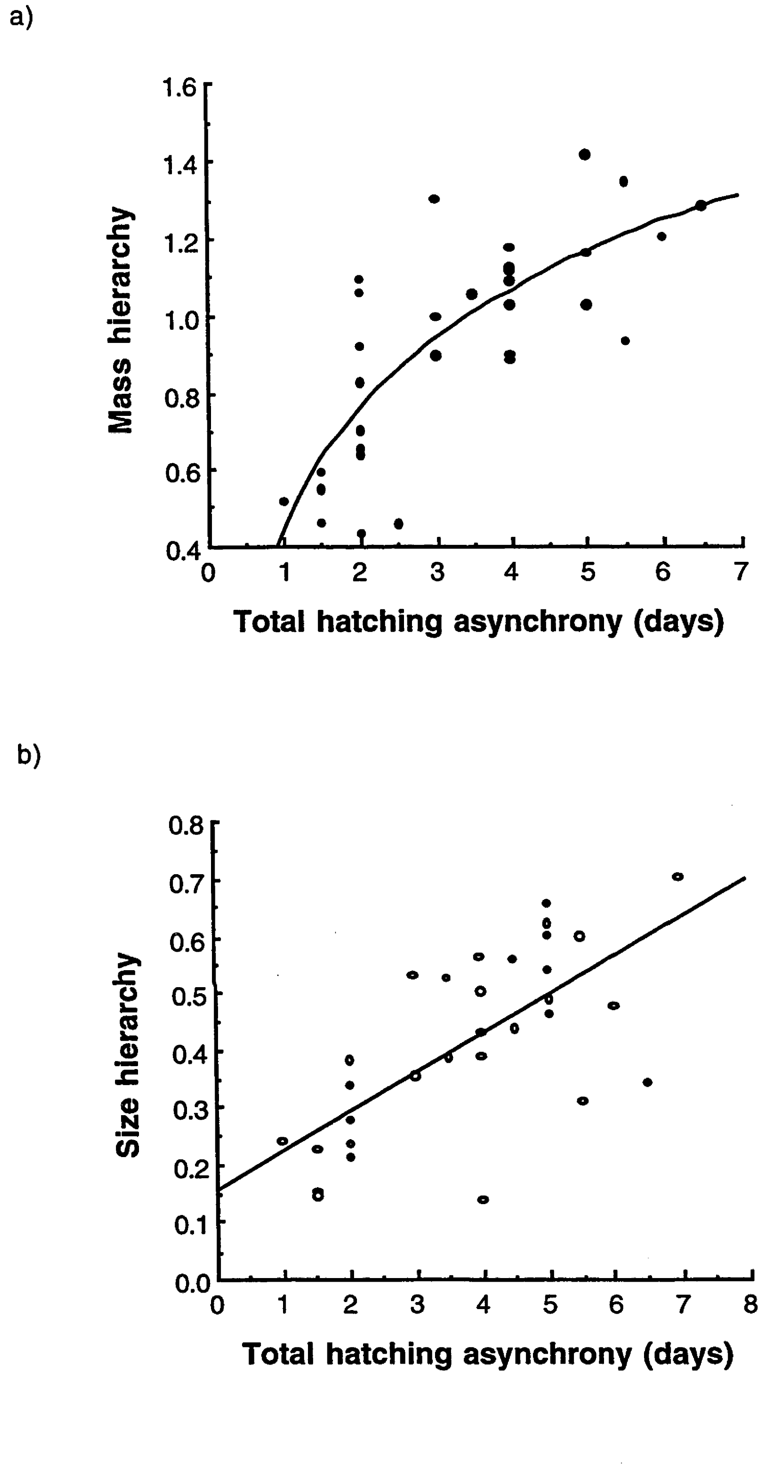

Fig. 3. a) The relationship between mass hierarchies and hatching asynchrony in crimson rosella broods (Predicted relationship - Mass hierarchy = 0.44+1.02 * Log(hatching interval); Regression, controlling for laying date, $t = 7.5$, $p < 0.0001$, $n = 34$). b) The relationship between size hierarchies and hatching asynchrony (Predicted relationship - Size hierarchy = 0.15 + 0.07 * hatching interval; Regression, $t = 5.3$, $p < 0.0001$, $n = 32$).

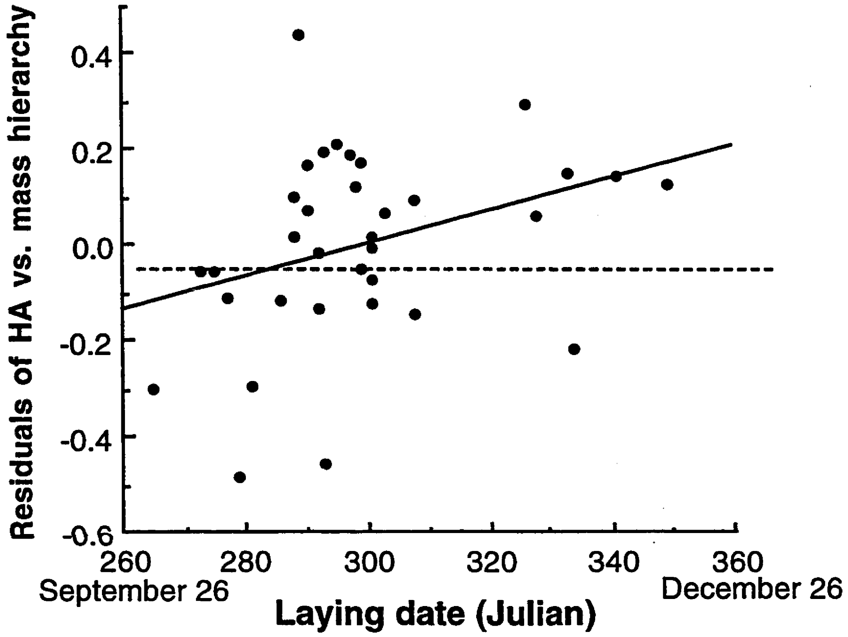

Fig. 4. The residuals of mass hierarchy regressed against hatching asynchrony plotted against laying date for rosella broods. The residuals were positively correlated to laying date (residuals = -1.02 + 0.003 * (laying date); Regression analysis, controlling for hatching asynchrony - t = 2.1, p = 0.04, n = 34).

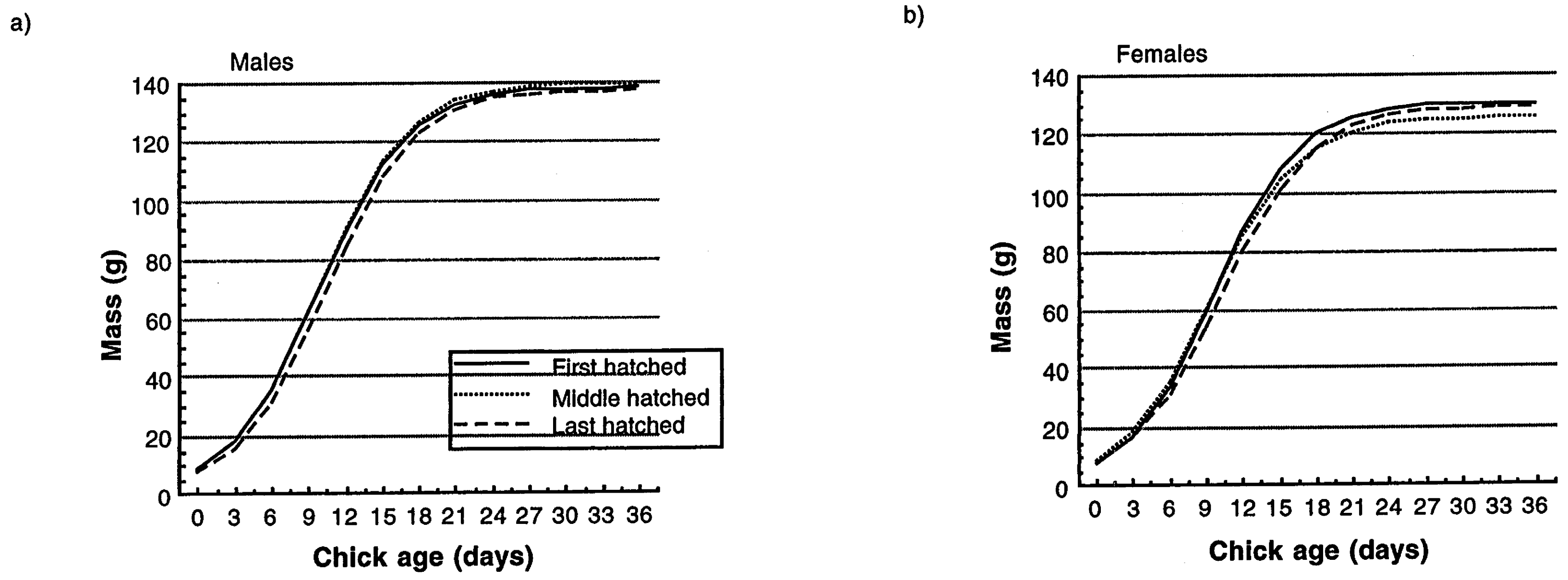

Fig. 5. Predicted logistic growth curves for the mass of crimson rosella chicks presented separately for a) males (first-hatched n = 15, middle-hatched n = 28, last-hatched n = 10) and, b) females (first-hatched n = 25, middle-hatched n = 31, last-hatched n = 20). Logistic curves were calculated using the mean parameter values from individually fitted curves for chick categorised as first, middle and last-hatched.

second, and chicks of either sex as "last-hatched" if they were penultimate or last-hatched in a brood. I have only considered pairwise comparisons for each sex where the chicks differ by at least 2 ranks. These criteria were met in only a subsample of broods, particularly for males since last-hatched males are much less common than last-hatched females. Analysis on this subset of data suggested that first-hatched male chicks were heavier, but not larger at fledging than last-hatched male chicks (Table 3). There were no pairwise differences in linear rates of mass gain or linear rates of increase of wing growth. In contrast, no measure of female chick growth differed in pairwise comparisons (Table 3). Despite the fact hatching rank potentially affected male mass at fledging, no hatching rank * sex interactions were detected in the mixed models (Table 1), suggesting that the subsample of data used in pairwise comparisons was biased

Patterns of annual and seasonal variation did not consistently affect nestling mass, or growth (Table 1). However, asymptotic tibia length varied between years, primarily due to shorter tibias in 1993 (Predicted asymptotic values (in mm) - Males 1993 = 55.0 ± 0.4; 1994 = 56.3 ± 0.5; 1995 = 57.3 ± 0.4; 1996 = 57.2 ± 0.8; Females, 1993 = 53.8 ± 0.4; 1994 = 53.5 ± 0.3; 1995 = 55.6 ± 0.3; 1996 = 54.5 ± 0.5). Annual differences in tibia length may reflect differing resource levels since the longest tibias were recorded in the wettest year; however, there were no interannual differences in mass or wing linear growth rates to support this view (Table 1).

Although few explanatory variables related to chick growth, growth rates were not constant between nestboxes. For each response variable tested, significant variation occurred between nestboxes even after the final model was fitted (Change in deviance for model with and without nestbox as a random factor: asymptotic mass, $\chi^2 = 84.9$, df = 1 $p < 0.0001$; mean maximum mass, $\chi^2 = 42.7$, df = 1, $p < 0.0001$; linear mass growth rate, $\chi^2 = 6.0$, df = 1, $p < 0.02$; tibia, $\chi^2_{1,}=10.2$, $p<0.005$; linear wing growth rate, $\chi^2 = 11.1$, df = 1, $p < 0.001$). Thus other unmeasured variables such as parental age, parental condition, or genetic factors also affect nestling growth.

Table 3. Summary of pairwise comparisons between first and last-hatched rosella chicks (see Results for definition) summarised separately for, a) male and b) female nestlings for the five measures of nestling growth analysed: Asymptotic mass (g), Mean maximum mass (g), asymptotic tibia length (mm), linear rate of mass gain (g/day), and linear rate of increase in wing length (mm/day). For each variable, mean paired differences (first - last hatched), standard deviations and the number of broods (in brackets) in each comparison are presented. The results of paired t-tests and probability levels are included for each variable.

a) Male nestlings

Growth variable	**Mean paired difference ± sd**	**Paired T-statistic**	**2-tailed sig**
Asymptotic mass	6.6 ± 6.4 (9)	3.1	0.02
Mean maximum mass	7.5 ± 7.6 (8)	2.8	0.03
Asymptotic tibia length	-0.95 ± 0.94 (7)*	-2.7	0.04
Linear rate of mass gain	0.45 ± 1.1 (9)	0.87	0.26
Linear rate of wing growth	0.14 ± 0.47 (9)	0.92	0.39

* Note for this comparison, last-hatched males were significantly larger than first-hatched males, as indicated by the minus sign

b) Female nestlings

Growth variable	**Mean paired difference ± sd**	**Paired T - statistic**	**2-tailed sig**
Asymptotic mass	1.1 ± 7.0 (19)	0.71	0.48
Mean maximum mass	2.5 ± 7.3 (19)	1.51	0.15
Asymptotic tibia length	0.74 ± 2.4 (18)	1.31	0.21
Linear rate of mass gain	0.22 ± 1.1 (18)	0.87	0.40
Linear rate of wing growth	-0.04 ± 0.64	-0.29	0.78

NESTLING MORTALITY

Twenty-two percent of all chicks hatched (43/198), died during the nestling period. Overall mortality during the nestling period tended to be higher for chicks hatching last (Percent dying - first-hatched = 18% (8/44), middle-hatched = 17% (19/110), last-hatched = 34% (15/44); $\chi^2 = 5.7$, df = 2, $p < 0.10$). Increased mortality of last-hatched chicks was entirely due to mortality immediately after hatching. Early mortality occurred in 10 cases (23% of all chick mortality) and always involved last-hatched, or in one case, both penultimate and last-hatched chicks (Percent dying immediately after hatching - First and middle-hatched = 1% (1/154), last-hatched = 20% (9/44); $\chi^2 = 28.4$, df = 2, $p < 0.0001$). In contrast, nestling mortality over the remainder of the nestling period did not differ between hatching ranks (First hatched = 18% (8/44; middle hatched = 17% (18/109); last hatched = 17% (6/35); $\chi^2 = 0.16$, df = 2, $p > 0.97$).

The probability of early brood reduction increased over the breeding season (Fig. 6). However, brood reduction did not increase with hatching asynchrony (Logistic regression, model improvement statistic; $\chi^2 = 0.7$, df = 1, $p = 0.39$), or brood size ($\chi^2 = 0.4$, df = 1, $p = 0.52$). Brood reduction might be more likely when the interval between the penultimate and last-hatched chick was large. However, there was no different in the hatching intervals between the penultimate and last-hatched chicks for broods that had brood reduction and those that did not (final hatching interval: brood reduced = 1.7 ± 0.3 days, n = 10; non-brood reduced = 1.6 ± 0.4 days, n = 11). Broods which hatched a higher proportion of their eggs tended to have a higher probability of brood reduction (Logistic regression, ${\chi^2}_1 = 3.59$, $p = 0.06$; Proportion hatched: brood reduced broods = 0.89; non-brood reduced broods = 0.73, n = 28).

POST-FLEDGING SURVIVAL

A total of 11% (18/168) of rosellas banded as nestlings were resighted as juveniles in or adjacent to the study area. Most individuals were sighted more than once (mean=2.8; range= 1 - 12), and several were observed paired and defending hollows, suggesting that they were resident in the area. Male juvenile rosellas were more likely to

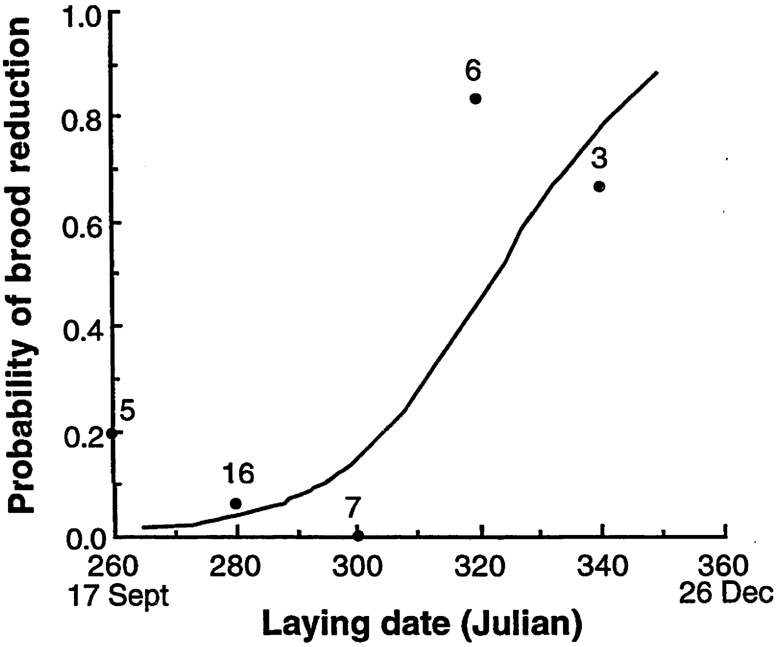

Fig. 6. The probability of brood reduction in rosella broods versus laying date for all years combined (Logistic regression, $\chi^2 = 12.3$, df = 1, $p < 0.001$). The fitted line, and the proportion of broods experiencing brood reduction over each 20 day intervals are shown. The number of broods sampled are indicated above each dot.

be sighted than females (25% (15/61) of males vs. 4% (3/80) of females resighted; $\chi^2 = 10.3$, df = 1, $p < 0.0001$). If post-fledging survival of males and females is equal, this suggests that female crimson rosellas move further from their natal area before breeding. I have assumed that any juvenile male in the area was equally likely to be resighted, however, since females may have survived but moved beyond the vicinity of the study area, I have not included them in survival analyses. Survival of male rosella chicks did not differ between chicks hatched first, middle or last in a brood (first = 25% (3/12), middle = 20% (7/35), last = 44% (4/9); $\chi^2 = 0.92$, df = 2, $p > 0.9$). Surviving male chicks were not heavier at fledging, larger at fledging and did not fledge earlier in the season than chicks who did not survive (Table 4).

Table 4. A comparison of chick size and mass at fledging for male crimson rosella chicks that survived to at least 3 months post fledging and chicks that did not. Two measures of chick mass at fledging (asymptotic mass and the mean maximum mass; see Methods) asymptotic tibia length and laying date were compared between individuals who survived and those who did not survive. Sample sizes are presented in brackets. Test statistics for t-tests and p-values are reported for each variable. There were also no significant differences between the characteristics of surviving and non-surviving chicks detected by a logistic regression.

Variable	Males surviving	Males not surviving	T - statistic	2-tailed sig
Asymptotic mass	139.6±3.3 (13)	139.0±1.6 (43)	- 0.2	0.88
Mean maximum mass	141.5±3.7 (11)	141.2±1.5 (42)	- 0.1	0.94
Asymptotic tibia length	56.6±0.3 (13)	56.5±0.3 (40)	- 0.0	0.97
Laying date	298.9±6.6 (14)	300.5±4.3 (40)	0.2	0.84

Discussion

The surprising result of this study is that high levels of hatching asynchrony in crimson rosella broods did not reduce the growth of later hatched chicks, and only affected survival immediately after hatching. Overall, neither hatching asynchrony nor hatching order affected the growth rates, size at fledging, or post-fledging survival of rosella chicks, but may have reduced mass at fledging for last-hatched male chicks. In contrast, hatching asynchrony in most species leads to poor growth and sometimes to lower post-fledging survival of last-hatched chicks (Table 5).

HATCHING ASYNCHRONY AND SIZE HIERARCHIES IN BROODS

Hatching asynchrony in rosella broods averaged 3.6 days, longer than that observed in 85% of the bird species summarised by Clark & Wilson (1981). Hatching asynchrony in broods never exceeded 1 week, although laying could take up to 2 weeks, suggesting that females initiated incubation midway through egglaying. Hatching asynchrony and mass hierarchies observed in crimson rosella broods were highly variable and not strongly related to brood size. This contrasts with most asynchronous species studied, where hatching spreads and size hierarchies increase with brood size (fieldfares *Turdus pilaris*, Wiklund 1985; European blackbirds *Turdus merula*, Magrath 1992; green-rumped parrotlets, Waltman & Beissinger 1992; white-winged choughs *Corcorax melanorhamphos*, Heinsohn 1995; American kestrels *Falco sparverius*, Wiebe & Bortolotti 1994a), suggesting that females initiate incubation relative to the first laid egg, leading to longer hatching spreads as clutch size increases. In crimson rosellas, the weak relationship between hatching asynchrony and clutch size and the increase in hatching asynchrony over the breeding season suggests that females varied when they initiated incubation in response to factors other than clutch size.

Some of the variation in hatching patterns observed in rosellas was due to hatching failure. Hatching failure is common in rosellas, averaging 34% of all eggs laid in this study (Chapter 2). Relatively high rates of hatching failure appear to be characteristic of parrots and similar levels have been described in several species (33%, long-billed corellas *Cacatua pastinator pastinator*, Smith 1991; 32% (mean for all areas),

Table 5. Summary of patterns of growth and survival for last-hatched nestlings in asynchronously hatching species. Only studies on wild birds are included.

Order* / Species (*after Sibley et al. 1990)	**Nestling growth reduced?**	**Post-fledging Survival reduced?**	**Reference**
Passeriformes			
Arabian babblers *Turdoides squamiceps*	yes	unknown	Ostreiher 1997
Blue tits *Parus caeruleus*	yes	yes/no	Nur 1984; Slagsvold et al. 1995
European Blackbirds *Turdus merula*	yes	yes	Magrath 1989; 1991
Marsh Tits *Parus palustris*	yes	unknown	Nilsson & Svensson 1996
Starlings *Sturnus vulgaris*	yes	yes	Stouffer & Power 1990
Pied flycatcher *Ficedula hypoleuca*	yes	unknown	Slagsvold 1986
Tree Swallows *Tachycineta bicolor*	yes	unknown	Zach 1982
White-winged choughs *Corcorax melanorhamphos*	yes	no	Heinsohn 1995; Boland et al. 1997
Psittaciformes			
Crimson rosellas *Platycercus elegans*	no	no	this study
Green-rumped parrotlets *Forpus passerinus*	yes	no	Stoleson & Beissinger 1997
Major Mitchell's cockatoo *Cacatua leadbeateri*	yes	no	Rowley & Chapman 1991
Long-billed corella *Cacatua pastinator*	yes	no	Smith 1991
Coraciiformes			
Blue-throated bee-eaters *Merops viridis*	yes	unknown	Bryant & Tatner 1990
European bee-eaters *Merops apiaster*	yes	no	Lessels & Avery 1989
White-fronted bee-eaters *Merops bullockoides*	yes	unknown	Emlen et al. 1991
Ciconiiformes			
American Kestrels *Falco sparverius*	yes	unknown	Wiebe & Bortolotti 1995
Black kites *Milvus migrans*	yes	unknown	Veiga & Hiraldo 1990
Magellanic penguins *Spheniscus magellanicus*	yes	unknown	Blanco et al. 1996
Maguari storks *Ciconiia maguari*	no	unknown	Thomas 1984
Red kites *Milvus milvus*	yes	yes	Veiga & Hiraldo 1990
Shag *Phalacrocorax aristotelis*	no	unknown	Amundsen & Stokland 1988
White-fronted bee-eaters *Merops bullockoides*	yes	unknown	Emlen et al. 1991

white-tailed black cockatoos, Saunders 1982; 30%, galahs *Cacatua roseicapillus*, Rowley 1990; 32% Puerto Rican parrots *Amazona vittata vittata*, Snyder, Wiley & Kepler 1987). In this study, the probability of an egg hatching did not vary with laying sequence (Krebs, unpublished data), so failure to hatch was not simply due to neglect of last laid eggs. Regardless of whether hatching failure occurred or not, there was substantial variation in hatching asynchrony at all brood sizes. In large rosella broods, up to four chicks could hatch on one day, or chicks could hatch at one day intervals.

Hatching asynchrony and size hierarchies increased with laying date, suggesting that more synchronous broods may be advantageous early in the breeding season. However, because large clutch sizes only occurred early in the breeding season, it was difficult to assess whether hatching asynchrony varied due to ecological factors associated with laying date, or due to differences between females. Either way, the variability of hatching patterns in rosella broods suggests that the onset of incubation varied between individual females. Mass hierarchies also increased with laying date independent of hatching asynchrony, suggesting that female rosellas use two mechanisms to set the size hierarchy within the brood, firstly by varying the onset of incubation and secondly by increasing or decreasing the feeding rates to early hatched chicks.

Females in some species can alter incubation patterns in response to food availability, but whether this is due to energetic constraints during egg-laying or facultative manipulation of hatching intervals is less clear. Supplementary food in marsh tits (*Parus palustris*) lead to females initiating incubation earlier than control females, suggesting that the timing of incubation was energetically constrained (Nilsson 1993). Females Marsh tits therefore appear to trade-off between foraging and incubation, regardless of the resulting hatching patterns. In contrast, in American kestrels, supplementary food lead females to delay incubation and reduce hatching asynchrony in broods (Wiebe & Bortolotti 1994a). Since the advantages of differing hatching patterns depended on food availability in American kestrels, females altered incubation patterns to produce levels of hatching asynchrony best suited to predicted levels of food (Wiebe & Bortolotti 1994b).

I have no data to suggest that energetic constraints explained the incubation patterns observed in crimson rosellas. Rosellas competed intensely for nesting hollows and one or both members of the pair defended the hollow. Females spent long periods of time in the nestbox during egg-laying and presumably could begin incubation early in laying, although in some clutches they did not initiate incubation until late in the laying sequence. Female rosellas are also fed by their mate from before egglaying until the brood is one week old, suggesting that they do not have to trade-off between foraging and initiating incubation. If energetic constraints determined the incubation patterns observed in rosellas, a female who was poorly fed by her mate may be forced to increase her foraging time during egglaying and delay the onset of incubation. However, the observed seasonal decreases in clutch size and increases in hatching asynchrony in rosellas do not support this hypothesis. Pairs breeding early in the season are generally older, more experienced, or in better condition than pairs breeding late in a season (e.g. sparrowhawks *Accipter nisus*, Newton 1986; European kestels *Falco tinnunculus*, Village 1990; kittiwakes *Rissa tridactyla*, Thomas & Coulson 1988; female great tits *Parus major* , Perrins & McCleery 1989; pied flycatcher *Ficedula hypoleuca*, Harvey, Stenning & Campbell 1988). If incubation patterns in rosellas were the result of energetic constraints, pairs breeding early would be predicted to have higher hatching asynchrony than pairs breeding later in the season, opposite to the pattern observed in this study.

CONSEQUENCES OF ASYNCHRONOUS HATCHING

Effects on chick size and post-fledging survival

Despite the substantial hatching asynchrony observed in crimson rosellas, variation in chick sizes at fledging and chick growth rates were unrelated to differences in hatching asynchrony and mass/size hierarchies. Rosella broods in this study never hatched synchronously, so potentially all last-hatched chicks were at a competitive disadvantage. Last-hatched chicks did not grow more poorly than first-hatched chicks. Linear growth rates of chick mass and wing length did not differ between hatching ranks in multivariate analyses and pairwise tests. In addition, last-hatched chicks did not have smaller tibias, a measure of skeletal size, than first-hatched chicks in any analysis, in fact last-hatched male chicks had significantly larger tibias (Table 3). However, asymptotic mass decreased with hatching rank in multivariate analysis, although asymptotic and mean maximum masses were lighter only for last-hatched male chicks in pairwise comparisons. Thus, last-hatched male and female rosella chicks grew at the same rate as first-hatched chicks over most of the nestling period and reached the same size at fledging. Last-hatched males however, were estimated to be lighter than their earlier hatched male siblings and potentially in poorer condition at fledging.

Differences in male mass at fledging were small and averaged 6 g, or 5% of male weight at fledging. Several lines of evidence suggest that the measured differences are not biologically meaningful. First, the high degree of hatching asynchrony in many rosella broods may result in underestimates for the mass of last-hatched chicks at fledging (see Methods). Second, fledging ages in parrots are variable, and underweight nestlings may be able to increase their condition by remaining in the nest for a few extra days (Stamps et al. 1985; Rowley 1990; Rowley & Chapman 1991). Third, post-fledging survival of last-hatched chicks was not reduced, and males with low fledging weights were not less likely to survive in this study.

It is not clear why last-hatched male and not female chicks should have lower masses at fledging. The larger sex in dimorphic species may have a competitive advantage in interactions over food (Teather 1992; Anderson et al. 1993; Price, Harvey & Ydenberg 1996). First-hatched male rosellas, particularly in broods with large hatching asynchronies may have a competitive advantage relative to last-hatched chicks because size differences will be largest about halfway through the nestling period. Any competitive disadvantage would affect later hatched male chicks more than female chicks because male energy requirements should increase more rapidly over the nestling period. Alternately, if male size affects subsequent breeding success, it may be advantageous for parents to preferentially feed first-hatched male, but not first-hatched female chicks. Interestingly, most last-hatched chicks in rosella brood are female (74%, 23/31 broods). Thus female rosellas may avoid producing males late in the laying sequence to minimise the costs of competitive disparities for last-hatched chicks.

Equal growth rates have rarely been described in asynchronously hatching species (Table 5). Thomas (1984) found no differences in the growth of nestlings hatched four days apart in maguari storks (*Ciconiia maguari*), although she measured only one brood. Despite hatching at one day intervals, nestling shag (*Phalacrocorax aristotelis)* had similar weights at fledging during a year of high food availability (Amundsen & Stokland 1988). In the majority of species, asynchronous hatching leads to decreased growth and increased mortality of later hatched nestlings (Table 5). Last-hatched chicks in asynchronous broods may have reduced growth and survival because parents are not able to provide sufficient food for the whole brood, and older chicks have first access to food (e.g. Forbes & Ankney 1987; Ploger & Mock 1986; Osorno & Drummond 1995; Blanco, Yorio & Boersma 1996). Even when food is abundant, later hatched chicks may grow poorly. For example, in green-rumped parrotlets, supplemental feeding in large broods only slightly improved the low survival rates of last-hatched chicks and did not increase the survival of penultimate chicks (Stoleson & Beissinger 1997). Stoleson and Beissinger (1997) argued that this was due to parents being unable to distribute food to later hatched chicks because of the large competitive asymmetries between chicks. Last hatched chicks in large highly asynchronous broods may also be vulnerable to being crushed or smothered in the nest by their much larger sibs (Stoleson & Beissinger 1997).

If the size differences between chicks in asynchronous broods reflect differences in competitive abilities, equal growth rates suggest that food distribution is under parental rather than chick control. Selective feeding of chicks, not determined by competitive interactions, has been shown in several species (budgerigars *Melopsittacus undulatus* , Stamps et al. 1985; pied flycatchers, Gottlander 1987; tree swallows, Leonard & Horn 1996; American kestrels, Anderson et al. 1993; white-winged choughs, Boland, Heinsohn & Cockburn 1997). In most studies, selective feeding was only observed when food was abundant. Small and underweight chicks were selectively fed by females in captive budgerigars with *ad lib* food (Stamps et al. 1985). Female pied flycatchers selectively fed small chicks in brood, but this preference disappeared when the brood hunger was experimentally increased (Gottlander 1987). In addition, selective feeding of last-hatched chicks, may not be sufficient to overcome their overall competitive inferiority in highly asynchronous species. In white-winged choughs, groups supplemented with food preferentially fed last-hatched chicks. Last-hatched chicks were more likely to survive in these broods, however, they still grew more slowly and had lower fledging weights than first hatched chicks (Boland et al. 1997).

Brood reduction

Although I could find no effect of asynchronous hatching on the growth or survival of crimson rosella chicks for most of the period of parental care, last-hatched chicks were more likely to die shortly after hatching than other chicks. Two lines of evidence suggest that this early mortality was due to parental refusal to feed recently hatched chicks rather than competition between chicks. First, even in broods with long hatching intervals, the largest chicks in a brood would not be coordinated enough to dominate parental feeds during the first few days of a last-hatched chick's life. Chicks younger than one week old rarely begged when their parents entered the nestbox and most feedings began when parents approached and offered food to inert chicks (unpublished data). Second, newly-hatched chicks that had died had empty crops. Third, videotapes showed that parents in many broods actively sought out small chicks to feed, unconstrained by chick behaviours (unpublished data).

The ability to reduce brood size may be important in rosellas, not due to unpredictable food supplies, as originally suggested by Lack (1947), but because of high levels of hatching failure. Rosellas forage primarily on seeds (Forshaw 1981), and although food availability varies between seasons, mainly due to rainfall patterns, overall levels of food availability do not change unpredictably over the breeding season. However, hatching failure was common in rosellas broods. In species with obigate siblicide, last-laid eggs appear to function mostly as replacement chicks in the event of random mortality or hatching failure (Mock & Parker 1986; Anderson 1990; Evans 1996). Last-hatched young in species with passive brood reduction can also function as replacement chicks, especially when hatching failure is high (Wiebe 1996). Forbes et al. (1997) have shown that last-hatched nestlings were more likely to survive in broods with hatching failure in red-winged blackbirds (*Agelaius phoeniceus*). Since high levels of hatching failure in rosellas results in initial clutch sizes not reliably correlating to brood sizes, a female may lay a larger clutch than desired and reduce the brood size through brood reduction if too many eggs hatch. Consistent with this hypothesis, brood reduction in rosellas tended to increase with the proportion of eggs successfully hatched. The probability of early brood reduction also increased over the breeding season as would be predicted if large broods were less successful or more costly to raise late in the breeding season.

Nevertheless, it seems unlikely that asynchronous hatching in rosellas has evolved simply as an adaptation to allow brood reduction. First, brood reduction was uncommon and its occurrence did not differ between years apparently differing in food availability. Second, the probability of early brood reduction in rosellas was not positively correlated with the degree of hatching asynchrony, suggesting that large hatching intervals were not necessary to allow rapid early mortality of nestlings. Several studies have noted that hatching asynchrony is not necessary to create competitive asymmetries between chicks, and strong dominance hierarchies for food were observed even in experimentally synchronised broods (Bengtson & Ryden 1983; Slagsvold 1986; Wiebe 1995; Drummond, Gonzalez & Osorno 1986; Mock & Ploger 1987). Thus, some degree of hatching asynchrony may minimise the costs of brood reduction, but it is not clear that increasing levels of hatching asynchrony will further decrease costs.

Why do crimson rosellas hatch asynchronously?

It is difficult to identify a single factor explaining asynchronous hatching in rosellas. Breeding in rosellas, as well as in parrots in general, is characterised by two day (or longer) egg-laying intervals, relatively long incubation and nestling periods, and asynchronous hatching (Saunders, Smith & Campbell 1984; Ricklefs 1993). Ricklefs (1993) has argued that this suite of life history characteristics is commonly associated and may relate to longevity benefits derived from longer embryonic and nestling development times and a reduction of sibling competition between developing embryos. In addition, the costs of asynchronous hatching in rosellas may be relatively low in comparison to synchronous hatching, particularly if low predation rates on incubating females and young in nesting hollows minimises the costs of longer incubation and nestling periods. Thus, the costs of asynchronous hatching in rosellas may be mainly in maintaining an equitable food distribution to the brood, whereas synchronous hatching may lead to additional costs such as reduced egg viability (Arnold, Rohwer & Armstrong 1987), increased levels of sibling competition (Hahn 1981), or increased food demands by the brood (Hussell 1972).

Regardless of the ultimate function of hatching asynchrony in rosellas, the variation in hatching intervals and size hierarchies observed in this study suggests that the costs and benefits associated with a particular degree of hatching asynchrony varies between individuals. Optimal levels of hatching asynchrony might vary between individuals due to the age or experience of a female, her condition or the quality of her mate. Several other studies have proposed that optimal breeding behaviour may vary between individuals. For example, female magpies (*Pica pica*) adjusted their clutch size to match territory quality (Hogstedt 1980) and optimal clutch sizes for female great tits varied between individuals (Pettifor et al. 1988). Few studies of hatching asynchrony have focussed on individual variation within populations. Wiebe and Bortolotti (1994) showed that females could alter their levels of hatching asynchrony in response to male provisioning during egglaying. However, the only study which has specifically tested whether individual optimisation explained the variation in hatching asynchrony observed within a population, found that individual house wrens (*Troglodytes aedon*) did no better or worse when hatching asynchrony in their nest was experimentally altered (Harper et al. 1994). In rosellas, seasonal increases in hatching asynchrony suggests that high quality females, or individuals breeding early in the season, benefit from increased synchrony of hatching. Early rosella broods, were often large, relatively synchronous, and appeared extremely healthy throughout the nestling period, suggesting that relative synchrony was advantageous for some individuals. Experimental manipulations of hatching asynchrony in crimson rosellas would be useful to determine the relative costs and benefits of hatching asynchrony in this species.

WHY ARE EQUAL GROWTH RATES RARE?

This study has shown that reduced growth and survival of last-hatched nestlings is not an unavoidable cost of hatching asynchrony, as suggested by several authors (Clark & Wilson 1981; Slagsvold 1985; Stoleson & Beissinger 1995; Nilsson & Svensson 1996). However, in most species, the costs of producing equal growth rates in asynchronous broods may be higher than the benefits. The major costs to parents of maintaining an equitable distribution of food are likely to be overriding competitive interactions between chicks (Amundsen & Stokland 1988; Stoleson & Beissinger 1995). Mock (1985) proposed that levels of sibling competition within broods are determined by the extent to which food deliveries can be monopolised by a single chick. Crimson rosellas may have lower levels of sibling competition within broods because parents distribute food through many small regurgitations over a single visit, making it difficult and perhaps costly for one chick to monopolise food. In addition, feeding visits to the brood were infrequent and load sizes were large (up to 25% of adult body weight; unpublished data), which should satiate chicks of high competitive ability, and produce a more equitable distribution of food (Forbes 1993).

Another way parents can directly overcome differences in the competitive abilities of chicks is by selectively feeding small or underweight individuals. This behaviour has been observed in another species of parrot, the budgerigar, where selective feeding produced equal growth rates of nestlings in captivity (Stamps et al. 1985). Selective feeding however, reduced the efficiency with which food was distributed and so may be costly to parents (Stamps et al. 1985). Although reduced feeding efficiency may restrict the extent of selective feeding in species with high delivery rates, the costs should be relatively low in rosellas due to infrequent food deliveries. Thus rosellas may be able to use selective feeding of last-hatched nestlings to maintain equal growth. If there are competitive differences between male and female nestlings in broods, the costs and benefits of selective feeding to parents may also differ between the sexes within a brood.

Equal growth rates are not characteristic of parrots as a group (Table 5), but several aspects of their breeding biology may allow the evolution of more complex food allocation within the brood. Parrots have long nestling periods for their body size, twice that of Columbiformes, and 60% higher than Falconiformes (Saunders, Smith & Campbell 1984) probably because of reduced predation pressure during the nestling stage as hole nesters (Lack 1968). Chick ages at fledging are highly variable in rosellas and other species of parrots and fledging can be very asynchronous (Krebs unpublished; Rowley 1990; Rowley & Chapman 1991; Waltman & Beissinger 1992). In addition, post-fledging survival in parrots does not appear to be strongly dependent on size or condition of nestlings at fledging (Smith 1991; Rowley & Chapman 1991; Stoleson & Beissinger 1997; this study). These traits may allow parents to engage in provisioning behaviours that potentially reduce the growth of all members of the brood but maximise the number of nestlings produced.

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Chapter 4

Complex patterns of food allocation in asynchronously hatching broods of crimson rosellas

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RUNNING HEAD: Krebs et al.: Complex food allocation in rosellas

Complex patterns of food allocation in asynchronously hatching broods of crimson rosellas

ABSTRACT

In birds, asynchronous hatching typically leads to lower growth and survival of last-hatched chicks. However, the growth of crimson rosella, *Platycercus elegans,* chicks is equal, although first-hatched chicks can be as much as seven times heavier than last-hatched chicks at the end of hatching. I examined the delivery and distribution of food to 18 rosella broods by videotaping feeds and simultaneously recording mass changes in the nestbox using a digital balance. Parents visited the nest infrequently and delivered loads of up to 25% of their body weight during a feeding visit. Male rosellas consistently delivered larger loads and consequently had higher feeding rates (g/h) than females. Parents distributed food between chicks by direct regurgitation in a series of up to 52 food transfers. Overall, chicks of all hatching ranks received equal numbers of transfers, but parents differed in how they distributed food within the brood. Males fed first-hatched chicks more than last-hatched chicks, whereas females distributed food equally to all chicks. Selective feeding of small chicks might be costly to females since they delivered food more slowly than males and spent more time in the nestbox. Thus female rosellas may invest more in current reproduction than males. Parents also distributed food differently to male and female chicks. Large males were fed more than all other nestlings, while female nestlings were fed equally irrespective of size. This study confirms that complex patterns of parental allocation occur in wild populations.

INTRODUCTION

Competition for food within broods of nestling birds is ubiquitous, and ranges in severity from siblicide in some species (Fujioka 1985, Drummond et al. 1986, Mock 1987; Bryant & Tatner 1990) to intensive begging behaviours and scramble competition in most (Bengtson & Ryden 1981, 1983; Harper 1986; Redondo & Castro 1992). In most species parents distribute food by feeding the closer or more responsive chick (Teather 1992; McRae et al. 1993; Kilner 1995; Leonard & Horn 1996; Ostreiher 1997). This behaviour tends to favour larger chicks, since they can compete for superior feeding positions and solicit more vigorously. For example, in red-winged blackbirds, *Agelaius phoeniceus*, chicks that were first offered food were closer to the parent, reached higher and begged sooner than those not offered food (Teather 1992). Thus by simply distributing food to predictable locations, parents passively create a feeding hierarchy within the brood.

Whether distributing food based on the outcome of competitive interactions between young is congruent with parental interests, chick interests or both is unclear. Parents should favour an even distribution of food if young benefit equally from a unit of parental investment (Clutton Brock 1991). However feeding the largest nestling may maximize the number of surviving young if food is limited (Lack 1947). If young behave more selfishly than is optimal for parents, conflict between parents and offspring as well as competition between nestlings over the distribution of food may occur (Trivers 1974).

Competition among nestlings can be costly for parents. Higher levels of fighting and scramble competition can increase the brood's food consumption (Mock & Ploger 1987; Wiebe & Bortolotti 1994). In addition, begging can increase both the risk of predation (Haskell 1994; Leech & Leonard 1997), and the energetic costs of nestlings (Leech & Leonard 1996; McCarty 1996). Competitive interactions within the nest may also restrict the ability of parents to distribute food to all chicks in a brood, leading to poor growth and survival of small or later hatched chicks even when food is abundant (e.g. Bryant 1978; Slagsvold 1986; Lessells & Avery 1989; Stoleson & Beissinger 1997).

The costs of chick competition to parents, and the benefits of competitive behaviours to chicks, should be reduced if parents are able to control the distribution of food. However, parental control has been shown in remarkably few studies. Partly this is because, in nonexperimental studies, it is difficult to infer parental control over the distribution of food when large chicks are fed most, since these chicks are also favoured in competitive interactions. By contrast, it is difficult to envisage sibling competition leading to high feeding rates for the smallest chick within broods. Thus for nonexperimental studies, only high feeding rates to small chicks suggest that parents are able to control the distribution of food.

Selective feeding of nestlings of low competitive ability has been described in one species in captivity (budgerigars, *Melopsittacus undulatus* : Stamps et al. 1985), one species in the wild (tree swallows, *Tachycineta bicolor*: Leonard & Horn 1996) and in two other species only when food was abundant (pied flycatchers, *Ficedula hypoleuca:* :Gottlander 1987; white-winged choughs, *Corcorax melanorhamphos* : Boland et al. 1997). The rarity of selective feeding across species could reflect higher costs to parents relative to benefits. Although parents can benefit from feeding smaller, less competitive chicks by increasing their quality and probably survival, choosing a particular nestling to feed may increase the time and energy required to distribute food within the brood (Stamps et al. 1985; Gottlander 1987).

Selective feeding of small chicks is not only rarely observed, but rarely observed in male parents (see Westneat et al. 1995 for an example). This suggests that the sexes can differ in their desired distributions of food. Sexual differences in food allocation may arise if the benefits of feeding individual chicks differs for males and females. For example, males could vary their feeding to nestlings based on the probability of paternity, whereas females who are equally related to all offspring will not (Westneat & Sherman 1993). Higher rates of female mortality may lead females to invest more in current reproduction, making them more willing to pay the costs associated with preferential feeding (Slagsvold et al. 1995). Alternatively, if parents differ predictably in food delivery rates, sexual differences in feeding patterns could be a consequence of sibling competition and be driven solely by differences in chick behaviour (Slagsvold 1997).

In this study, I examined the patterns of food delivery and allocation within wild broods of an Australian parrot, the crimson rosella, *Platycercus elegans*. Crimson rosella broods hatch highly asynchronously which results in large size asymmetries within the brood for most of the nestling period and first-hatched nestlings can be seven times heavier than last-hatched young at the end of hatching. Despite initial size disparities, all nestlings have equal growth rates and fledge at similar sizes (Chapter 3), suggesting that the distribution of food within rosella broods is not based on competitive interactions between nestlings. In addition male nestlings are 10% heavier at fledging than females, suggesting they may have higher energy requirements. I examined food allocation within broods and ask: (1) does nestling size or hatching rank affect food allocation? (2) does the distribution of food differ for different sex nestlings?, (3) do male and female parents differ in how they distribute food within the brood?

METHODS

Species and General Methods

Crimson rosellas *Platycercus elegans*, are a broad-tailed parrot (140g) which commonly breeds in eastern Australia. The sexes have similar plumage, but males are about 15% larger than females and have slightly broader bills (E. Krebs unpublished data). Rosellas breed in socially monogamous pairs (Forshaw 1981). The female incubates the eggs and broods small nestlings and the male feeds her until the youngest chick is approximately 5 days old at which point both parents directly feed the young. Crimson Rosellas are typically single-brooded and lay from three to eight eggs (mean ± SE = 5.3 ± 0.1, N = 71 broods). Females usually lay eggs at 2 day intervals and initiate incubation in the middle of the laying sequence so that broods hatch asynchronously over 1.5 to 7 days (mean ± SE = 3.6 ± 0.2, N = 46). Rosella chicks fledge approximately 35 days after hatching. Broods can fledge asynchronously over several days, although it was not possible to obtain detailed information on fledging intervals.

In 1993 and 1994, I placed a total of 46 nestboxes in dry sclerophyll eucalypt forest (*Eucalyptus rossi, E. macrorhyncha*) in Black Mountain Nature Reserve, Canberra, Australia. Nestboxes were spaced 50 m apart in a grid system and mounted approximately 4 m above the ground. Each box had a hinged lid, and was fitted with a removable nest floor supported by wooden blocks. The nest floor could be accessed by a small door on the front of the box. Eighty percent of all boxes were occupied by rosellas in each year, although high levels of egg destruction by conspecifics meant that not all birds successfully raised chicks.

Nestboxes were inspected at least weekly during the laying period. In most cases, I visited boxes daily during the predicted hatching period until all nestlings had hatched. Where the order of hatching was observed directly I assigned a hatching order to each chick (first, second, etc.) and a hatching time to the nearest 0.5 day, based on the dryness of a chick's down and its crop contents. When more than one chick hatched on the same day, hatch time was assigned based on a combination of wing chord and dryness of the down. If chicks were so similar in size that it was unclear which chick had hatched first, I assigned tied hatching ranks. In broods where several chicks had already hatched, chicks were assigned ranks retrospectively using a regression of wing chord on age for all chicks of known hatching times. These broods were never more than 4 days old, and I never noted rank reversals early in the nestling period.

All newly hatched chicks were marked by trimming the down on different parts of the body, and older chicks were marked with a single colour band to allow individual recognition. Nestlings were weighed to the nearest 0.1 g at hatching and subsequently to the nearest 1 g using Pesola spring balances.

Sexing nestlings

Nestlings were difficult to sex because size differences become most apparent late in the nestling period and because mass and size measurements are overlapping for the sexes across broods. Therefore, to assign sex unambiguously to all nestlings, I took a 100-µL blood sample from the brachial vein of each chick at least 15 days after hatching, extracted the DNA and used a PCR based sex-specific genetic marker to identify male and female nestlings (see Griffiths et al. 1998, for details of the method).

Feeding Observations

I examined parental feeding behaviour in 18 rosellas broods, nine in 1994 and nine in 1995. Crimson rosellas eat a wide variety of seeds, buds, fruits and some insects (Magrath & Lill 1983) which they collect in their crop. Parents feed chicks by directly regurgitating seeds into their mouths in a series of food transfers. This presents two difficulties for quantifying the distribution of food within the brood. First, the number of food transfers by a parent to each chick on each feeding visit needs to be quantified. To do this, I used a miniature black and white CCD video camera with infrared illumination to videotape feeding visits(Oatley Electronics, NSW) attached to the lid of the nestbox. The output was recorded on to a portable video recorder (Sony VideoWalkman GVS50) located on the ground below the nestbox. Chicks were marked with a unique number of black paint spots (nontoxic tempera paint) to allow individual recognition.

Although the number of transfers indicates the relative distribution of food to chicks during each feeding visit, a second difficulty is that the amount of food delivered by parents also varies between visits and nests. Therefore, I needed to quantify the mass of food delivered to the nest during each visit. To do this, I simultaneously recorded mass changes in the nestbox by placing a portable digital balance (Sartorius PT6) under the false nest floor. Output from the balance was monitored by a portable computer (Zenith Supersport 286) running specially designed software (NestBug; Szep et al. 1995). This software continuously recorded any mass changes (feeding deliveries) within the nestbox over the day.

To standardize between broods with varying hatching asynchrony, I monitored broods based on the age of last-hatched chicks. This meant that mean brood age would increase with hatching asynchrony, but ensured that food allocation to the last-hatched, and least competitive, chick was not confounded by age differences between broods. Monitoring protocol differed somewhat between the two years. In 1994, I monitored broods at 8, 15, and 22 days after the last chick hatched. Mass changes in each nestbox were recorded for approximately 12 h, from 0630 to 1830 hours. Broods were videotaped for the first and last 3h of the day, for a total of 6h. In 1995, because of an ongoing experiment, I monitored broods only 8 and 15 days after the last chick hatched. I recorded mass changes and videotaped broods for 6 hours continuously starting between 0900 and 1000 hours. Both these protocols allowed four to eight feeding visits over the day to be examined in detail.

All chicks were weighed at the beginning and end of each monitoring session. In most cases, I set up equipment and weighed and marked chicks before parents returned for the first morning feed, in order to minimize disturbance to the parents. Parents did not appear to be deterred from visiting the nestbox by the appearance of monitoring equipment and entered and fed chicks 5 - 15 min after arriving back at the box.

Analysis

Mass data

The computer recorded an event as occurring when the mass from the digital balance changed more than 75 g. This value was chosen to maximise the probability of detecting a parental visit and to minimise the probability of nestling movements triggering a false visit. Data recorded from the digital balance consists of a series of masses (up to 120 readings) that were saved before and after adults entered or left the box. These raw data files were edited for consistency and two types of anomalous readings were removed: (1) extremely brief visits (< 10 s) resulting in very short weighing series; and (2) highly variable, rapidly repeated measurements that occurred when a parent was only partially standing on the nest floor. The edited files were summarized using NestBug Visit Analyser Software (Szep et al. 1995), which calculated mean masses and excluded outliers (any points changing the mean more than 0.1 g). Parental masses on entering the nestbox were calculated by subtracting the nest mass just prior to a feeding visit from the total mass in the box during a visit. Similarly, parental masses on leaving the box were calculated by subtracting the total mass in the box just prior to a parent leaving from the nest mass after leaving. Load size was estimated by subtracting the parent's mass on entering the nestbox from its mass on leaving. Occasionally, especially in boxes with older broods, parents would enter the box and feed chicks standing on an internal wire ladder, and only intermittently touch the nest floor. Feeds from the ladder produced short and unreliable weighing sequences and were used only to record the time of the feeding visit.

Video analysis

To analyse each videotaped feed I used a desktop video player (Sony E6500) that allowed slow motion and frame by frame playback. The sex of the parent entering the box was identified by bill morphology and pair specific plumage differences or the presence of leg bands. I recorded the time of day, the length of a feed, and the number and sequence of food transfers to each chick. The proportion of food transfers to each chick correlated strongly to its mass gain over the day (ln(proportion food transfers) over 6h versus mass gain over that period, controlling for variance between boxes and brood ages; deviance $\chi^2_1 = 21.1$, $P < 0.0001$). Therefore I have assumed that all food transfers are equal in size both between chicks and over the entire sequence of a feed. Although I have no way of testing this assumption directly, all bill contacts, even those at the end of a feeding bout appeared to involve at least some food transfer.

Statistics

To examine the overall patterns of feeding by parents I used the following dependent variables: the number of feeding visits (number of visits / h, visit rate), food delivered per feed (g, load size), and the total feeding rate (g delivered / h, feeding rate). To assess how food was distributed within the brood, I examined the number of transfers obtained by each chick during a feeding visit. The number of transfers was square-root transformed to satisfy the distributional and variance assumptions of subsequent modelling.

I fitted separate models for each dependent variable and examined the effect of seven explanatory variables: year, brood age (days after the last chick hatched), brood size, total hatching asynchrony (in days), sex of feeder, chick sex and chick hatching rank. To examine the effect of hatching order in broods of differing sizes, I grouped chicks as first-, middle- and last-hatched for each brood. Consequently, there were more middle-hatched chicks than first or last for broods with more than three chicks. Size hierarchies based on hatching order were stable at each brood age measured, especially for tibia length and feather development. Weight hierarchies were sometimes reversed at 22 days between first- and middle-hatched chicks because females are lighter at fledging than males, but this never occurred for last-hatched chicks, regardless of sex. Thus hatching order categories were affected by the distribution of each sex and the total hatching asynchrony of the brood, however I have controlled for this variation between broods using multivariate statistics.

Although the unit of replication in this study was the nestbox, I were interested in differences in food distribution between chicks of different hatching ranks across nestboxes. Analysing this statistically therefore requires models appropriate for multilevel data. Since the data were unbalanced, and therefore unsuitable for conventional 'analysis of variance' (and particularly repeated measures designs), I used a general procedure for estimation (Restricted maximum likelihood, REML) of mixed models incorporating random and fixed effects.

I fitted a fixed model by initially including all appropriate explanatory variables and two-way interactions. Nestbox was included in models as a random term, except in the modelling of food transfers to individual chicks, where nestbox, brood age, and feeding visit were included as additional random terms, and excluded as response variables. Terms were dropped from the full model in a stepwise procedure by assessing the change-in-deviance between the full model and the sub-model, which is approximated by a Chi-square distribution, (GENSTAT 5 Commitee 1993). Any significant terms were included in subsequent model fitting. The final model was selected by sequentially dropping nonsignificant interactions and then nonsignificant main effects, until only significant terms remained. To avoid any confounding order effects, any term that was close to significant ($P < 0.20$) was re-evaluated by adding and dropping it from the final model.

To compare the predictability with which chicks obtained food transfers during feeds, I used a mixed model to examine random effects. Brood size, chick rank, parental sex and load size were included as fixed effects, and box, chick, brood age and feed were included as random terms. The fitted random model provided estimates of variance in numbers of food transfers for chicks for all combinations of random terms within the model. This allowed variance to be quantified at several different levels.

For analyses that did not require a mixed model, I used least squares statistics. In all analyses, residual plots and normal probability plots were examined for unequal variances and deviations from normality and transformations applied if necessary. I report main effects or interaction terms from a model where they are significant, a statistical trend ($0.05 < P < 0.10$), or of particular biological relevance. Means and standard errors are reported throughout unless otherwise indicated.

RESULTS

Patterns of Food Delivery

Males and females did not differ in the number of visits they made to the nestbox ($\chi^2_1 = 1.0$, $P > 0.25$), and in 63% of visits both parents entered the box within 10 min of each other. In total, pairs of rosellas made 0.75 ± 0.03 feeding visits / h to the nestbox. The number of visits varied with brood age and decreased when the brood was 22 days old ($\chi^2_2 = 6.6$, $P < 0.02$; Fig. 1). However, the number of visits did not increase with brood size ($\chi^2_1 = 1.7$, $P > 0.10$) or total hatching asynchrony ($\chi^2_1 = 0.0$, $P > 0.90$).

Males delivered larger loads of food to the nestbox than females (males = 10.9 ± 0.7 g, N (number of measured loads) = 89, females = 9.0 ± 0.6 g, N = 74 ; $\chi^2_1 = 4.7$, $P < 0.05$). However, since males are larger than females, loads as a proportion of body mass did not vary between the sexes (males = 0.082 ± 0.007, females = 0.077 ± 0.004; Paired t test: $t_{16} = 0.6$, $P = 0.53$). Load sizes varied between 1 and 32 g of food during a feeding visit. Load sizes did not differ between brood ages ($\chi^2_2 = 1.5$, $P > 0.25$), or brood sizes ($\chi^2_1 = 0.5$, $P > 0.25$), but increased with total hatching asynchrony ($\chi^2_1 = 6.2$, $P < 0.02$; Fig. 2).

Male rosellas fed broods at a higher rate than females ($\chi^2_1 = 6.8$, $P < 0.01$; Fig. 3). Combined pair feeding rates to the brood ranged between 3.6 and 14.3 g/h (mean = 8.4 ± 0.4 g/h, N=38). Feeding rates varied with brood age and were lowest when the brood was 22 days old ($\chi^2_2 = 8.7$, $P < 0.02$; Fig. 3) and increased with brood size ($\chi^2_1 = 6.1$, $P < 0.02$; Fig. 4a; b; c), but not hatching asynchrony ($\chi^2_1 = 1.2$, $P > 0.25$).

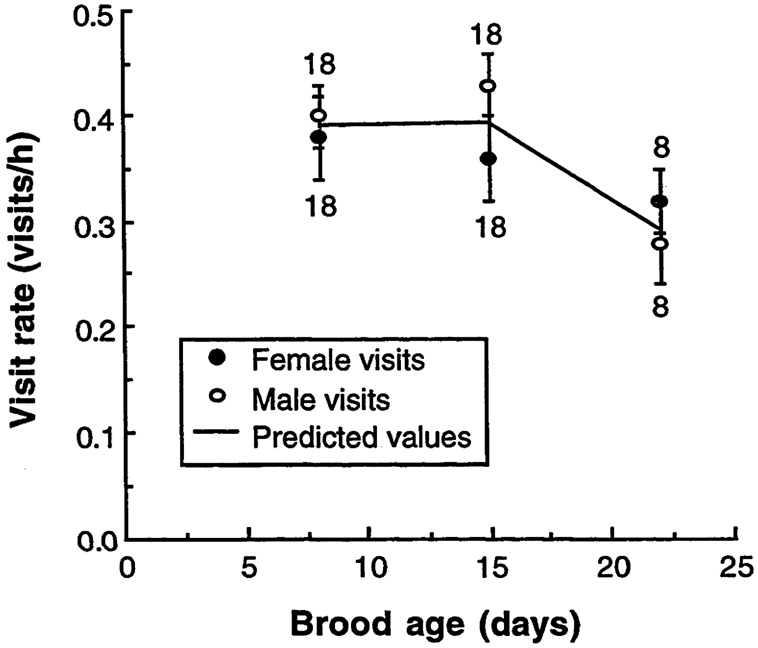


Figure 1. Number of feeding visits to the nestbox by male and female rosellas measured at three brood ages (see Methods). The line represents predicted values from the fitted model, and points represent the mean and standard error for the data in each category. The number of broods in each category is indicated over each point for males or under each point for females. There were no significant differences between the sexes (see text).

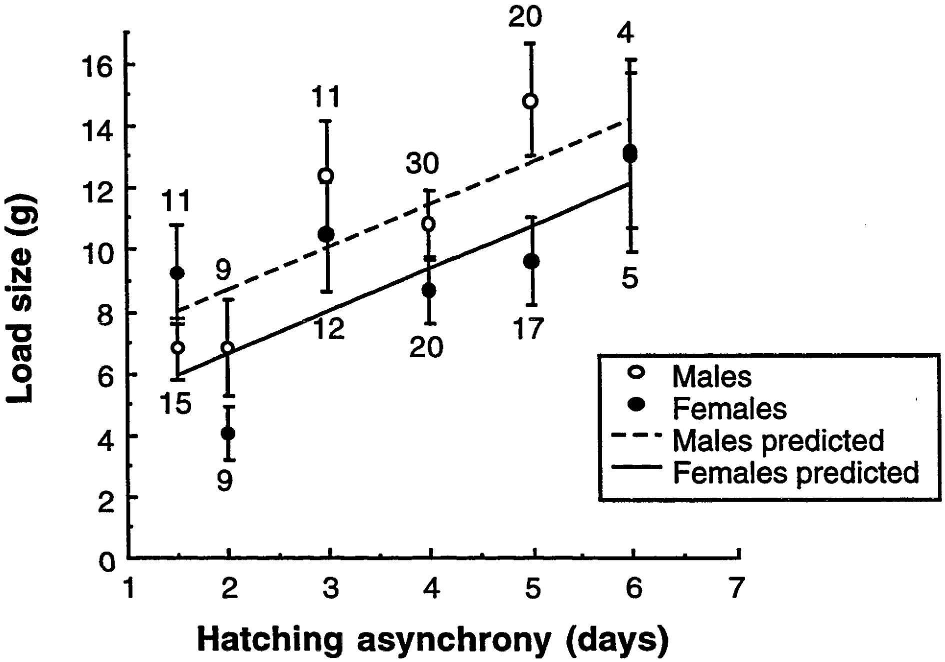


Figure 2. The relationship between load size delivered and hatching asynchrony of the brood for male and female rosellas. The lines represent predicted values from the fitted model for males and female, and points represent the mean and standard error for data in each category. The number of loads measured are indicated above each point for males and below each point for females.

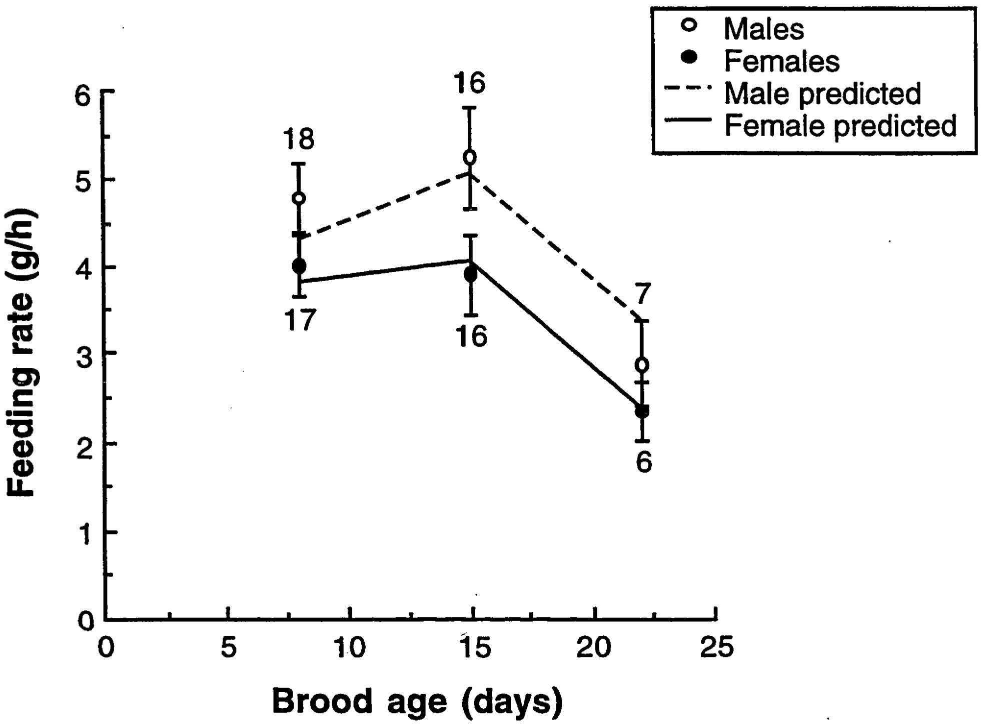
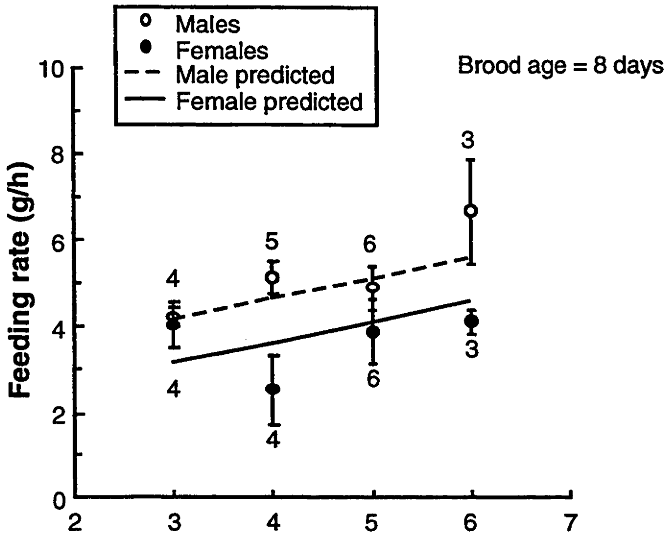


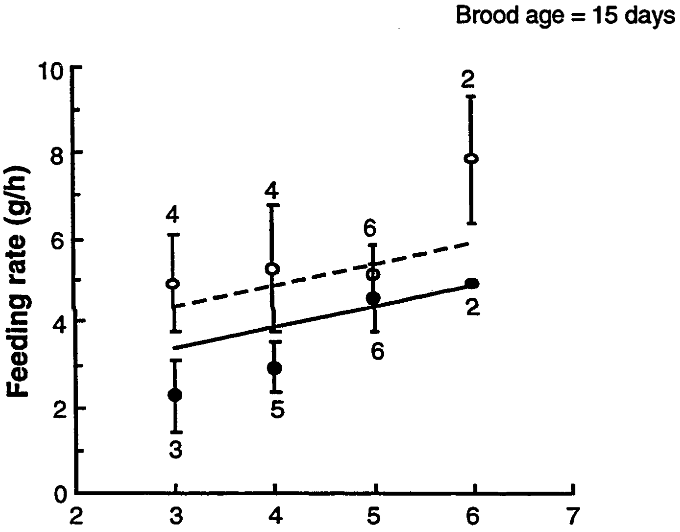
Figure 3. Male and female feeding rates to the brood measured at three brood ages. The lines represent predicted values for males and females from the fitted model and points represent the mean and standard error for data in each category. The number of broods measured are indicated above each point for males and below each point for females.

Figure 4. The relationship between feeding rate by males and females and brood size presented separately for brood ages: (a) 8 days, (b) 15 days, and (c) 22 days. The lines represent predicted values for each sex from the fitted model and points represent the mean and standard error of the data in each category. The number of broods in each category are indicated above each point for males and below each point for females.

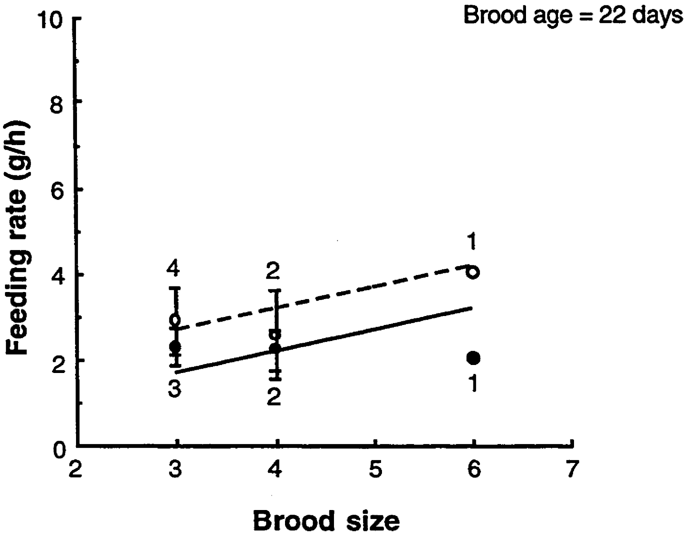
(a)


Males
Females
Male predicted
Female predicted
Brood age = 8 days
Feeding rate (g/h)
0
2
4
6
8
10
2
3
4
5
6
7
4
5
6
3
4
4
6
3

(b)


Brood age = 15 days
Feeding rate (g/h)
0
2
4
6
8
10
2
3
4
5
6
7
4
4
6
2
3
5
6
2

(c)


Brood age = 22 days
Feeding rate (g/h)
Brood size
0
2
4
6
8
10
2
3
4
5
6
7
4
2
1
3
2
1

No aspect of food delivery differed between the two years of the study (number of feeding visits: $\chi^2_1 = 2.4$, $P > 0.10$; load sizes: $\chi^2_1 = 0.1$, $P > 0.50$; and feeding rates: $\chi^2_1 = 0.6$, $P > 0.25$).

Distribution within the Brood

The number of food transfers distributed by parents during a feeding visit, varied between 2 and 51 (mean = 15 ± 0.6, N = 201) and increased with the load size delivered ($\chi^2_1 = 45.6$, $P < 0.001$). Overall, chicks of each hatching rank obtained an equal number of transfers ($\chi^2_2 = 4.4$, $P > 0.10$). Even in broods with high hatching asynchrony, last-hatched chicks did not receive fewer transfers (Hatching asynchrony * chick rank interaction: $\chi^2_2 = 1.6$, $P > 0.25$). However, parents differed in their distribution of food to chicks of differing ranks. Male rosellas distributed significantly more transfers to first-hatched chicks whereas females distributed equal number of transfers to first-, middle- and last-hatched chicks in the brood (sex * chick rank interaction: $\chi^2_3 = 10.8$, $P < 0.005$; Fig. 5a, b). Since there were no statistically significant differences in the number of transfers received by different chicks, male and female food distributions must partially complement each other (Fig. 5a, b).

The number of food transfers received by male and female nestlings differed according to hatching rank. First-hatched male chicks obtained more transfers than female chicks of all ranks, and middle- and last-hatched male chicks (chick sex * rank interaction: $\chi^2_2 = 8.9$, $P<0.02$; Fig. 6). Sex differences in parental food distribution and sex differences in food obtained by chicks implies that male parents fed early-hatched male nestlings more than other nestlings, however this three-way interaction was not statistically significant (parental sex * chick sex * rank interaction: $\chi^2_2 = 1.9$, $P > 0.25$; Figs 5, 6).

Male rosellas distributed food more quickly than females, spending significantly less time per food transfer (males = 9.7 ± 0.6 s/transfer, females = 11.3 ± 0.8 s/transfer; Paired t test: $t_{17} = 2.2$, $P = 0.04$). In addition, females spent more time in the nestbox before and/or after feeds, whereas males only rarely remained in the nestbox longer than necessary to feed chicks (proportion of visits lasting more than one minute longer than

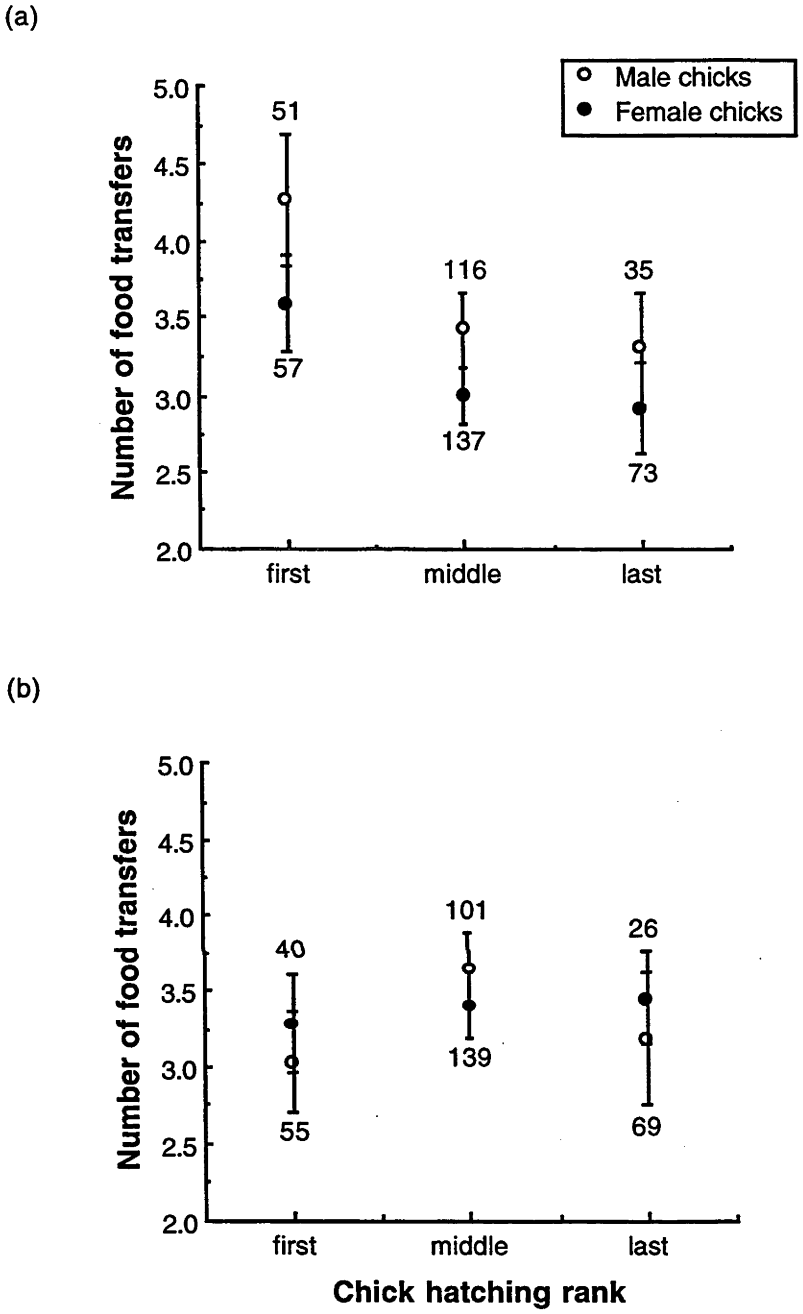


Figure 5. The number of transfers distributed to first, middle and last-hatched chicks plotted separately for (a) male and (b) female feeding visits. Dots represent the mean number of food transfers (± SE) for male and female chicks in each category calculated across all brood ages. The number of feeding bouts (food transfers / chick / feeding visit) for chicks in each category are indicated above each point for males and below each point for females.

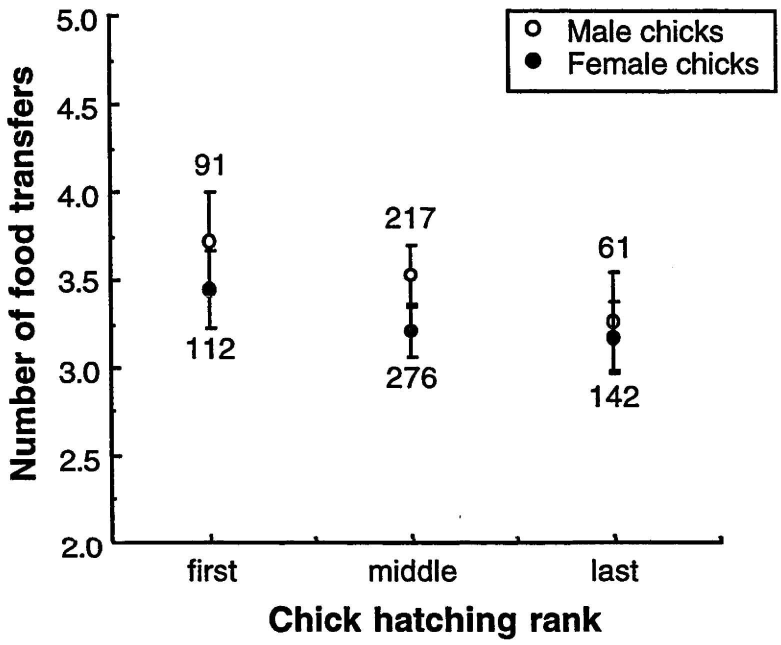


Figure 6. The number of food transfers distributed to first middle and last hatched chicks. Dots represent the mean number of food transfers (± SE) and for male and female chicks in each category calculated across all brood ages. The number of feeding bouts (food transfers / chick / feeding visit) in each category are indicated above each point for males and below each point for females.

the time spent feeding: males = 3% (1/34); females = 46% (13/28); $\chi^2_1 = 11.6$, $P < 0.001$)

If females distributed food equally by allocating a fixed number of transfers to each chick and males distributed food unequally, possibly to the hungriest chicks, the variance in numbers of food transfers should differ between the sexes. Female feeds should have lower variance than males, regardless of the total number of food transfers during a feed. This prediction was not supported, variances in female and male transfers to chicks over all feeds were equal (estimated variance in numbers of transfers to individual chicks for all feeds; females = 0.39 ± 0.03; males = 0.42 ± 0.03).

When food is distributed preferentially to the largest chicks in a brood, the mean number of transfers might not vary between chicks when food is abundant. However, if first-hatched chicks have first access to food, their food intake should vary less than that of last-hatched chicks. Alternatively, if competitive interactions do not determine access to food, variance in the number of food transfers to a chick should not differ between first and last-hatched chicks. The latter pattern was supported in rosella chicks (mean variance in number of transfers/chick/feeding visit, for all brood ages combined: first-hatched = 6.1 ± 3.9; last-hatched = 5.8 ± 4.4; Paired t test: $t_{17} = 0.32$, $P = 0.75$). In addition, if the distribution of food within a brood is predictable and a particular chick (i.e. the largest chick) consistently dominates feeds, the variance in food transfers should be high between individual chicks and lower between feeding visits. By contrast, the variance in average food transfers between individual chicks was much lower than the variance in transfers between different feeds in rosellas (Table 1).

Table 1. Variance in the numbers of food transfers / chick / feeding visit grouped by nestbox, individual chick, brood age (8, 15 and 22 days after the last chick hatched) and feeding visits. Variance estimates would be expected to decrease at lower scales (i.e. variance between nestboxes higher than variance between chicks), however, variance between individual chicks (b) and chicks at different brood ages (d) is lower than expected. This suggests that variation in the number of food transfers is more homogeneous than expected between individual chicks.

Level examined	Variance in numbers of food transfers	SE of estimate
(a) All nestboxes	2.56	0.03
(b) Individual chicks	0.33	0.01
(c) Brood ages	0.96	0.02
(d) Chicks at each brood age	0.27	0.01
(e) Feed at each brood age	0.71	0.02
(f) Individual chicks during feeds	0.43	0.03

DISCUSSION

Crimson rosellas chicks hatched asynchronously over 2 to 7 days, leading to large size differences within broods (Chapter 3). Despite these size disparities, chicks of all hatching ranks grew equally well, in contrast to the rank-related growth rates observed in most asynchronously hatching species (Slagsvold 1986; Mock & Ploger 1987; Lessells & Avery 1989; Bryant & Tatner 1990; Heinsohn 1995; Ostreiher 1997; Stoleson & Beissinger 1997). As these patterns of growth predict, nestling rosellas obtained equal numbers of food transfers during feeding visits, and the variance in numbers of food transfers suggested that no nestling consistently dominated feeds. However, the equality in food allocation was achieved through a complex pattern of food distribution by parents. Male and female parents distributed food differently based on hatching rank and nestling sex, demonstrating that overall patterns of food delivery reveal surprisingly little about the patterns or mechanisms of food allocation within the brood.

Patterns of Food Delivery

Loads delivered to crimson rosella broods were variable in size and parents were capable of bringing loads up to 25% of their body mass in a single visit. Male rosellas brought larger loads and delivered more food to the brood at all ages than females. Higher feeding rates by males are rarely observed in socially monogamous species (Clutton Brock 1991) and male feeding rates were much lower than female rates in budgerigars (Stamps et al. 1987). Male and female rosellas, like many parrots, maintain year round, relatively stable pair bonds where males invest heavily in breeding by provisioning the female prior to egg laying, and throughout incubation until they feed chicks directly. Higher male feeding rates, however, probably do not represent greater parental effort by male rosellas because the loads delivered were proportional to body size for both sexes, and females also incurred the costs of egg laying (Heaney & Monaghan 1995) and incubation (Heaney & Monaghan 1996).

Patterns of food allocation within rosella broods suggest that despite large size and age asymmetries within nests, large chicks do not monopolise food at the expense of smaller chicks. Parents could achieve an equitable distribution of food within the nest either by altering the patterns of food delivery to the nest, or directly by controlling which chick obtains food during a feeding visit. Forbes (1993) argued parents could reduce sibling competition within the brood by clumping the temporal spacing of feeding visits. This should satiate large chicks and increase the amount of food that is distributed to smaller chicks. However, rosellas do not appear to use this mechanism to regulate the distribution of food. Food transfers in rosellas are not distributed in an orderly fashion based on nestling rank and large chicks do not receive first access to food (E. Krebs, unpublished data). In addition, the proportion of temporally clumped feeds in a nestbox tended to be negatively correlated with the level of hatching asynchrony in a brood (proportion of feeds within 10 min versus total hatching asynchrony/brood size: $F_{16,1} = 3.2$, $P = 0.09$). Thus feeding visits were more clumped at relatively synchronous nests.

A second way that rosella parents could structure feeds to reduce competitive asymmetries is by feeding infrequently, but distributing large amounts of food. In this study, overall feeding rates increased with brood size, but the amount of food delivered at each feeding visit increased more strongly with the degree of hatching asynchrony (see Fig. 2). This suggests that parents delivered larger loads to broods with large size asymmetries possibly to ensure that small chicks were fed. Mock (1985) first proposed that the ability of young to monopolize prey would affect the degree of sibling competition. In great blue herons, *Ardea herodias*, broods fed on fish too large for an individual to swallow, were less aggressive than broods fed on small, easily swallowed fish (Mock 1985). Although rosellas cannot alter prey sizes, load sizes were strongly correlated with the number of food transfers during a feeding visit and larger loads would allow parents to increase of the number of transfers within a feed. If large numbers of food transfers increase the cost of monopolizing food for chicks, larger loads should produce a more equitable distribution of food than smaller loads.

Distribution within the Brood

Why do males and females distribute food differently?

In this study, male crimson rosellas distributed food unequally within the brood and fed large chicks more than small chicks. Rosella chicks begged for food and attempted to position themselves near to a parent's beak. Since large chicks have a competitive advantage during scramble competition, food allocation favouring large chicks could occur as a result of sibling competition. Many studies have found that chicks of high competitive ability are more successful in obtaining food than chicks of low ability (Bengtsson & Ryden 1983; Teather 1992; Price & Ydenberg 1995). Furthermore, experiments have shown that distribution of food within the nests is controlled by chick interactions and not parental preferences in several species: starlings, *Sturnus vulgaris* (Kacelnik et al. 1995), canaries, *Serinus canarius* (Kilner 1995), and Arabian babblers, *Turdoides squamiceps* (Ostreiher 1997). Alternatively, large chicks obtain more food in some species because parents are more responsive to begging of large chicks (blue-footed boobies, *Sula nebouxii*: Drummond et al. 1986; black-legged kittiwakes, *Rissa tridactyla*: Braun & Hunt 1983; yellow-headed blackbirds, *Xanthocephalus xanthocephalus*: Price & Ydenberg 1995). Thus, feeding patterns by male crimson rosellas are consistent either with food distribution based on the outcome of competition between chicks, or selective feeding of large chicks.

In contrast to the hierarchical distribution of food to the brood by males, female crimson rosellas distributed food equally and fed all chicks irrespective of their size. Sex differences in nestling food allocation have been observed in several species: budgerigars (Stamps et al. 1985); pied flycatchers (Gottlander 1987); red winged blackbirds (Westneat et al. 1995; and tree swallows (Leonard & Horn 1996). More often, only females are observed to distribute food to small or undersized nestlings (but see Westneat et al. 1995). Distributing food equally to nestlings in broods with a size hierarchy can occur only if females preferentially feed nestlings of low competitive ability, or allocate a fixed amount of food to each chick irrespective of competitive interactions. Distributing food in this way may reduce nestling competition by preventing selfish chicks from monopolizing food, and should increase the growth and survival of last-hatched chicks. However, if preferential feeding is costly to parents, parental survival, or the growth and survival of the whole brood could be reduced by redirecting resources to small nestlings when food is scarce. Consistent with this, preferential feeding of less competitive chicks was not observed when food was scarce in pied flycatchers and white-winged choughs (Gottlander 1987, Boland et al. 1997).

To date, there is little consensus as to why the sexes might distribute food differently to young (see Slagsvold 1997 for a review). Patterns of food distribution might differ between the sexes if the costs or benefits of feeding certain chicks were higher for males or females. Since distributing food selectively to chicks requires that adults discriminate between chicks and feed the appropriate individual, this style of feeding should be less efficient than feeding based on the outcome of competitive interactions. Selective feeding by female budgerigars is less efficient than nonselective feeding, females regurgitate food to young at half the rate of males (Stamps et al. 1985).

Female crimson rosellas were also less efficient at distributing food than males, spending 16% longer per food transfer. However, this difference is unlikely to add significantly to a female's energetic costs since it would increase the length of an average feed by only 23 s.

Differences in the sexes' ability to discriminate between nestlings might also increase the cost of selective feeding to one parent. In many species brooding is done only by females, allowing them to be better attuned to variation in offspring need than males (Gottlander 1987). Female rosellas spent more time in the nestbox than males, both brooding early in the nestling period and staying longer in the box during feeding visits. Whether this increased the female's ability to discriminate between chicks based on hunger or condition is unclear. However, it seems unlikely that the ability to discriminate between the sizes of nestlings differs between male and female crimson rosellas because the size asymmetries within broods are large, making the costs of discrimination low.

Preferential feeding by females may result from differences in the benefit males and females obtain by feeding chicks of poor competitive ability. Males may feed selectively if the probability of paternity decreased with the laying sequence (Gottlander 1987; Westneat & Sherman 1993). Although the relationship between laying sequence and extrapair paternity is unknown in rosellas, this explanation is unlikely. Extrapair paternity appears to be rare in rosellas (0%, N = 13 nestlings, 3 broods, E. Krebs unpublished data). Furthermore, no general pattern of paternity and laying sequence has been observed between species (Riley et al. 1995; Westneat et al. 1995).

If the survival of adult females is lower than that of males, females may invest more in current reproduction than males, and spend more energy to ensure that all nestlings are fed (Slagsvold et al. 1995). In birds, mortality is generally higher in females (Breitwisch 1989) and, in parrots, it is higher in females in Major Mitchell cockatoos, *Cacatua leadbeateri* (Rowley & Chapman 1991), white-tailed black cockatoos, *Calyptorhynchus funereus* (Saunders 1982), and green rumped parrotlets, *Forpus passerinus* (Stoleson & Beissinger 1997). Although mortality rates of adult male and female crimson rosellas are unknown, two observations suggest mortality was higher for females in the study population. First, incubating females were occasionally killed on the nest, and second, the adult sex ratio appeared to be male biased since first year females were frequently paired to older males.

Slagsvold (1997) has suggested that different allocation patterns by parents can arise through sibling competition alone. If parents differ predictably in the amount of food they deliver, and the position from which they feed, dominant chicks might attempt to be fed by the parent with the highest feeding rate. In rosellas, the largest chicks in the brood receive more transfers from males than other chicks and males fed at higher rates than females. However, several aspects of rosella breeding biology suggest that this pattern is not due to chick behaviour. Rosella parents feed infrequently, transfer food many times during a feed, move around the nestbox and refuse to feed certain chicks. Large rosella chicks could preferentially associate with male parents when parents feed simultaneously in the nestbox, but these feeds are uncommon.

Why do parents distribute food differently to male and female nestlings?

Rosellas also allocated food according to nestling sex. First- and middle-hatched male nestlings were fed more than last-hatched male and all female nestlings. Differential food allocation based on nestling sex could arise by active parental discrimination, or as a nonselected result of differences in nestling behaviour. To date, there is little evidence for active discrimination in favour of one sex in birds. Sex differences in nestling behaviour have been observed in several species. In budgerigars, female-biased broods begged at higher rates and are fed more than male-biased broods but within broods parents showed no preference for feeding male or female chicks (Stamps et al. 1985, 1987). Differences in male and female begging behaviours have been observed in several dimorphic species. For example, male nestlings beg more intensely than females in red-winged blackbirds (Teather 1992), and yellow-headed blackbirds (Price & Ydenberg 1995) and females beg more than males in American kestrels (Anderson et al. 1993). Furthermore, Price & Ydenberg (1995) observed that male yellow-headed blackbirds nestlings were more sensitive to changes in food delivery than females and escalated their begging rates more quickly after food deprivation. If sex differences in nestling behaviour are important in rosellas, male nestlings, especially first hatched nestlings, should beg more intensely within broods than female nestlings.

Increased food allocation to nestlings of the larger sex in dimorphic species could reflect higher energetic requirements rather than parental favouritism. Male energetic expenditure and food consumption is higher than for females in nestlings of two highly dimorphic species: great-tailed grackles, *Quiscalus mexicanus* (Teather 1987; Teather & Weatherhead 1988), and red-winged blackbirds (Fiala & Congdon 1983). Differences in energetic consumption however, may not be as great as body size differences would predict. For example, male great-tailed grackle nestlings which weigh 30% more than females consume only 15% more food (Teather 1987). Crimson rosellas have a relatively small size dimorphism, in this study males were only 10% larger than females at fledging, and size differences did not emerge until day 15. Nevertheless, assuming male and female rosellas have similar energetic efficiencies, males, at least late in the nestling period, should have higher energetic requirements than females. Thus, food allocation in crimson rosellas is consistent with increased male energetic requirements.

Does hatching asynchrony affect food distribution?

If competitive interactions within the brood allow large chicks to monopolize food, food distribution should be more skewed in broods with larger hatching intervals. This pattern has been observed in studies which have experimentally manipulated hatching asynchrony. Food is distributed relatively equally in synchronous cattle egret *Bubulcus ibis*, broods and very unequally in brood with double the normal degree of hatching asynchrony (Ploger & Mock 1986). Similarly, food in synchronous broods of blue-footed boobies is distributed much more equally than in asynchronous nests (Osorno & Drummond 1995). However, synchronised broods of both species fight at much higher rates than asynchronous broods, suggesting that synchronous hatching decreases the cost of a skewed food distribution at the expense of increasing the total levels of sibling competition within the brood.

Rosellas did not appear to manipulate the distribution of food within the brood by altering the degree of hatching asynchrony. Neither food distribution nor growth rates (Chapter 3) of chicks within rosella broods changed with increasing hatching asynchrony and food was evenly distributed to nestlings, even in broods with large size differences. The costs of large competitive asymmetries within the broods in rosellas was reduced by parents by altering the amount and the distribution of food within broods. Control over the distribution of food in rosella broods, may be facilitated by a feeding ecology which allows infrequent, but large feeds. Further work examining parental responses to chick solicitation at different hunger levels should clarify the extent to which food distribution is under chick or parental control, how chicks of different ranks respond to changes in food availability, and how the cues that male and female parents use to distribute food differ. More detailed studies of food distribution are needed in species like rosellas with large hatching asynchronies and infrequent food deliveries if we are to understand the costs and benefits of differing patterns of parental food allocation and how these constraints may differ between the sexes.

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Chapter 5

Mothers adaptively alter the distribution of food within broods of asynchronously hatching crimson rosellas

Mothers adaptively alter the distribution of food within broods of asynchronously hatching crimson rosellas

Abstract

Food allocation in many asynchronously hatching species favours large, competitively-superior chicks. In contrast, food is distributed equally within broods of crimson rosellas, implying that parents do not simply feed the most competitive chick. I used temporary chick removals to manipulate hunger of individual chicks or the whole brood. This allowed me to assess how mothers and fathers allocated food to hungry nestlings of different hatching ranks under differing levels of competition for food. When an individual chick within the brood was hungry, it obtained more food and had gained the same mass by the end of the day as during the control, irrespective of hatching rank. Mothers did not allocate food differently within the brood when an individual chick of either hatching rank was hungry, and were apparently able to control the distribution of food by refusing to feed first-hatched chicks when they were hungry and by moving more during feeds. In contrast, fathers only allocated more food to last-hatched chicks when an individual chick within the brood was hungry. When the whole brood was hungry, first-hatched chicks obtained more food relative to the control. This was because mothers preferentially fed first-hatched chicks when all chicks were hungry. Fathers fed all chicks equally in the control and brood removal treatments. Both parents responded to increased brood hunger by moving more between food transfers, but did not alter which chicks they refused to feed when the brood was hungry. The patterns of food allocation in rosellas suggest that both mothers and fathers were able to discriminate and selectively feed chicks, but that parents responded differently to chick hunger and levels of competition within the brood. Mothers appeared to regulate the distribution of food within crimson rosella broods, and skewed the allocation of food in a way consistent with a strategy of adaptive brood reduction.

Introduction

The growth of altricial nestlings is dependent not simply on the amount of food delivered to the brood by parents, but also how food is distributed within the brood. An equal distribution of food will maximise the growth of all young, but may depress the growth rate of the whole brood if feeding rates are low. On the other hand, an unequal distribution of food can maximise the quality of any young fledged, particularly if food is scarce, but can result in poor growth of some chicks even when feeding rates are high. Poor nestling growth is costly to parents since it can reduce nestling survival (Bryant and Tatner 1990; Wiebe 1996; Ostreiher 1997), and post-fledging survival (Perrins 1965; Nur 1984; Magrath 1991).

Despite the differing consequences of patterns of food distribution within the brood, parents typically exert little direct control, allowing competitive interactions between chicks to determine access to food. For example, parents often feed the chick who begs first or reaches higher (Smith and Montgomerie 1991; Teather 1992; Leonard and Horn 1996), or obtains a certain position within the nest (Gottlander 1987; McRae et al. 1993; Kacelnik et al. 1995; Kilner 1995).

Parents can indirectly control the distribution of food within the brood by hatching young asynchronously. Asynchronous hatching produces an age and size hierarchy within the brood which leads to competitive asymmetries between chicks. If parents in asynchronously hatching species, distribute food based on the outcome of chick interactions, food distribution favours larger early-hatched chicks (e.g. great tits *Parus major*, Bengtsson and Ryden 1983; cattle egrets *Bubulcus ibis*, Mock and Ploger 1987; blue-footed boobies *Sula nebouxii*, Osorno and Drummond 1995; and yellow-headed blackbirds *Xanthocephalus xanthocephalus*, Price and Ydenberg 1995).

Asynchronous hatching can benefit parents by increasing feeding efficiency (Hahn 1981; Stamps et al. 1985; Gottlander 1987) and by promoting efficient brood reduction when food is scarce (Lack 1947). Since the competitive asymmetries produced by hatching patterns determine access to food, small chicks will starve first and parents do not need to actively manipulate food distribution.

Hatching asynchrony can be costly to parents because competitive differences between nestlings may lead to large chicks monopolising more food than is optimal for parents (Mock and Parker 1997; Parker et al. 1989), and parents and offspring may disagree over the timing and extent of brood reduction (O'Conner 1978; Forbes 1993). Consistent with this prediction several studies have reported that last-hatched chicks have poor growth and survival, even when food is abundant (Bryant 1978; Werschkul 1979; Slagsvold 1982; Stoleson and Beissinger 1997).

By actively allocating food within the brood, parents can fine-tune or alter the distribution of food and minimise any costs associated with sibling competition. One way to fine-tune the distribution of food is by allocating food selectively to nestlings. Parents could ensure an equal distribution of food by selectively feeding last-hatched nestlings, or reinforce competitive disparities by selectively feeding first-hatched nestlings. Selective feeding of large nestlings is difficult to infer from observational data since these chicks can also compete more effectively for food. However, parents in some species appear to favour first-hatched chicks by being more responsive to their begging (e.g. black legged kittiwakes *Rissa tridactyla*, Braun and Hunt 1983; great tits, Bengtsson and Ryden 1983; yellow headed blackbirds, Price and Ydenberg 1995). Selective feeding of last-hatched nestlings has been described in several asynchronously hatching species: captive budgerigars (*Melopsittacus undulatus*, Stamps et al. 1985), pied flycatchers (*Ficedula hypoleuca,* Gottlander 1987), tree swallows (*Tachycineta bicolor*; Leonard and Horn 1996), red-winged blackbirds (*Agelaius phoeniceus* Westneat et al. 1995) and white-winged choughs (*Corcorax melanorhamphos*, Boland et al. 1997).

In the majority of cases only females are observed to selectively feed last-hatched chicks (but see Westneat et al. 1995). It is unclear whether females are more likely to engage in selective feeding because the costs, such as discriminating between nestlings, are relatively lower, or because the benefits from improved growth of last-hatched chicks are relatively greater (see Slagsvold 1997 for a review of hypotheses). Since females set the initial size disparities within the brood through incubation patterns (Magrath 1992) and can manipulate them depending on food availability in some species

(Wiebe and Bortolotti 1994; Green and Krebs 1995; Wiebe et al. 1998), females may be more likely than males to actively alter the distribution of food within broods.

If parents facultatively adjust the distribution of food within broods to maximise the number and quality of young, selective feeding of last-hatched chicks should occur only when food is abundant, whereas selective feeding of first-hatched chicks should occur when food is scarce. Patterns of food distribution have been shown to depend on food availability in two species. Female pied flycatchers selectively feed small chicks under 'normal' conditions, but distributed food to large chicks when the brood was deprived of food (Gottlander 1987). Food distribution within broods of white-winged choughs typically favours large chicks, but groups given supplemental food selectively fed small chicks (Boland et al. 1997).

Crimson rosellas (*Platycercus elegans*) are Australian parrots which hatch asynchronously and have complex patterns of food allocation within broods. Despite large initial size disparities, nestlings of all hatching ranks grow at the same rate (Chapter 3). I manipulated the hunger of first- and last-hatched nestlings independently or at the same time to examine how parents responded to hungry nestlings when hunger within the brood was relatively low or high. I predicted that parents should selectively allocate food to last-hatched chicks when brood hunger is low, but shift the distribution of food in favour of first-hatched chicks when brood hunger was high. I also examined whether mothers and fathers distribute food in the same way.

Methods

SPECIES AND GENERAL METHODS

Crimson rosellas are broad-tailed parrots which breed commonly in eastern Australia. The sexes have similar plumage, but males are about 15% larger than females and have slightly broader bills (Krebs unpublished data). Rosellas breed in socially monogamous pairs (Forshaw 1981). The female alone incubates the eggs and broods small nestlings. Males feed incubating and brooding females until the brood is approximately 5 days old, at which point both parents feed the young directly. Crimson rosellas are typically single-brooded and lay from 3 to 8 eggs (mean ± sd = 5.1 ± 0.1, n = 64). Females usually lay eggs at 2 day intervals and initiate incubation in the middle of the laying sequence so that broods hatch asynchronously over 1.5 to 7 days (mean ± se = 3.5 ± 0.5) (Chapter 2).

In 1993 and 1994, I placed a total of 46 nestboxes in dry sclerophyll eucalypt forest (*Eucalyptus rossi, E. macrorhyncha*) in Black Mountain Nature Reserve, Canberra, Australia. Nestboxes were spaced 50 metres apart in a grid system and mounted approximately 4 metres above the ground. Each box had a hinged lid, and was fitted with a removable nest floor supported by wooden blocks. The nest floor could be reached by a small door on the front of the box. Eighty percent of boxes were occupied by rosellas in each year, although high levels of egg destruction meant that not all birds raised chicks.

I visited boxes daily during the predicted hatching period until all nestlings had hatched. Where the order of hatching was observed directly I assigned a hatching rank to each chick (first, second, etc.) and a hatching time to the nearest 0.5 day, based on the dryness of a chick and its crop contents. Where more than one chick hatched on the same day, hatch time was assigned based on a combination of wing chord and dryness of the down.

Newly hatched chicks were marked by trimming down on different parts of the body, and older chicks were marked with a single colour band. Nestlings were weighed to the nearest 1 g using Pesola spring balances.

Sexing nestlings

I sexed nestlings from DNA extracted from blood and used a PCR based sex-specific genetic marker (see Griffiths et al. 1998 for details of the method).

Feeding observations

Rosella parents feed chicks by regurgitating seeds directly into their mouths in a series of food transfers. To quantify the number of food transfers a parent makes to each chick during a feeding visit, I videotaped feeding visits using a miniature black and white CCD video camera with infra-red illumination (Oatley Electronics, NSW) attached to the lid of the nestbox. The output was recorded onto a portable video recorder (Sony VideoWalkman GVS50) located on the ground below the nestbox. Chicks were marked with a unique number of black paint spots (non-toxic tempera paint) to allow individual recognition.

Although the number of transfers indicates the relative distribution of food to chicks during each feeding visit, the amount of food delivered by parents also varied between feeding visits (Chapter 4). To quantify the size of parental food deliveries, I simultaneously recorded mass changes in the nestbox by placing a digital balance (Sartorius PT6) under the false nest floor. Output from the balance was monitored by a portable computer (Zenith Supersport 286) running specially designed software (NestBug; Szép et al. 1995). This software continuously recorded any mass changes (feeding deliveries) within the nestbox over the day.

MANIPULATION OF CHICK HUNGER

I deprived nestlings of food for short periods in nine experimental broods in 1995 to examine whether hunger altered the distribution of food within the brood. I manipulated hunger in two ways by: (i) removing an individual chick within the brood ('Individual hunger experiment') and (ii) removing the whole brood ('Brood hunger experiment'). In the individual hunger experiment I deprived first- and last-hatched chicks of food separately to assess the effect of hatching rank. Individual broods vary in their growth rates (see Chapter 3), therefore I chose an experimental design which allowed each brood to be used as its own control. Treatments were sequentially applied to a particular brood over 7 days (Table 1). Broods were not visited on days following chick removals ("rest days"; Table 1). I alternated the order in which I removed first and last-hatched chicks in the individual hunger experiment. This experimental design minimised inter-brood variation between control and experimental manipulations, but resulted in brood age increasing over subsequent treatments (Table 1). Within an experiment, control and removal treatments were separated by a maximum of 3 days (Table 1), a small difference relative to the 35 day nestling period. Nestling growth was linear over the brood ages monitored and size asymmetries within brood were stable

Table 1. Summary of experimental design used to manipulate individual chick and brood hunger in nine experimental broods. Brood ages were measured from the day the last chick hatched.

Experiment	Day	Brood age	Treatment
(i) Individual chick removal	1	8	Control 1
	2	9	Removal 1
	3	10	Rest day
	4	11	Removal 2
	5	12	Rest day
(ii) Brood removal	6	13	Control 2
	7	14	Brood removal

within each experiment, but decreased by 14% (paired difference = 5.0 ± 2.1 g) between the two experiments. Thus differences between the individual and brood hunger experiments might be confounded by brood age.

Experimental broods had four to seven nestlings. To standardise broods with varying degrees of hatching asynchrony, I began experimental manipulations when the last-hatched chick was 8 days old. I removed target chicks from the brood prior to the first feeding visit of the day, and returned them three hours later. Removed chicks were kept in warm, dark box, and appeared to suffer no long term effects. Removals resulted in target chicks missing 2 to 4 feeding visits by parents (mean mass gain in control chicks = 4.1 g; mass loss in removal chicks = -2.4 g). I assume that the mass loss during chick removals resulted in increased nestling hunger. When removing single chicks I did not provide a replacement chick during the removal period, but when I removed the whole brood I substituted 2 to 4 chicks of a similar age. Consequently the brood size experienced by parents during the three hour removal period was smaller than their "normal" brood size.

On each monitoring day, I weighed each chick at approximately 0630, prior to removals, 0930, after any removals, and 1530. I recorded feeding visits to the nestbox for 9 hours, from approximately 0630 to 1530 hours and videotaped feeding visits in each box for 6 continuous hours starting at approximately 0930, after removed chicks were returned to the nestbox. In most cases, I set up equipment and weighed and marked chicks before parents returned for the first feed of the morning, thereby minimising disturbance. Parents did not appear to be deterred from visiting the nestbox by the appearance of monitoring equipment and they entered and fed chicks 5 to 15 minutes after arriving back at the box, as observed at unmanipulated boxes.

ANALYSIS

Mass data

The mass of food delivered to the nestbox was estimated by subtracting a parent's mass on entering the nestbox from its mass on leaving. The computer recorded a visit as occurring when the reading from the digital balance changed by more than 75 g. At each visit, a series of masses (maximum = 120) were saved before and after parents entered or left the box. Raw data files were edited for consistency and two types of anomalous readings were removed: (i) extremely brief visits (< 10 s) resulting in very short weighing series; and (ii) highly variable, rapidly repeated measurements which occurred when a parent was only partially standing on the nest floor. The edited files were summarised using NestBug Visit Analyser Software (Z. Toth, unpublished), which calculated mean masses and excluded outliers changing the mean more than 0.02 g. Occasionally, especially in boxes with older broods, parents would enter the box and feed chicks standing on an internal wire ladder, and only intermittently touch the nest floor. Feeds from the ladder produced short and unreliable weighing sequences and were only used to record the time of the feeding visit and where possible, the amount of food delivered.

Video data

To analyse parental behaviour during each feeding visit I used a desktop video player (Sony E6500) that allowed slow motion and frame by frame playback. The sex of the parent entering the box was identified by bill morphology and pair specific plumage differences or the presence of leg bands. I recorded time of day, the length of a feed, and the number and sequence of food transfers to each chick. Parents were recorded as refusing to feed a chick when they jerked their head away or physically turned away from a chick who was soliciting or trying to grab their bill. Parental movements during feeds were measured as the beak to beak distance (mm) between a parent, just prior to regurgitating food at a given transfer, to the parent just prior to the subsequent transfer. I used the mean distance moved between transfers during a feeding visit in analyses.

The number of food transfers during a feed was strongly correlated to the load size delivered by parents (controlling for variance between boxes; change in deviance $\chi^2{}_1 = 46.5$, $p < 0.001$) and the number of transfers to each chick correlated strongly to their mass gain (ln(food transfers) over 6 hours vs. mass gain over that period, controlling for variance between boxes and brood ages; change in deviance $\chi^2{}_1 = 21.1$, $p < 0.001$). Therefore I have assumed that all food transfers are equal in size. Although I have no way of testing this assumption directly, all bill contacts appeared to involve at least some food transfer.

Statistics

I analysed the results using models appropriate for multilevel data because hatching ranks and treatments were replicated within nestboxes. My data were unbalanced, and therefore unsuitable for conventional 'analysis of variance' (and particularly repeated measures designs), so I used a mixed model incorporating random and fixed effects (REML Restricted Maximum Likelihood; GENSTAT 5 Committee 1993).

I was unable to control experimentally for differences in the sex ratio of broods, since the DNA sexing technique had not yet been developed. However, retrospective sexing showed that the sexes were relatively evenly distributed among first- and last-hatched chicks (5/9 first-hatched chicks and 3/9 last-hatched were male). Since sample sizes for males and females within each hatching rank were too small for strong inference, I statistically removed the effect of sex by including it in the random structure of models.

To evaluate how parents responded to changes in chick hunger, I compared chicks on control and removal days. I fitted separate models for individual chick and brood hunger experiments and for the following response variables: feeding rates (g/h) for both parents combined, and separately for fathers and mothers; load sizes (g) delivered by fathers and mothers; food transfers (proportion) allocated to a chick, for both parents combined, and separately for fathers and mothers; distance moved between food transfers (mm) by fathers and mothers; and the number of times a chick was refused food by fathers and mothers. I used the proportion of food transfers received by each chick in preference to the number of transfers because the proportion is less affected by load size, brood size or brood age.

I fitted models using hunger treatment (control vs. removal), chick hatching rank (first vs. last) and their two-way interaction as explanatory variables. Nestbox, chicks within boxes and chick sexes within boxes were included in all models as random terms, except those examining feeding rates and load sizes, which included only nestbox. Variables were then dropped from the model in a stepwise procedure by assessing the change-in-deviance, which approximates a Chi-squared distribution, between the full model and the sub-model (GENSTAT 5 Commitee 1993). Significant terms were included in subsequent model fitting. The final model was selected by sequentially dropping non-significant interactions and then non-significant main effects, until only significant terms remained.

When complex modelling was not required I used paired t-tests to examine differences between variables. In all analyses frequency histograms, residual plots and normal probability plots were examined for unequal variances and deviations from normality, and transformations applied if necessary. I have reported main effects or interaction terms from a model where they were significant ($p < 0.05$, or there was a statistical trend ($0.05 < p < 0.10$). Means and standard errors are reported throughout, except where otherwise indicated.

Results

CHANGES IN FOOD ALLOCATION

Individual chick hunger experiment

Hungry chicks of both hatching ranks received more food transfers, and gained more mass during the post-removal period (Table 2a; 3a; Figure 1; 2a). Consequently, chicks had gained the same mass by the end of the day in the removal treatment as in the control (Table 3b; Figure 2b).

Although parents compensated hungry chicks by feeding them more, changes in food allocation were mainly the result of redistribution within the brood, since neither total feeding rates nor load sizes increased when chicks were hungry (Table 4).

Parents did not respond in the same way to hungry first- or last-hatched chicks. Fathers allocated more transfers to first-hatched chicks than to last-hatched chicks during the control period (Figure 3a). However, when a chick was hungry, fathers tended only to increase the amount of food allocated to last-hatched chicks (Table 2b; Figure 3a). In contrast, mothers did not allocate more food to first- or last-hatched chicks when they were hungry (Table 2c; Figure 3b).

Brood hunger experiment

When the whole brood was hungry only first-hatched chicks obtained more food transfers (Table 2a; Figure 4). The food delivered was not adequate for the entire brood since hungry chicks of both hatching ranks gained more mass in the post-removal period, but lost mass over the whole day relative to the control (Table 3a; b; Figure 5a; b).

Despite the reduced growth parents did not increase their feeding rates or load sizes when the whole brood was hungry (Table 4)

Mothers were primarily responsible for changes in the distribution of food within hungry broods. Mothers fed last-hatched chicks more than first-hatched chicks during the control period (Table 2c; Figure 6b). However, when the whole brood was

Table 2. Model fitting results for proportion of food transfers to chicks during the (i) individual hunger and (ii) brood hunger experiments.

a) total transfers to chicks

Term dropped from model	**Change in Deviance (df = 1)**	**P-value**
(i) individual hunger experiment		
hunger*hatching rank	0.4	ns
hatching rank	1.4	ns
hunger	4.7	< 0.05
(ii) brood hunger experiment		
hunger*hatching rank	4.5	< 0.05
hatching rank	0.8	ns
hunger	0.5	ns

b) transfers by fathers

Term dropped from model	**Change in Deviance (df = 1)**	**P-value**
(i) individual hunger experiment		
hunger*hatching rank	3.4	< 0.10
hatching rank	3.6	< 0.10
hunger	1.1	ns
(ii) brood hunger experiment		
hunger*hatching rank	1.3	ns
hatching rank	0.2	ns
hunger	0.0	ns

c) transfers by mothers

Term dropped from model	**Change in Deviance (df = 1)**	**P-value**
(i) individual hunger experiment		
hunger*hatching rank	0.9	ns
hatching rank	1.9	ns
hunger	0.8	ns
(ii) brood hunger experiment		
hunger*hatching rank	8.2	< 0.005
hatching rank	0.0	ns
hunger	0.1	ns

Table 3. Model fitting results for mass gain of chicks during the post-removal period and over the whole day for (i) individual and (ii) brood hunger experiments

a) mass gain by chicks over the post-removal period

Term dropped from model	**Change in Deviance (df = 1)**	**P-value**
(i) individual hunger experiment		
hunger*hatching rank	0.1	ns
hatching rank	1.8	ns
hunger	4.4	< 0.05
(ii) brood hunger experiment		
hunger*hatching rank	0.5	ns
hatching rank	0.3	ns
hunger	6.5	< 0.025

b) Mass gain by chicks over the whole day

Term dropped from model	**Change in Deviance (df = 1)**	**P-value**
(i) individual hunger experiment		
hunger*hatching rank	0.6	ns
hatching rank	1.4	ns
hunger	1.5	ns
(ii) brood hunger experiment		
hunger*hatching rank	0.2	ns
hatching rank	0.2	ns
hunger	6.5	< 0.025

Table 4. Summary of parental feeding rates calculated separately for fathers, mothers and for both parents combined, for broods (N = 9) under each treatment. Load sizes delivered by fathers and mothers are also presented. Probability values are reported for the change in deviance for a model with and without hunger treatment. There were no significant interactions between the sex of parents and feeding rate or load size (all $p > 0.75$)

(i) individual chicks hungry

Treatment	**Control period**	**First-hatched hungry**	**Last-hatched hungry**	**P - value**
Male feeding rate (g/h)	4.5 ± 0.6	5.1 ± 0.5	5.4 ± 0.8	> 0.10
Female feeding rate (g/h)	3.3 ± 0.5	4.1 ± 0.6	4.2 ± 0.5	> 0.10
Total feeding rate (g/h)	7.8 ± 0.7	9.2 ± 0.7	9.7 ± 1.0	> 0.10
Male load size (g)	12.4 ± 1.6	13.2 ± 1.3	14.9 ± 1.6	> 0.50
Female load size (g)	10.4 ± 1.3	13.1 ± 1.3	12.3 ± 1.1	> 0.50

(ii) brood hungry

Treatment	**Control period**	**Brood hungry**		**P - value**
Male feeding rate (g/h)	4.2 ± 0.7	4.9 ± 0.8	-	> 0.10
Female feeding rate (g/h)	3.7 ± 0.4	4.5 ± 0.7	-	> 0.10
Total feeding rate (g/h)	7.9 ± 0.8	9.4 ± 1.1	-	> 0.25
Male load size (g)	10.9 ± 1.3	11.2 ± 1.3	-	> 0.90
Female load size (g)	10.8 ± 1.1	10.4 ± 0.9	-	> 0.90

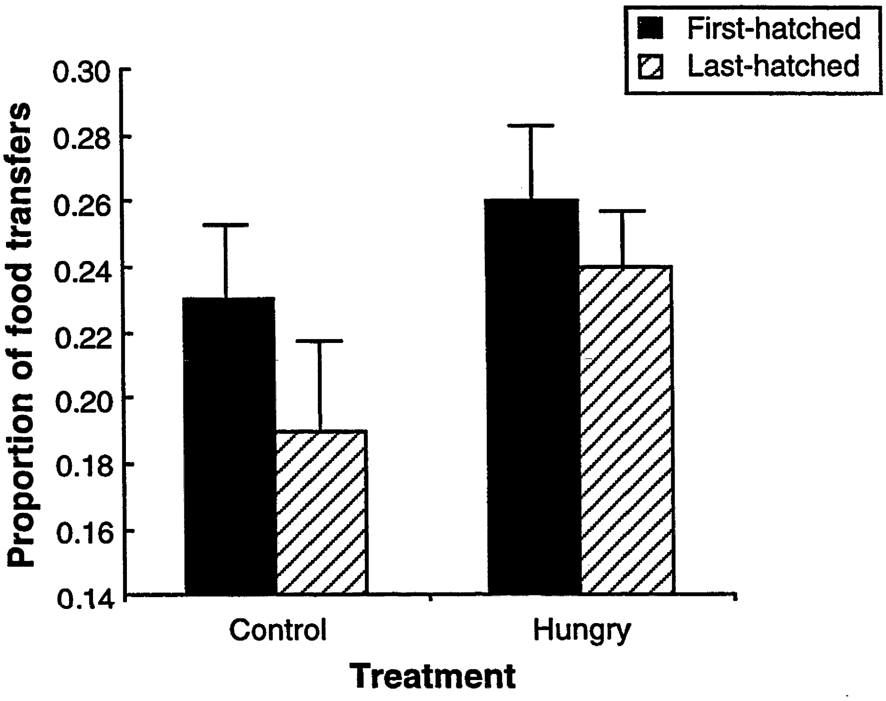
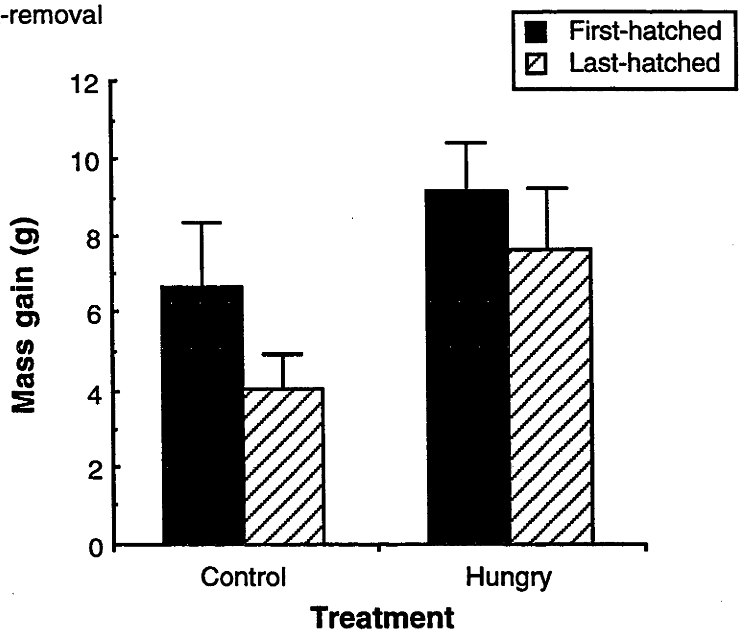


Figure 1. The proportion of food transfers (mean ± se) obtained by first and last-hatched chicks during the control period and when each chick was hungrier than the rest of the brood (n = 9 broods).

a) Post-removal



b) Whole day

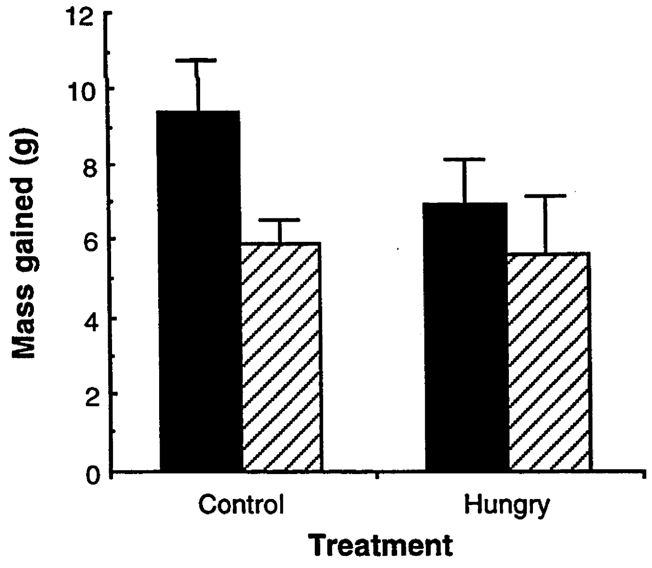
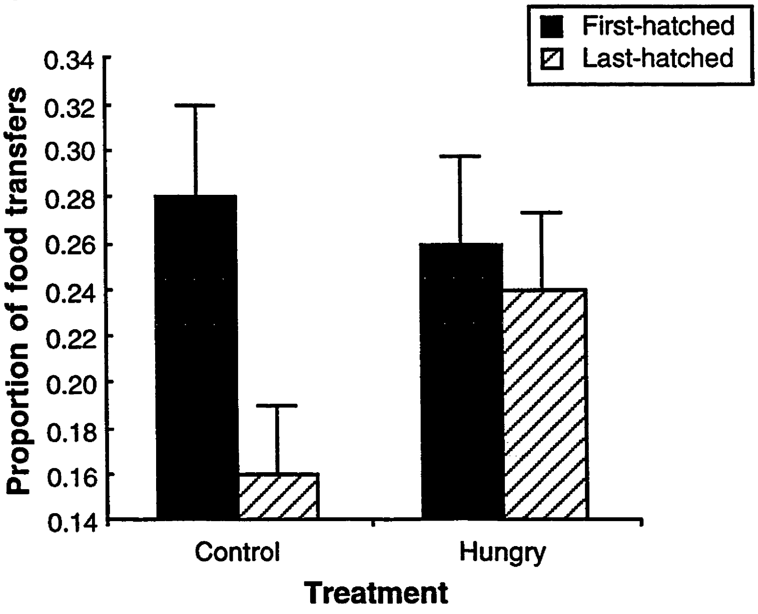


Figure 2. Mass gained (mean ± se) by first and last-hatched chicks during the control period and when each chick was hungrier than the rest of the brood (n = 9 broods), plotted separately for, a) the post removal period (6 hours) and b) over the whole day (9 hours).

a) fathers



b) mothers

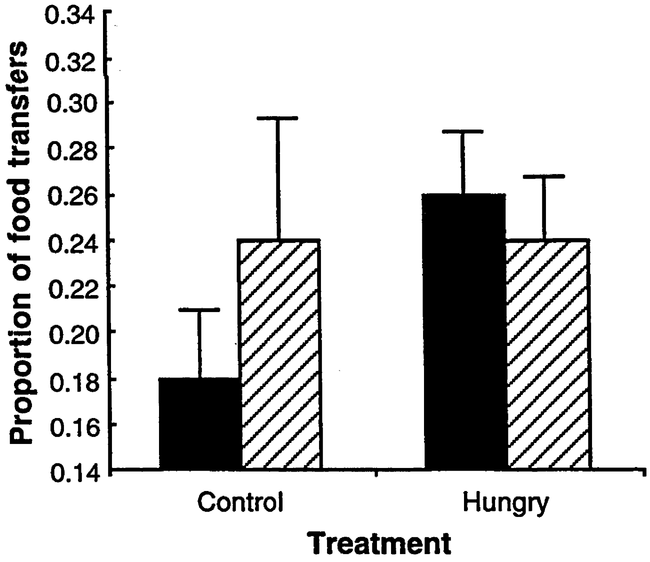


Figure 3. The distribution of food during the individual hunger experiment plotted separately for a) fathers and b) mothers. The proportion of food transfers (mean ± se) obtained by first- and last-hatched chicks are shown for the control period, and when individual chicks were hungrier than the rest of the brood (n = 9 broods).

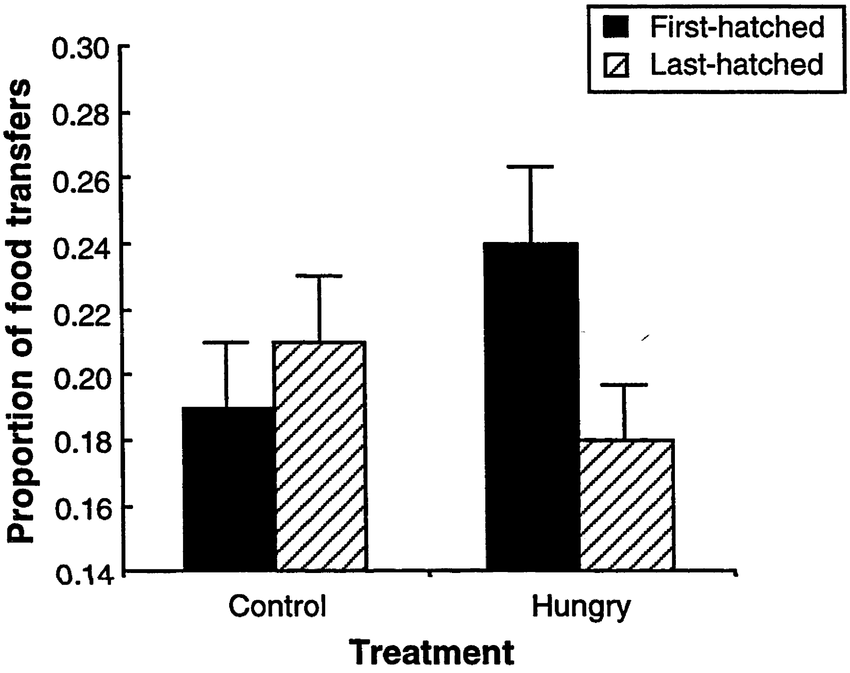
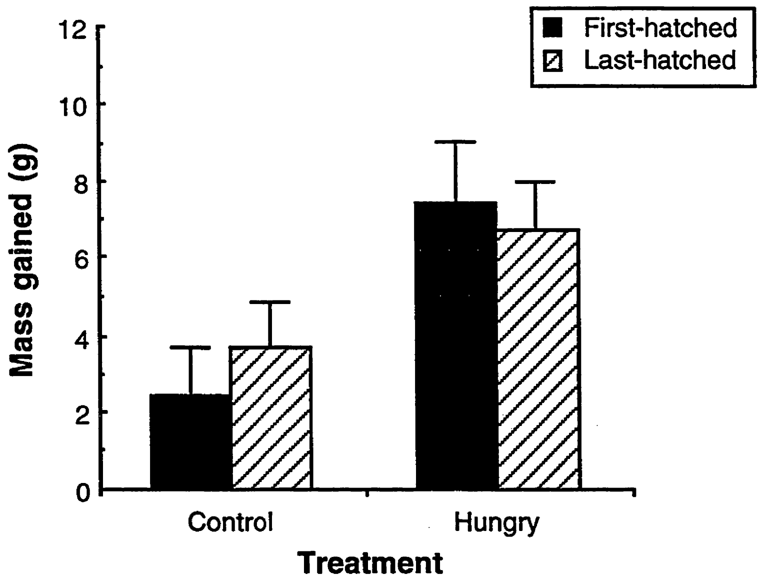


Figure 4. The proportion of food transfers (mean ± se) obtained by first and last-hatched chicks during the control period and when the entire brood was hungry (n = 9 broods).

a) Post-removal



b) Whole day

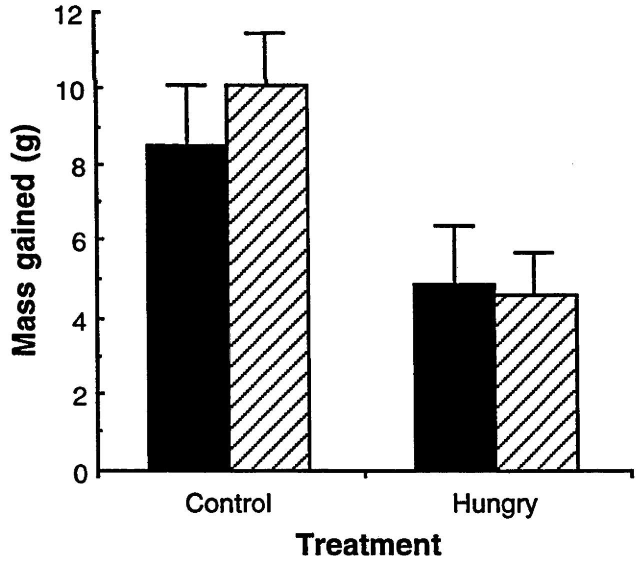
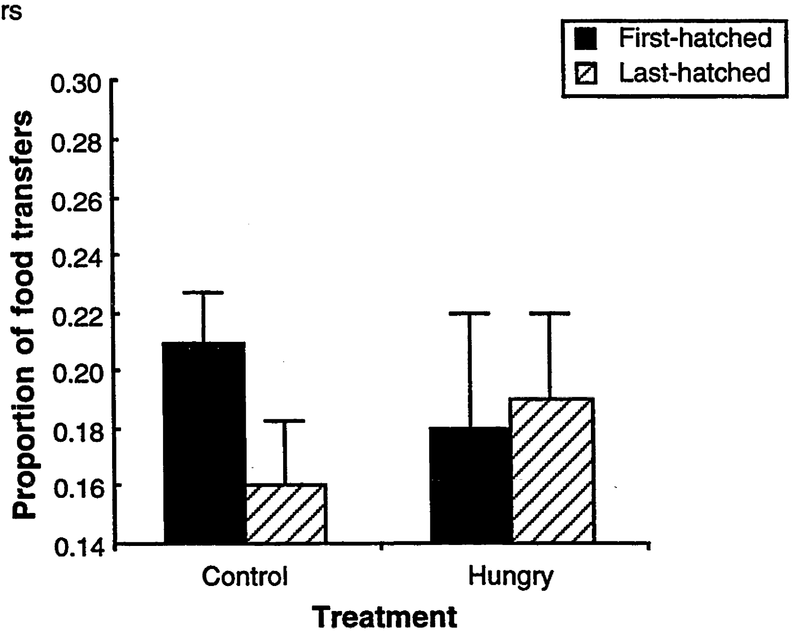


Figure 5. Mass gained (mean ± se) by first and last-hatched chicks during the control period and when the entire brood was hungry (n = 9 broods), plotted separately for, a) the post removal period (6 hours) and b) over the whole day (9 hours).

a) fathers



b) mothers

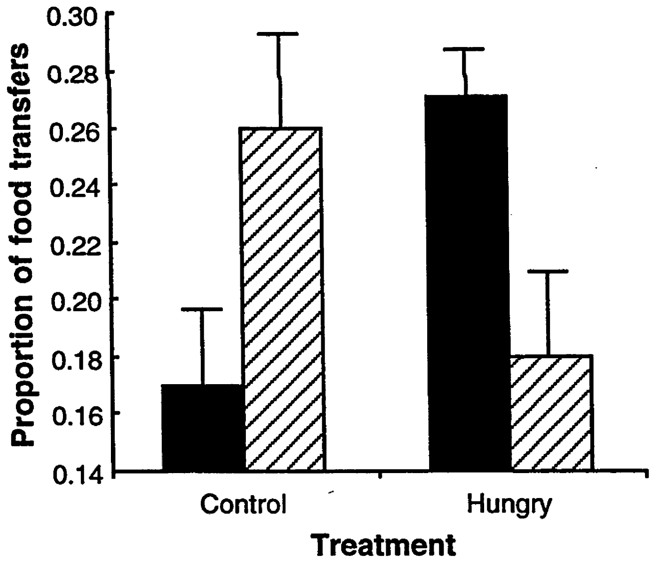


Figure 6. The distribution of food during the brood hunger experiment plotted separately for a) fathers and b) mothers. The proportion of food transfers (mean ± se) obtained by first- and last-hatched chicks are shown for the control period, when the entire brood was hungry (n = 9 broods).

hungry, mothers dramatically increased the number of transfers to first-hatched chicks and decreased the number of transfers to last-hatched chicks (Table 2c; Figure 6b). In contrast, fathers fed first- and last-hatched chicks equally both in the control period and when the brood was hungry (Table 2b; Figure 6a).

MECHANISMS OF PARENTAL CONTROL

Individual chick hunger experiment

A parent could reduce the ability of individual chicks to monopolise transfers by increasing the distance it moved its head between sequential regurgitations. Increased scramble competition within rosella broods appeared to result in chicks frequently attempting to grab a parent's bill. The distance parents moved in between food transfers increased as the brood aged, as expected if this behaviour acts to reduce competition within the brood (brood age 8 = 58.5 ± 3.4 mm, brood age 14 = 76.0 ± 4.5 mm; paired t-test - $t = -2.8$, $df = 16$, $p = 0.01$).

Parents also sometimes refused to feed chicks who were actively soliciting food. Overall, mothers and fathers were equally likely to refuse to feed chicks during a feed (total number during a feed: mothers = 4.4 ± 0.8, fathers = 3.9 ± 1.2; paired t-test; $t = -0.5$, $df = 8$, $p = 0.61$), but mothers refused to feed chicks more often when they were hungry (mothers = 3.4 ± 0.6, fathers = 1.5 ± 0.5; paired t-test; $t = 2.9$, $df = 8$, $p = 0.01$).

As the patterns of food distribution suggest, mothers engaged in behaviours to reduce the ability of first-hatched chicks to monopolise food when they were hungry. When first-hatched chicks were hungry, mothers responded by moving further between consecutive food transfers and refused to feed hungry first-hatched chicks more often than hungry last-hatched chicks (Table 5b; 6b; Figure 7; 8).

In contrast to mothers, fathers did not alter their behaviours towards hungry chicks. The distance fathers moved between consecutive transfers was not related to hatching ranks or hunger (control period = 53.7 ± 4.2 mm, first-hatched hungry = 63.4 ± 4.9 mm, last-hatched hungry = 65.3 ± 3.4 mm; Table 5a). Fathers also did not differ in the number of times they refused to feed chicks of different hatching ranks, or hunger

Table 5. Model fitting results for parental head movements during feeds for the (i) individual and (ii) brood hunger experiments

a) movements between transfers by fathers

Term dropped from model	**Change in Deviance (df = 1)**	**P-value**
(i) individual hunger experiment		
hunger*hatching rank	2.2	ns
hatching rank	0.0	ns
hunger	0.6	ns
(ii) brood hunger experiment		
hunger*hatching rank	0.0	ns
hatching rank	0.0	ns
hunger	14.1	< 0.001

b) movements between transfers by mothers

Term dropped from model	**Change in Deviance (df = 1)**	**P-value**
(i) individual hunger experiment		
hunger*hatching rank	4.4	<0.05
hatching rank	0.0	ns
hunger	0.0	ns
(ii) brood hunger experiment		
hunger*hatching rank	0.1	ns
hatching rank	0.0	ns
hunger	4.5	< 0.05

Table 6. Model fitting results for feeding refusals by parents during the (i) individual and (ii) brood hunger experiments

a) refusals to feed chicks by fathers

Term dropped from model	**Change in Deviance (df = 1)**	**P-value**
(i) individual hunger experiment		
hunger*hatching rank	0.4	ns
hatching rank	1.4	ns
hunger	0.9	ns
(ii) brood hunger experiment		
hunger*hatching rank	0.4	ns
hatching rank	8.3	< 0.005
hunger	0.0	ns

b) refusals to feed chicks by mothers

Term dropped from model	**Change in Deviance (df = 1)**	**P-value**
(i) individual hunger experiment		
hunger*hatching rank	5.2	< 0.025
hatching rank	4.6	< 0.05
hunger	8.9	< 0.005
(ii) brood hunger experiment		
hunger*hatching rank	0.1	ns
hatching rank	6.3	< 0.025
hunger	1.3	ns

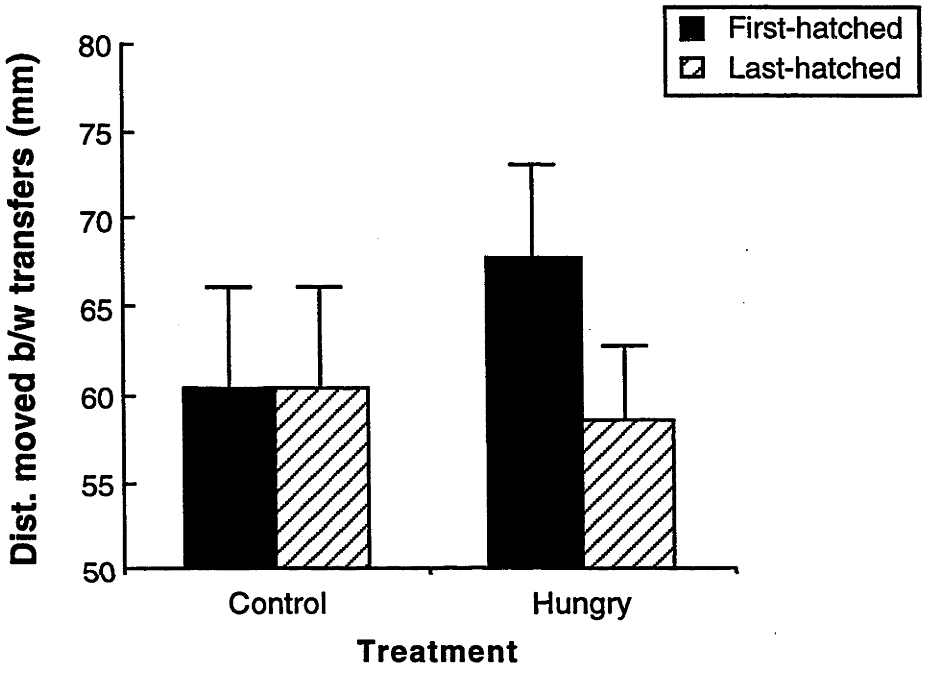


Figure 7. The distance (mean ± se) mothers moved in between transfers during the control period and when first and last-hatched chicks were hungrier than the rest of the brood (n = 9 broods).

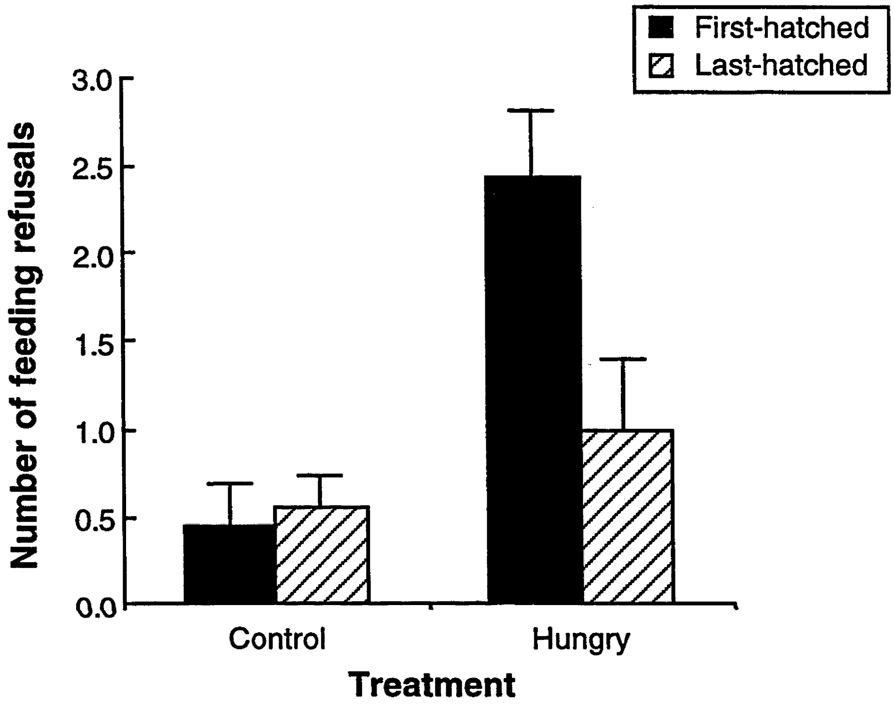


Figure 8. The number of times (mean ± se) mothers refused to feed first and last-hatched chicks in a feed during the control period and when chicks were hungrier than the rest of the brood (n = 9 broods).

levels (first-hatched: control = 1.2 ± 0.5, hungry = 1.1 ± 0.4; last-hatched: control = 1.1 ± 0.5, hungry = 0.4 ± 0.3; Table 6a).

Brood hunger experiment

When the whole brood was hungry and competition for food high, both parents increased the distance they moved between consecutive food transfers relative to the control period (Table 5; Figure 9).

Although the distribution of food would predict that the frequency of feeding refusals should increase at least for fathers when the brood was hungry, this pattern was not observed. Fathers and mothers refused to feed first-hatched chick more often than last-hatched chicks during this experiment, but the number of refusals did not change when the brood was hungry (Figure 10a,b; Table 6).

Discussion

Food was allocated to crimson rosella chicks in a way that would facilitate brood reduction. When only a single chick within the brood was hungry, parents were able to compensate the chick without significantly reducing food to other chicks in the brood. However, when the whole brood was hungry, parents were unable to compensate all chicks for the mass lost during the removal period and so redistributed food to first-hatched chicks. Thus when food appeared to be insufficient for the whole brood, parents reallocated food to older chicks at the expense of last-hatched chicks. If this pattern of food allocation continued, it would result in efficient brood reduction.

Mothers were primarily responsible for adaptive shifts in food allocation within the brood. When a single chick within the brood was hungry, mothers continued to feed all chicks irrespective of hunger and engaged in behaviours which reduced the ability of first-hatched chicks to monopolise food. However when the whole brood was hungry, mothers re-allocated food to first-hatched chicks at the expense of last-hatched chicks. In contrast, fathers reallocated food to last-hatched chicks when they were individually hungry, but distributed food equally to all chicks when the brood was hungry. Both parents moved more during feeding visits when the brood was hungry and refused to

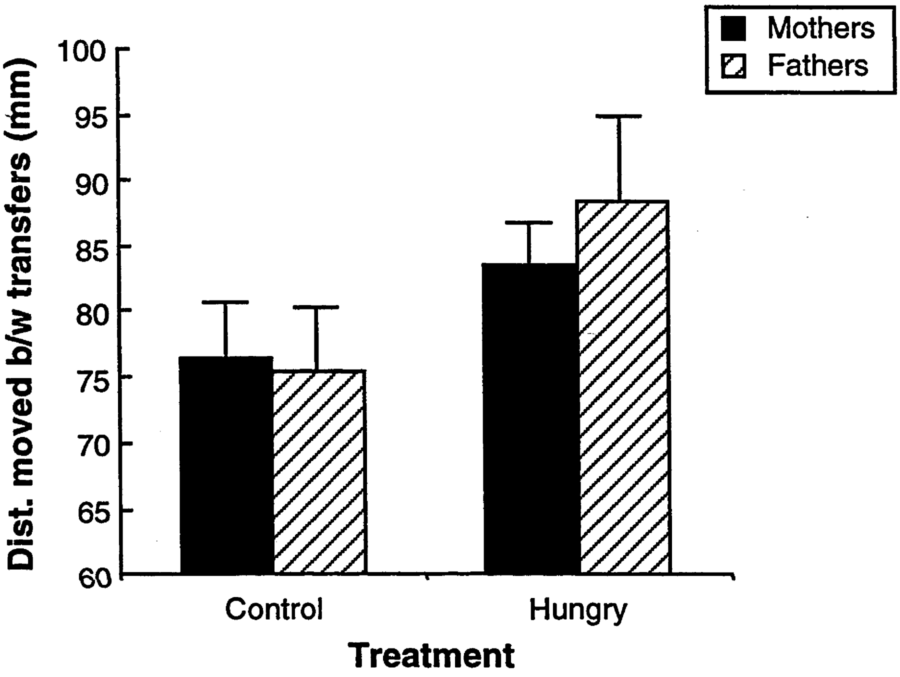
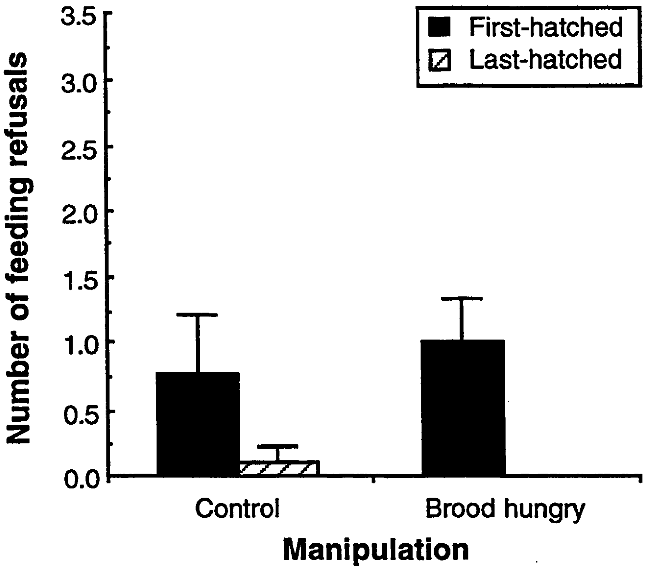


Figure 9. The distance (mean ± se) parents moved between consecutive food transfers during the control period and when the entire brood was hungry (n = 9 broods).

a) fathers



b) mothers

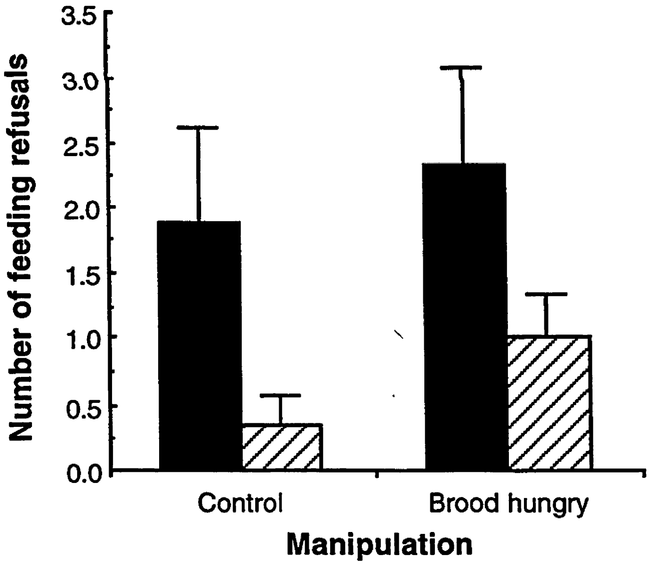


Figure 10. The number of times (mean ± se) parents refused to feed first and last-hatched chicks in a feed during the control period and when the brood was hungry (n = 9 broods), plotted separately for a) fathers and b) mothers.

feed first-hatched chicks more often than last-hatched chicks, behaviours which potentially increased parental control of food allocation.

FOOD ALLOCATION TO BROODS WITH HUNGRY CHICKS

In contrast to most species, rosellas did not significantly increase their feeding rates or load sizes in response to short-term increases in chick or brood hunger. Increases in feeding rates in response to both short term and long term increases in brood hunger have been observed in great tits (Bengtsson and Ryden 1983), red-winged blackbirds (Whittingham and Robertson 1993; Burford et al. 1998; but see Clark and Lee 1998), pied flycatchers (Ottoson et al. 1997), and yellow-headed blackbirds (Price 1998). Although mean feeding rates by rosellas increased in the predicted direction, the lack of increase was not simply a statistical artefact of small sample sizes. Only five out of nine pairs increased their feeding rates when a chick or the brood was hungry, suggesting not all pairs were able or willing to increase food delivery.

It is unclear whether rosella parents were unable or unwilling to increase the food delivered to hungrier broods. Foraging ability can restrict increases in feeding rates in some species. For example, red-winged blackbird parents increased feeding rates, but decreased the size of loads delivered to broods following food deprivation, leading to reduced growth by nestlings (Whittingham and Robertson 1993). Rosella parents may differ in their foraging abilities since growth rates between broods are variable. Alternatively, parents may be unwilling to increase feeding rates to the brood if it increases the costs of reproduction (Korpimaki 1988). Crimson rosellas are likely to be conservative in their energy expenditure on reproduction since they are relatively long lived (Forshaw 1981) and can defer breeding when food availability is low (Chapter 2).

FOOD ALLOCATION WITHIN BROODS WITH HUNGRY CHICKS

The individual and brood hunger experiments were likely to signal two different things to parents provisioning a brood. Increasing the hunger of a single chick creates higher than normal variability in chick hunger within the brood. Unequal hunger could indicate that food delivery is adequate for the brood, but that the previous distribution of food had been uneven. Alternatively, if there is conflict between parents and offspring over how food should be distributed within the brood, unequal hunger could be interpreted by parents as an attempt by a selfish chick to monopolise food. Increased hunger by the whole brood, on the other hand, should signal to parents that current levels of food delivery are insufficient to sustain adequate growth of all chicks.

Individual hunger experiment

Rosella mothers distributed food in such a way as to ensure that the smallest and least competitive chick in the brood obtained food, regardless of chick hunger. Mothers did not change how they distributed food within broods when either first- or last-hatched chicks were hungry. Since large differences in size exist within broods, food distribution should favour first-hatched chicks in the absence of parental selectivity for less competitive chicks. However, in this experiment and in unmanipulated nests (Chapter 4) mothers fed chicks equally, irrespective of differences in competitive ability, suggesting that mothers controlled the allocation of food within the brood.

If mothers distribute food selectively to last-hatched chicks, why did they not feed last-hatched chicks more when they were hungry? Rosella mothers did not respond to sudden variations in demands for food by chicks, and may allocate a fixed amount of food to each chick, irrespective of chick hunger when brood hunger is low. This behaviour would minimise the ability of more competitive chicks to monopolise food, and allow food to be distributed more evenly. Thus, under natural conditions, not responding to individual chick hunger would increase the food allocated to less competitive, last-hatched chicks.

A fixed pattern of food allocation contrasts with previous studies manipulating individual nestling hunger, which consistently find that parents allocate more food to hungry nestlings (Teather 1992; Kacelnik et al. 1995; Kilner 1995; Price and Ydenberg 1995). This difference is not surprising, since parents in most species allow competition between chicks to determine access to food, and hungry chicks should compete harder to obtain food.

Parents can control the distribution of food within broods directly by selectively feeding or refusing to feed certain chicks. In this study, mothers attempted to maintain an equitable distribution of food by refusing to feed large, competitively superior chicks more often when they were hungrier than the rest of the brood. Parents are observed to selectively feed chicks in a few other species (e.g. Stamps et al. 1985; Gottlander 1987; Leonard and Horn 1996; Westneat et al. 1995; Boland et al. 1997), however, to my knowledge, only the study on budgerigars by Stamps and colleagues (1985) has documented mothers refusing to feed certain chicks (but see Forbes and Ankney 1987; Leonard et al. 1988; for refusals in precocial species).

Parents can also indirectly regulate the distribution of food within the brood by increasing the costs to chicks of monopolising food. For example, distributing food through many small regurgitations may reduce levels of competition for food, making it difficult for an individual chick to increase its share. Rosella parents may also indirectly control the distribution of food by frequently altering their position during feeds by moving their head and body. Similar behaviours are described by Stamps et al. (1985) in budgerigars, where females move around the box and resume feeding particular chicks when interrupted. A general pattern of moving further during feeds should decrease the ability of a single chick to monopolise food transfers, reducing nestling competition. Consistent with this function, the distance rosella parents moved during feeds increased with the age of the brood. Mothers also moved further during feeds when first-hatched chicks were hungry, which could be a response to an increase in competitive behaviours by these chicks.

Parents may be more likely to engage in behaviours that directly control the distribution of food in species like parrots because the relative costs of distributing food are low. Rosellas feed only about once per hour, deliver large amounts of food, and feed each chick several times during a feeding visit by regurgitating small amounts of food (see Chapter 4). In contrast, many passerine species deliver food many times per hour and deliver small loads, which they feed to a single chick. For example in great tits, parents feed about once per minute with each visit lasting one second (Ryden and

Bengtsson 1980). In species which feed frequently, even small increases in the time spent at each feeding visit would lead to large increases in the total time spent feeding.

In contrast to mothers, fathers altered their distribution of food within rosella broods only when last-hatched chicks were hungry. Since fathers did not allocate more food to hungry first-hatched chicks, they also appear to be able to control the distribution food within broods. The mechanisms used by fathers to change the allocation of food within the brood are not clear since they did not refuse to feed large chicks more frequently, nor increase the distance they moved during feeds. If fathers are responding simply to changes in chick solicitation this would suggest that only last-hatched chicks within the brood begged harder when hungry.

Brood hunger experiment

If increased hunger by the whole brood signals that current food delivery is inadequate, parents would be predicted to respond by increasing feeding rates or by preferentially feeding older chicks. Rosella parents did not significantly increase their feeding rates and chicks in hungry broods gained only half the mass they gained during controls. Rosellas did the latter: the distribution of food shifted from a pattern of equal allocation to one that favoured first-hatched chicks. Despite the pattern of food allocation, statistical models did not detect a greater mass gain by first-hatched chicks than last-hatched chicks. The reasons for this are not clear, but a direct comparison of the differences in mass gained suggests that first-hatched chicks did gain slightly more mass, as expected (differences in mass gained in post-removal period (removal - control): first-hatched = 4.8 ± 2.3 g, last-hatched = 2.7 ± 1.8 g; paired t-test, $t = 2.4$, $df = 8$, $p = 0.04$). Differences in mass gain may have been lower than the differences in food allocation suggested if larger, first-hatched chicks had higher metabolic costs (Teather and Weatherhead 1988).

Food allocation which consistently favoured first-hatched chicks would lead to poor growth and probably lower survival of last-hatched chicks. Death of last-hatched chicks through starvation is frequently observed in asynchronously hatching species (Magrath 1990; Stoleson and Beissinger 1995). Lack (1947) first proposed that hatching asynchrony may function to facilitate efficient brood reduction when food was limited. Hatching asynchrony allows adaptive brood reduction in some species (European blackbirds *Turdus merula*, Magrath 1989; American kestrels *Falco sparverius*, Wiebe and Bortolotti 1994; white-winged choughs, Boland et al. 1997), although it can have different functions in others (e.g. Hahn 1981; Hussell 1972; Stoleson and Beissinger 1997). In rosellas, parents actively promoted or prevented brood reduction by altering food allocation within the brood.

The extent to which parents in other species adaptively alter food allocation is unclear because few studies have examined food distribution within the brood under varying food conditions. Several studies, however, have manipulated brood hunger or food availability and noted changes in food distribution within the brood. For example, Bengtsson and Ryden (1983) observed that great tits feed large chicks within the brood more than small chicks, and that this difference became more pronounced when brood hunger was increased. Female pied flycatchers distributed food evenly to all nestlings under control conditions, but began to feed large chicks in the brood after a brief period of food deprivation (Gottlander 1987). Groups of white-winged choughs normally feed large chicks more than small chicks, and brood reduction is common. However, when groups were supplemented with food, birds fed small chicks more than large chicks within the brood, increasing their probability of survival (Boland et al. 1997).

Mothers appear to control the overall patterns of food distribution within the brood in rosellas. While fathers allocated food equally to nestlings during control and brood removal treatments, mothers strongly altered their food distribution by increasing the proportion of food to first-hatched chicks and decreasing the proportion to last-hatched chicks. Redirecting food away from last-hatched chicks suggests that mothers were attempting to reduce brood size to ensure the survival of some young. Interestingly, mothers also controlled brood size by selectively starving nestlings at hatching under some circumstances (Chapter 2). Although active behaviours to adaptively alter the distribution of food within broods have rarely been described, the fact that mothers typically engage in selective feeding (e.g. Stamps et al. 1985; Gottlander

1987; Leonard and Horn 1996) suggests that they control food allocation in other species.

The shift in food allocation in favour of first-hatched chicks in hungry rosella broods was not due to intensified competitive interactions between chicks restricting the ability of parents to control the distribution of food. Both mothers and fathers moved further during feeds when the brood was hungry, a behaviour which should reduce competitive interactions and increase parent's control over food distribution. First-hatched chicks would have been favoured by competitive asymmetries during this experiment since they were still considerably larger than last-hatched nestlings. Despite these competitive differences, fathers fed nestlings equally throughout the control and brood removal treatments, suggesting they selectively fed last-hatched nestlings. Thus parents were able to control the distribution of food, but females preferentially distributed food to first-hatched chicks.

If parents are able to control the distribution of food within broods, it is not clear why I did not detect a greater number of refusals when the brood was hungry. Refusals were potentially more difficult to detect when the brood was hungry because feeding visits were highly chaotic; alternatively, parents may engage in other, unmeasured behaviours to control the distribution of food

WHY DO MOTHERS AND FATHERS ALLOCATE FOOD DIFFERENTLY?

It is not clear why mothers and fathers allocated food differently to hungry chicks within rosella broods. If the costs and benefits of food allocation differed for the sexes, parents would be expected to consistently invest more in either large or small chicks. However this was not the pattern observed in rosellas, mothers and fathers responded to the same changes in hunger in entirely different ways. Fathers responded more to variation in chick hunger within the brood, suggesting they re-allocate food based on short-term changes in hunger. In contrast, mothers appear to allocate food adaptively to maximise the long-term survival prospects of the brood. Mothers maximised the growth rates of all chicks when feeding conditions were adequate, but when conditions appeared to deteriorate, maximised quality of any young fledged by redirecting food to larger, older chicks within the brood. Thus, mothers and fathers appear to have entirely different strategies for allocating food. These patterns contrast strongly with previous studies that have manipulated chick hunger, which generally find no differences between parental responses to hungry chicks (e.g. Whittingham and Robertson 1993; Kilner 1995; Kacelnik et al. 1995; Burford et al. 1998; but see Gottlander 1987 for female differences).

Mothers may be more likely to allocate food based on long-term survival prospects of the brood because they have better knowledge of its condition than fathers (Gottlander 1987). This is potentially the case in rosellas since mothers spend more time associating with the brood during early brooding and feeding visits (Chapter 4). Mothers may also invest more in current reproduction if females have higher mortality (Slagsvold et al. 1995). Female mortality may be higher than males in rosellas, but the fact the fathers provision at higher rate than mothers suggests that males do not invest less in current reproduction (Chapter 4). Alternatively, the patterns of food allocation in crimson rosellas may represent highly coevolved behaviours in a species with biparental care and long-term monogamy. Complex patterns of food allocation may be possible in rosellas both because parents can precisely control the distribution of food within the brood, and because a long nestling period allows the opportunity to readjust its distribution.

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Chapter 6

Signalling by hungry chicks: Who controls the distribution of food within rosella broods?

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Abstract

Begging by altricial nestlings can signal both hunger and competitive ability, consequently parents do not always respond to begging in a straightforward way. I examined the interactions between nestlings and parents in crimson rosellas (*Platycercus elegans*), a species where parents engage in complex patterns of food allocation. I manipulated the hunger of individual chicks and the entire brood, to assess how chick solicitation and parental feeding behaviour changed with hunger and nestling competition. When individual chicks were made hungry they did not increase their begging or position themselves closer to a feeding parent. Last-hatched chicks begged more than first-hatched chicks irrespective of hunger. Parents in general, tended to feed chicks who were hungrier and closer but the sexes behaved in different ways: mothers fed first-hatched chicks in proportion to their begging intensity, whereas fathers fed last-hatched chicks in proportion to their begging. Since fathers generally allocate more food to first-hatched chicks and mothers to last-hatched chicks, begging rates appear to be used by parents to adjust food allocation to other chicks within the brood. When the whole brood was hungry, chicks increased their begging intensity but did not position themselves closer to a feeding parent. Therefore, only when both hunger and nestling competition were increased within broods did nestlings beg more intensely. Parents fed first-hatched chicks and chicks who were closer during the brood hunger experiment, and did not change their distribution of food when the whole brood was hungry. Rosella parents are able to regulate the distribution of food to nestlings and mothers and fathers differ in their desired patterns of food allocation.

Introduction

Altricial nestlings use costly behaviours such as vocalising, posturing and competing for favoured positions when soliciting for food from parents. Conspicuous solicitation is energetically costly for nestlings. For example, begging by tree swallow nestlings (*Tachycineta bicolor*) increased metabolic rates around 27% above resting (McCarty 1996; Leech and Leonard 1996), although the costs can be lower in some species (McCarty 1996). Begging calls are also costly for parents and young because they increase the risk of predation. In two studies, artificial nests which broadcast begging calls were depredated at a higher rate than controls (Haskell 1994; Leech and Leonard 1997). Nests with high rates of begging calls had higher rates of predation than nests with low rates, hence the intensity of begging may also increase its costs (Haskell 1994).

Costly forms of solicitation by nestlings are likely to have evolved due to underlying conflict between parents and offspring over the optimal distribution of resources (Trivers 1974; McNair and Parker 1979). If begging is costly, it can honestly signal hunger, since the benefits of additional resources will be less than the costs to obtain them (Godfray 1991; 1995). Alternatively, costly begging may allow an evolutionarily stable compromise between the level of offspring solicitation and parental provisioning (McNair and Parker 1979; Parker 1985).

Begging intensity frequently correlates to changes in chick hunger. Nestlings beg harder when they are deprived of food and reduce their begging when fed (Bengtsson and Ryden 1983; Redondo and Castro 1992; Price et al. 1996; Leonard and Horn 1998) . Not surprisingly, parents frequently allocate more food to young who call more intensely (Redondo and Castro 1992; Teather 1992; Leonard and Horn 1996; Price et al. 1996), reach highest (Smith and Montgomerie 1991; Teather 1992; Leonard and Horn 1996) or obtain a certain position within the nest (Gottlander 1987; McRae et al. 1988; Kacelnik et al. 1995; Kilner 1995).

Although begging frequently provides information for parents on hunger, several factors can affect the intensity of begging. First, begging can increase in response to nestling competition within the brood. When one or more siblings are deprived of food, the others may beg more (e.g. American robins *Turdus migratorius*, Smith and Montgomerie 1991; yellow-headed blackbirds *Xanthocephalus xanthocephalus*, Price and Ydenberg 1995; and tree swallows, Leonard and Horn 1998). However, begging rates are not always sensitive to competition within the nest (see Kacelnik et al. 1995; Cotton et al. 1996; Ostreiher 1997). Second, offspring size can affect the intensity of begging, independent of nestling hunger. Nestlings often beg by stretching out and gaping towards the parent, and parents often feed chicks who reach highest (Smith and Montgomerie 1991; Teather 1992; Leonard and Horn 1996). In species where young hatch asynchronously, however, the difference in ages of chicks within the brood will predictably influence a nestling's intensity of begging. If parents simply feed young who reach highest, larger, older chicks will obtain more food. Third, begging is also highly variable (e.g. Hussell 1988; Redondo and Castro 1992) suggesting that early experience can increase or decrease begging levels. In budgerigar (*Melopsittacus undulatus*) broods begging was strongly influenced by early patterns of parental food allocation. Begging rates increased within hours in broods where fathers, who were responsive to chick begging, started to feed nestlings, but not in broods where only mothers fed young (Stamps et al. 1985; 1989).

If begging by nestlings does not reflect only hunger, parents should benefit by ignoring or devaluing begging under some circumstances. Parents in some species use physical characteristics of chicks, as well as begging to allocate food. In canaries (*Serinus canaria*) and great tits (*Parus major*), parents allocated food to nestlings based on mouth colour (Gotmark and Ahlstrom 1997; Kilner 1997), a signal which correlates strongly with hunger in young nestlings (Kilner 1997). American coot (*Fulica americana*) parents preferentially fed nestlings with orange head plumes, and solicitation by nestlings involved displaying their heads to parents rather than vocalising (Lyon et al. 1994). Parents selectively distribute food to chicks based on their size in pied flycatchers (*Ficedula hypoleuca*, Gottlander 1987), red-winged blackbirds (*Agelaius phoeniceus* , Westneat et al. 1996) and tree swallows (Leonard and Horn 1996), and on condition in budgerigars (Stamps et al. 1985).

Parents can also regulate the distribution of food within broods by responding flexibly to nestlings. Parents can bias the distribution of food by responding more to solicitation by certain chicks. For example, last-hatched chicks beg more intensely but are not fed more in some asynchronously hatching species (Bengtsson and Ryden 1983; Price and Ydenberg 1995; Lotem 1998). Mothers and fathers differ in how they allocate food to large and small nestlings, with mothers generally feeding smaller chicks (Stamps 1985; Gottlander 1987; Westneat et al. 1995; see Slagsvold 1997 for a review). Parents can alter the distribution of food within the brood to favour different chicks in response to changes in food availability (Gottlander 1987; Boland et al. 1997).

The allocation of food within broods of asynchronously hatching crimson rosellas (*Platycercus elegans*) is a consequence of complex distribution patterns by parents (Chapter 4). Mothers distributed food evenly to chicks irrespective of hatching rank. In contrast, fathers distributed more food to first-hatched chicks. These differences imply that parents are able to regulate the distribution of food to nestlings; however, they could also be the result of differences in chick behaviours towards parents. To assess whether the distribution of food is primarily under parental or chick control in rosellas, I increased hunger within the brood independently for a single chick, and for the entire brood together. This allowed me, first, to determine how changes in hunger affected solicitation by first- and last-hatched chicks and, second, to examine how parents and chicks responded to increased competition for food within the brood. If chicks determine the distribution of food within the brood, chick behaviours should strongly influence whether a nestling is fed or not, whereas if parents determine the distribution of food, food allocation should not always be based on nestling behaviours.

Methods

SPECIES AND STUDY METHODS

Crimson rosellas are a broad-tailed parrot which breeds commonly in eastern Australia. The sexes have similar plumage, but males are about 15% larger than females and have slightly broader bills (Krebs unpublished data). Rosellas breed in socially monogamous pairs (Forshaw 1981). The female incubates the eggs and broods small nestlings. Males feed incubating and brooding females until the brood is approximately 5 days old, at which point both parents feed the young directly. Crimson rosellas are typically single-brooded and lay from 3 to 8 eggs (mean ± sd = 5.1 ± 0.1, n = 64). Females usually lay eggs at 2 day intervals and initiate incubation in the middle of the laying sequence so that broods hatch asynchronously over 1.5 to 7 days (mean ± se = 3.5 ± 0.5; Chapter 2).

In 1993 and 1994, I placed a total of 46 nestboxes in dry sclerophyll eucalypt forest (*Eucalyptus rossi, E. macrorhyncha*) in Black Mountain Nature Reserve. Nestboxes were spaced 50 metres apart in a grid system and mounted approximately 4 metres above the ground. Each box had a hinged lid, and was fitted with a removable nest floor supported by wooden blocks. The nest floor could be reached by a small door on the front of the box. Eighty percent of all boxes were occupied by rosellas in each year, although high levels of egg destruction meant that not all birds raised chicks.

I visited boxes daily during the predicted hatching period until all nestlings had hatched. Where the order of hatching was observed directly I assigned a hatching rank to each chick (first, second, etc.) and a hatching time to the nearest 0.5 day, based on the dryness of a chick and its crop contents. Where more than one chick hatched on the same day, hatch time was assigned based on a combination of wing chord and dryness of the down. In broods where several chicks had already hatched, chicks were assigned ranks retrospectively using a regression of wing chord on age for all chicks of known hatching times. These broods were never more than 4 days old, and I never noted rank reversals early in the nestling period.

All newly hatched chicks were marked by trimming the down on different parts of the body, and older chicks were marked with a single colour band to allow individual recognition. Nestlings were weighed to the nearest 1 g, using Pesola spring balances.

Sexing nestlings

I sexed nestlings from DNA extracted from blood and used a PCR based sex-specific genetic marker (see Griffiths et al. 1998 for details of the method).

Feeding observations

Rosella parents feed chicks by regurgitating seeds directly into their mouths in a series of food transfers. To quantify the number of food transfers a parent makes to each chick during a feeding visit, I videotaped feeding visits using a miniature black and white CCD video camera with infra-red illumination (Oatley Electronics, NSW) attached to the lid of the nestbox. The output was recorded onto a portable video recorder (Sony VideoWalkman GVS50) located on the ground below the nestbox. Chicks were marked with a unique number of black paint spots (non-toxic tempera paint) to allow individual recognition.

Although the number of transfers indicates the relative distribution of food to chicks during each feeding visit, the amount of food delivered by parents also varied between feeding visits (Chapter 4). To quantify the size of parental food deliveries, I simultaneously recorded mass changes in the nestbox by placing a digital balance (Sartorius PT6) under the false nest floor. Output from the balance was monitored by a portable computer (Zenith Supersport 286) running specially designed software (NestBug; Szép et al. 1995). This software continuously recorded any mass changes (feeding deliveries) within the nestbox over the day.

MANIPULATION OF CHICK HUNGER

I deprived nestlings of food in nine experimental broods in 1995 to examine whether hunger altered the distribution of food within the brood. I manipulated hunger in two ways by: (i) removing an individual chick within the brood ('Individual hunger experiment') and (ii) removing the whole brood ('Brood hunger experiment'). In the individual hunger experiment I deprived first- and last-hatched chicks of food separately to assess the effect of hatching rank.

Individual broods vary in their growth rates (see Chapter 3), therefore I chose an experimental design which allowed each brood to be used as its own control. Treatments were sequentially applied to a particular brood over 7 days (see Chapter 5 for details). I alternated the order in which I removed first- and last-hatched chicks in the individual hunger experiment so that chicks of neither rank were consistently older during removals.

The experimental design chosen minimised inter-brood variation between control and experimental manipulations, but resulted in brood age increasing over subsequent treatments. Within an experiment, control and removal treatments were separated by a maximum of 3 days (Table 1), a small difference relative to the 35 day nestling period. Nestling growth was linear over the brood ages monitored and size asymmetries within a brood were stable within each experiment, but decreased by 14% (paired difference = 5.0 ± 2.1 g) between the two experiments.

Experimental broods had four to seven nestlings. To standardise between broods with varying degrees of hatching asynchrony, I began experimental manipulations when the last-hatched chick was 8 days old. I removed target chicks from the brood prior to the first feeding visit of the day, and returned them three hours later. Removed chicks were kept in a warm, dark box, and appeared to suffer no long term effects. Removals resulted in target chicks missing 2 to 4 feeding visits by parents (mean mass gain in control chicks = 4.1 g; mass loss in removal chicks = -2.4 g). I assume that the mass loss resulting from chick removals led to increased hunger by nestlings. When removing single chicks I did not provide a replacement chick during the removal period, but when I removed the whole brood I substituted 2 to 4 chicks of a similar age. Consequently the brood size experienced by parents during the three hour removal period was smaller than their "normal" brood size.

On each monitoring day, I measured and weighed each chick at approximately 0630, prior to removals, 0930, after any removals, and 1530. I recorded feeding visits to the nestbox for 9 hours, from approximately 0630 to 1530 hours and videotaped feeding visits in each box for 6 continuous hours starting at approximately 0930, after removal chicks were returned to the nestbox. In most cases, I set up equipment and weighed and marked chicks before parents returned for the first morning feed, thereby minimising disturbance. Parents did not appear to be deterred from visiting the nestbox by the appearance of monitoring equipment and entered and fed chicks 5 to 15 minutes after arriving back at the box, as observed at unmanipulated boxes.

ANALYSIS

Mass data

The mass of food delivered to the nestbox was estimated by subtracting a parent's mass on entering the nestbox from their mass on leaving. Data recorded from the digital balance consists of a series of weights (maximum = 120) which were saved before and after adults entered or left the box. These raw data files were edited for consistency and the edited files were summarised using NestBug Visit Analyser Software (Z. Toth, unpublished; see Chapter 4 for details).

Video data

I analysed each feeding visit using a desktop video player (Sony E6500) that allowed slow motion and frame by frame playback. Since parents regurgitate food to nestlings many times during a feed, examining interactions between chicks requires detailed assessment of nestling position and nestling and parental behaviour prior to each food transfer over the whole feeding visit. I did this by examining a single feeding visit by mothers and fathers under each control and experimental manipulation. In total, 90 feeding visits were examined. I selected the first feeding visit by each sex of parent after the experimental manipulations, provided the feed had at least twice as many transfers as chicks, and only one parent was present in the box. The sex of the parent entering the box was identified by bill morphology and pair specific plumage differences or the presence of leg bands. I recorded time of day, and the number and sequence of food transfers to each chick. The proportion of food transfers to each chick correlated strongly to their mass gain over the day (Chapter 4). Therefore I have assumed that all food transfers are equal in size, both between chicks and over the entire sequence of a feed. Although I have no way of testing this assumption directly, all bill contacts appeared to involve at least some food transfer.

To obtain detailed data of parent and chick interactions during feeding visits, I measured two variables: chick begging and the position of a chick relative to a feeding parent. Rosella chicks beg by vocalising, flapping their wings, and bobbing up and down. I assigned the begging of chicks to one of three categories: (i) not begging -

chicks not vocalising, wing flapping or bobbing; (ii) weak begging - chicks vocalising but without accompanying body movements; and (iii) intense begging - chicks vocalising strongly, flapping wings and bobbing up and down. The begging of target chicks was assessed prior to each consecutive transfer (i.e. after a transfer was completed and before the next transfer commenced). I assigned a nominal score of 1 (no begging), 2 (weak begging), or 3 (intense begging) to each begging category and calculated a mean score for each chick over each feeding visit.

Chick position was measured as the beak to beak distance (mm) from the target chick to the feeding parent and was assessed during the interval between food transfers (as above). Since chicks who are generally closer to parents during a feeding visit are likely to be fed more often, I used the mean position of a target chick during a feeding visit in subsequent analyses.

Statistics

I analysed the data using models appropriate for multilevel data because hatching rank and treatments were replicated within nestboxes. My data were unbalanced, and therefore unsuitable for conventional 'analysis of variance' (and particularly repeated measures designs), so I used a mixed model incorporating random and fixed effects (REML Restricted Maximum Likelihood; GENSTAT 5 Commitee 1993).

I was unable to control experimentally for differences in the sex ratio of broods, since the DNA sexing technique had not yet been developed. However, retrospective sexing showed that the sexes were relatively evenly distributed among first and last-hatched chicks (5/9 first-hatched chicks and 3/9 last-hatched were male). Since sample sizes for males and females within each hatching rank were too small for strong inference, I statistically removed the effect of sex by including it in the random structure of models.

To evaluate the impact of changes in chick hunger, I compared between chicks on control and removal days. Nestbox, chicks within boxes and chick sexes within boxes were included in all models as random terms. I fitted separate models for individual chick and brood hunger experiments and for the following response variables:

mean begging score, chick position relative to the parent and the proportion of food transfers obtained during a feed. I used the proportion of food transfers to each chick in preference to the number of transfers because the proportion is less affected by load size, brood size or brood age. I wanted to examine the relationship between chick solicitation and parental feeding behaviours, therefore I have evaluated how parents distributed food during each feeding visit where I have measured chick behaviours, although I have done so already for the larger data set in Chapter 5.

I fitted models assessing changes in begging scores and chick position using three explanatory variables: hunger treatment (control vs. removal), chick hatching rank (first vs. last), parental sex and all two and three-way interactions. To examine how parents distributed food relative to changes in chick behaviour, I included the following explanatory variables: hunger treatment, chick hatching rank, parental sex, begging score, chick position, and relevant two and three-way interactions. Variables were then dropped from the model in a stepwise procedure by assessing the change-in-deviance, which approximates a Chi-squared distribution, between the full model and the sub-model (GENSTAT 5 Commitee 1993). Significant terms were included in subsequent model fitting. The final model was selected by sequentially dropping non-significant interactions and then non-significant main effects, until only significant terms remained.

When complex modelling was not required I used paired t-tests to examine differences between variables. In all analyses, frequency histograms, residual plots and normal probability plots were examined for unequal variances and deviations from normality and transformations applied if necessary. I have reported main effects or interaction terms from a model where they are significant, or a statistical trend ($0.05 < p < 0.10$) and non-significant terms or interactions where they are of particular relevance. Means and standard errors are reported throughout, except where otherwise indicated.

Results

INDIVIDUAL HUNGER EXPERIMENT

An individual chick who was hungrier than the rest of the brood did not increase the intensity of its begging (hunger effect, $\chi^2_1 = 1.8$, $p > 0.10$; Figure 1a). Overall, last-

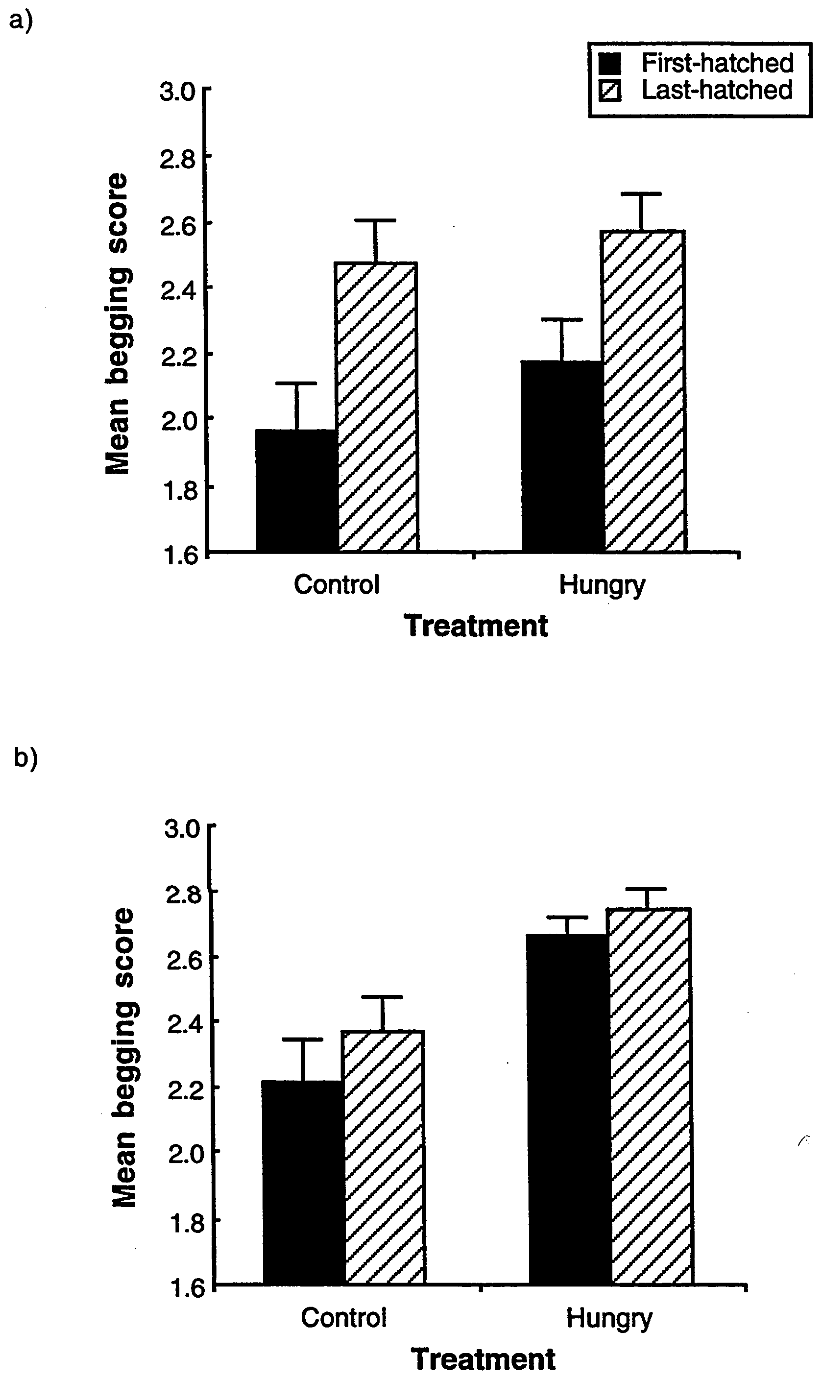

Figure 1. The begging scores of first- and last-hatched chicks during a feeding visit in control and experimental periods, plotted separately for when a) an individual chick and b) the whole brood was hungry (n = 9 broods).

hatched chicks begged more intensely than first-hatched chicks during both control and experimental periods (rank effect, $\chi^2_1 = 14.9$, $p < 0.001$; Figure 1a).

Hungry chicks were not positioned closer to a feeding parent than during the control period (hunger effect, $\chi^2_1 = 0.2$, $p > 0.75$; hunger*rank interaction, $\chi^2_1 = 0.0$, $p > 0.99$). However first-hatched chicks tended to be closer to fathers and last-hatched chicks tended to be closer to mothers during feeding visits, irrespective of nestling hunger (rank*parental sex interaction, $\chi^2_1 = 3.1$, $p < 0.10$; rank*parental sex*hunger interaction, $\chi^2_1 = 0.0$, $p > 0.99$; Figure 2).

Chicks tended to be fed more when they were hungrier than the rest of the brood, or when they were positioned closer to either parent (hunger effect, $\chi^2_1 = 3.7$, $p < 0.10$; position effect, $\chi^2_1 = 3.3$, $p < 0.10$; no significant interactions). Chicks were sometimes fed more when they begged more intensely, but the response depended on both parental sex and chick hatching rank (begging*parental sex*rank interaction, $\chi^2_1 = 7.2$, $p < 0.01$). To examine this complex relationship in more detail, I calculated correlation coefficients between chick's begging scores and the proportion of food transfers obtained separately for each hatching rank, parental sex, and hunger level (Table 1). Fathers fed last-hatched chicks in proportion to their begging both during the control and experimental periods, and appeared to be more responsive to begging by last-hatched chicks when they were hungry (Table 1). In contrast, mothers fed first-hatched chicks in proportion to their begging during the control and experimental periods, but appeared less responsive to begging when first-hatched chicks were hungry (Table 1).

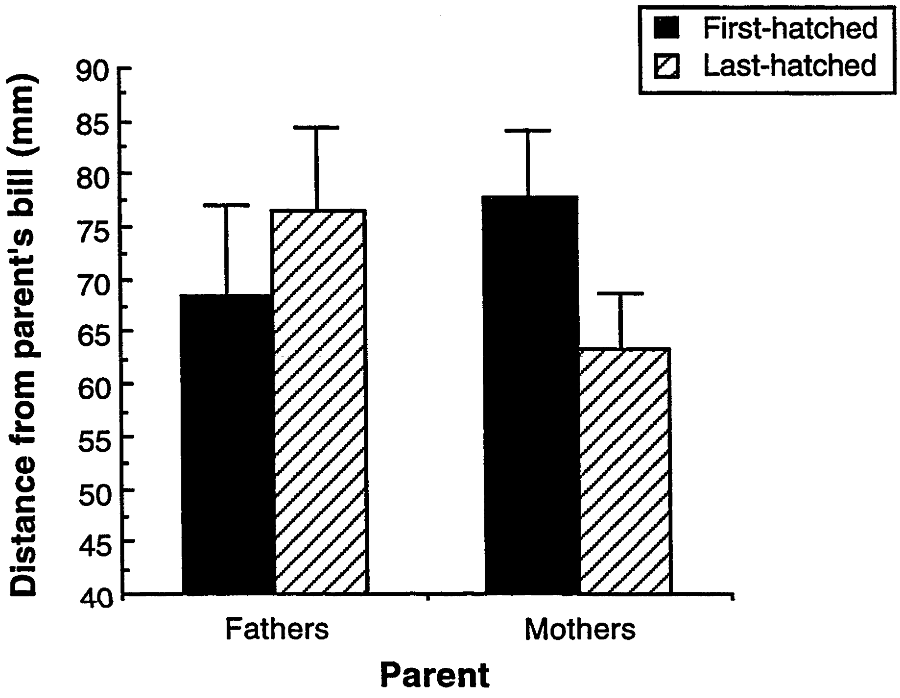

Figure 2. The proximity of chicks to parents (see Methods) during feeding visits by mothers and fathers in the individual chick hunger experiment, plotted separately for first and last-hatched chicks.

Table 1. Correlations between the proportion of food transfers obtained by a chick and its mean begging level during that feeding visit for control periods and when chicks were individually hungry. Feeding visits by mothers and fathers are presented separately.

	CONTROL		**HUNGRY**	
Parent feeding	**First-hatched**	**Last-hatched**	**First-hatched**	**Last-hatched**
Mothers	0.76 (9)	-0.29 (9)	0.38 (9)	-0.11 (9)
Fathers	0.05 (9)	0.55 (9)	-0.51 (8)	0.81 (8)

BROOD HUNGER EXPERIMENT

Chicks begged more intensely when the whole brood was hungry relative to the control period (hunger effect, $\chi^2_1 = 20.7$, $p < 0.001$; Figure 1b). Begging intensity did not differ between first- and last-hatched chicks during the control or experimental periods (rank effect, $\chi^2_1 = 0.5$, $p > 0.75$; rank*hunger interaction, $\chi^2_1 = 0.0$, $p > 0.99$).

Neither first- nor last-hatched chicks were positioned closer to parents when the whole brood was hungry (hunger effect, $\chi^2_1 = 0.0$, $p > 0.99$; hunger*rank interaction, $\chi^2_1 = 0.0$, $p > 0.99$). No measured variable predicted chick position during this experiment (all $\chi^2 < 2.0$).

Chicks were fed more when they were closer to a feeding parent ($\chi^2_1 = 30.4$, $p < 0.001$) regardless of brood hunger (position*hunger interaction, $\chi^2_1 = 1.5$, $p > 0.10$). Overall, first-hatched chicks were fed more than last-hatched chicks during both control and experimental periods (rank effect, $\chi^2_1 = 4.8$, $p < 0.05$; rank*hunger interaction, $\chi^2_1 = 1.7$, $p > 0.10$). Chicks were not fed more when they begged harder (begging effect, $\chi^2_1 = 0.15$, $p > 0.50$; no significant interaction.

CHANGES BETWEEN THE TWO EXPERIMENTS

Since the individual hunger and brood experiments were conducted at different brood ages, chick behaviours could change between the two periods due simply to nestlings being older. Mean begging scores of chicks did not increase when the brood was older (control at brood age 8 days = 2.2 ± 0.1, control at brood age 14 days = 2.3 ± 0.1, paired t-test $t = -0.5$, $df = 33$, $p = 0.60$). In contrast, chicks were positioned further from the feeding parent when the brood was older (8 days = 68.7 ± 4.3 mm, 14 days = 95.2 ± 7.1 mm, paired t-test, $t = -3.1$, $df = 33$, $p = 0.004$).

If competition for food is higher when the whole brood was hungry, the intensity of chick begging may increase simply due to the effects of competition. To assess this, I compared the difference in begging scores between hunger and control treatments during the brood and chick hunger experiments. The difference in begging intensity (hungry - control) was higher during the brood hunger experiment (chick hungry = 0.1 ± 0.1 $n = 9$; brood hungry = 0.4 ± 0.1, $n = 8$; $\chi^2_1 = 4.3$, $p < 0.05$).

Discussion

The unexpected result of this study was that rosella nestlings did not always beg more intensely when they were hungry. Chicks begged more intensely when all chicks in the brood were hungry, but not when only one chick was hungrier than the rest of the brood. When individual chicks were hungry, parents tended to feed them more, and responded in a complex way to begging. Fathers fed last-hatched chicks in proportion to how intensely they begged during a feed, especially when hungry. Mothers fed first-hatched chicks in proportion to their begging intensity, although the relationship was weaker when the chick was hungry. Parents did not respond more to the begging of particular chicks because they were closer to them, in fact the opposite pattern was observed. First-hatched chicks tended to be closer to fathers, whereas last-hatched chicks were closer to mothers during the individual hunger experiment. Parents in both the individual and brood hunger experiments fed chicks that were positioned closer to them, but hungry chicks were not closer to a feeding parent than during control periods.

CHANGES IN CHICK BEHAVIOURS

Changes in begging intensity correlate to changes in nestling hunger in most species (Bengtsson and Ryden 1983; Redondo and Castro 1992; Kacelnik et al. 1995; Price and Ydenberg 1995; Kolliker et al. 1998). For example, food deprived yellow-headed blackbirds nestling begged more intensely when deprived of food, and begged less intensely when fed (Price and Ydenberg 1995). In contrast, begging by rosella chicks did not reliably signal nestling hunger since chicks did not beg harder nor obtain a position closer to a feeding parent when individually deprived of food. Rosella nestlings may not have responded to removals if they were too short in duration to significantly increase hunger. This is unlikely to be the case, since nestlings consistently lost mass, and begging increased after the whole brood was deprived of food. In addition, parents were able to identify nestlings who had been removed, and feed them more. Thus chick removals most likely increased nestling hunger.

It is not clear how rosella parents were able to evaluate chick hunger. Since I only measured changes in the overall intensity of begging, individually hungry chicks potentially changed their begging in subtle ways, such as by increasing the volume or frequency of their vocalisations. Price and Ydenberg (1995) analysed several aspects of begging calls in yellow-headed blackbird chicks and found that intensity and order of begging, but not volume, increased when chicks were hungry. Subtle changes seem unlikely to explain the lack of measured response to hunger by individual rosella chicks. Similar measures of begging correlate strongly to changes in hunger in other studies (e.g. Smith and Montgomerie 1991; Redondo and Castro 1992; Leonard and Horn 1996) and the intensity of begging differed markedly between first- and last-hatched rosella chicks.

The benefits of increased begging by individually hungry chicks may be relatively low in rosellas because parents use multiple cues to evaluate nestling hunger. Nestlings often solicit for food in a number of ways, vocalising, posturing or competing for a certain position within the nest, and parents frequently allocate food based on a combination of these behaviours. For example, Teather (1992) found that parents tended to feed nestlings who begged first, reached the highest and were closest to the parent.

Parents may also use different aspects of nestling solicitation to distribute food under different conditions. In canaries, parents typically fed the closest chicks (Kilner 1995). However, when different sized chicks were individually deprived of food, parents allocated more food to all hungry chicks, even small nestlings who never moved closer to parents (Kilner 1995). Since rosella nestlings did not beg more intensely or get closer to parents, parents may use some other unmeasured cue to assess chick hunger. One physical cue which unambiguously signals the previous distribution of food is the crop sizes for each chick. Crop sizes in rosellas are conspicuous, especially when the brood is young, and directly correlated to food allocation.

If begging functions in rosella broods to signal overall food requirements of the brood, rather than individual hunger, the benefits of increased begging will also be low for individual chicks. Parents increase feeding rates to the nest in response to long term playbacks of brood begging calls in several species (pied flycatchers, Ottosson et al. 1997; yellow-headed blackbirds, Price 1998). Parents are also induced to continue provisioning at high rates when a cuckoo chick begs because their begging mimics the sound of begging by a whole brood (Davies et al. 1998). Rosellas did not increase provisioning in response to short term manipulations of individual or brood hunger (Chapter 5), however they might increase feeding rates in response to long term changes in brood begging.

Nestlings can vary not only in their short term hunger, but also in their condition, or mass required to fledge (Price et al. 1996). By removing chicks from the nest, I increased their short term hunger, but did not alter their long term nutritional requirements. Price et al. (1996) demonstrated that begging can vary according to the long term needs of nestlings. Male yellow-headed blackbirds are larger at fledging and consistently begged more than females. Female chicks in good condition begged less than females in poor condition after food deprivation (Price et al. 1996). Last-hatched nestlings will generally have higher long term needs and are observed to beg more in many asynchronously hatching species (e.g. great tits, Bengtsson and Ryden 1983; budgerigars, Stamps et al. 1985; yellow-headed blackbirds, Price and Ydenberg 1995;

barn swallows, Lotem 1998). Thus, last-hatched rosella nestlings may have begged more during the individual hunger experiment because they had higher long term needs.

Last-hatched rosella nestlings begged more than first-hatched nestlings, but only during the individual chick hunger experiment. The differences in the begging of first- and last-hatched chicks disappeared during the brood hunger experiment because first-hatched chicks begged more intensely (Figure 1). Since the size hierarchy within the brood decreased slightly between the two experiments (see Methods), this suggests that begging strategies by first-hatched chicks were sensitive to the magnitude of the size hierarchy as suggested by Parker et al. (1989).

Nestling competition may enhance changes in begging within rosella broods. When the whole brood was hungry, and competition for food relatively high, broods begged more intensely. Competition between nestlings can increase begging independently from changes in hunger (Smith and Montgomerie 1991; Price and Ydenberg 1995; Leonard and Horn 1998). Broods of American robins, begged more intensively after one nestling was deprived of food (Smith and Montgomerie 1991). Leonard and Horn (1988) found that tree swallow chicks begged less intensely in nests where half the chicks were deprived of food than in nests where the whole brood was deprived, although the proportion of chicks begging increased for both types of broods. This is consistent with the pattern observed in rosellas, begging rates increased relatively more when the whole brood was hungry. Thus begging levels in rosella broods are affected more strongly by nestling competition than by nestling hunger.

PARENTAL RESPONSES TO CHANGES IN CHICK BEHAVIOUR

Parent rosellas responded in a complex way to begging by chicks. Overall food allocation patterns during these experiments (Chapter 5) showed that mother and fathers distributed food differently to first- and last-hatched chicks during manipulations of chick hunger. Mothers allocated food equally to chicks during the individual chick hunger experiment, implying that they selectively fed last-hatched chicks of low competitive ability. Fathers, in contrast, favoured first-hatched chicks during the control period, and last-hatched chicks when they were hungry. Mothers did not change how they distributed food when a chick was hungry, and fathers did not feed hungry first-hatched chicks more, hence parents appear to allocate food in a relatively fixed way to these chicks. Since parents did not only feed their 'favourite' chicks, how did they allocate food to other chicks in the brood? The correlations between how much a chick was fed versus its begging score suggest that parents fed non-preferred chicks in proportion to their begging effort. Thus parents used begging to fine tune the distribution of food within the brood, although they use other cues when determining the overall patterns of food allocation.

Parents respond in complex ways to begging by nestlings in other species. Parents can be more or less responsive to begging by certain chicks. Last-hatched nestlings beg more intensely in many asynchronously hatching species, but obtain less food than first-hatched chicks (Bengtsson and Ryden 1983; Drummond 1986; Price and Ydenberg 1995; Lotem 1998). Parents can also differ in their responses to begging. In budgerigars, Stamps et al. (1985) found that mothers did not feed broods more if they begged more. However, fathers respond to begging, and rapidly increased their feeding rates when the brood begging increased. Kolliker et al. (1998) found that in great tits, mothers fed food-deprived chicks at a higher rate than fathers. This lead to nestlings selectively moving towards parents depending on their hunger level.

Although rosella parents did not respond to changes in begging by chicks they preferred to feed, these chicks tended to be positioned closer to the parent who fed them most; first-hatched chicks were found closer to fathers and last-hatched chicks, closer to mothers. Distance from a feeding parent frequently influences whether a nestling is fed (Smith and Montgomerie 1991; Teather 1992; Leonard and Horn 1996). In rosellas, nestlings were fed more when they were closer to parents. However it is difficult to know whether parents or chicks control their relative positions. Rosellas regurgitate and move many times during a feeding visit (Chapter 5), therefore, the distance between a chick and parent at one time is a composite of chick and parental movements. Proximity to the parent can be affected both by competition between nestlings, or parental behaviours (Kilner and Johnstone 1997). Since hungry chicks did not obtain positions closer to parents, despite the fact that parents fed close chicks more, parents may control the relative positions of chicks through their movements. If this is the case, chicks were fed more by a particular parent, because of parental preferences and not chick behaviours.

DO PARENTS OR CHICKS CONTROL THE DISTRIBUTION OF FOOD WITHIN BROODS?

The patterns of food allocation (Chapter 4) and the responses to hunger manipulations within broods (Chapter 5) suggest that parents largely control the distribution of food in crimson rosellas. Mothers and fathers allocated food differently to nestlings, but not because of differences in nestling behaviours as suggested by Slagsvold (1997). Neither begging intensity nor chick position differed towards mothers or fathers when a chick or the whole brood was hungry. In addition, the behaviours of nestlings observed in this study did not correlate consistently to nestling hunger, or predict the distribution of food within broods. Direct parental control of food allocation has not been observed in an experimental study (but see Stamps et al. 1985, and Kolliker et al. 1998 for non-experimental examples). In contrast, several experimental studies have shown that competition between nestlings determines the distribution of food (Ostreiher 1997; Kacelnik et al. 1995; Kilner 1995)

Ultimately this study raises more questions about food allocation in crimson rosellas than it answers. The lack of a strong relationship between nestling hunger and begging is difficult to reconcile with any model of the evolution of begging. Rosella parents allocate food based on chick size and hunger, and the priority given to each cue differs between the sexes. Experiments are required which control for variation in nestling hunger, and independently examine the effects of nestling competition and hunger (e.g. Kilner 1995). Rosella parents are clearly sensitive to variation in chick hunger, but how this is signalled, and why mother and fathers respond differently remains unclear. Rosella parents engage in behaviours apparently aimed at reducing competition within broods (Chapter 5). Since parental and nestling behaviours are closely co-evolved, the value of begging may be relatively low in this species because parents control the distribution of food.

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Chapter 7

Synthesis and future directions

Synthesis and Future directions

My work on crimson rosellas has shown that interactions between parents and young are complex, and structured differently from most other species studied. In this chapter I outline some of the unresolved issues arising from my research, and suggest the type of experiments which might begin to resolve them.

What is the function of hatching asynchrony in crimson rosellas?

Rosella broods hatch asynchronously with the time period ranging from 12 hours to seven days. Asynchronous hatching functions to facilitate brood reduction when food becomes scarce in some species (Lack 1947; Magrath 1989; Osorno and Drummond 1995). However, hatching asynchrony can also arise because of constraints on incubation patterns, or because it increases parental feeding efficiency (see Stoleson and Beissinger 1995 for a review). Hatching asynchrony might facilitate brood reduction in rosellas. The allocation of food within broods shifted in a way which would facilitate brood reduction when food became scarce. However, brood reduction in rosellas always occurred at hatching when last-hatched chicks were never fed and subsequently died. Furthermore, the probability of brood reduction was not related to the degree of hatching asynchrony suggesting a large size hierarchy is not necessary to allow brood reduction.

Rosellas can minimise the costs of large size hierarchies in asynchronously hatching broods by selectively feeding nestlings. Thus hatching asynchrony did not result in reduced growth and survival of later hatched chicks (cf. Bryant 1978; Werschkul 1979; Amundsen and Slagsvold 1991; Stoleson and Beissinger 1997). The costs of hatching asynchrony are low in rosellas because parents control the distribution of food and feed last-hatched chicks when food is abundant.

Some rosellas broods hatch relatively synchronously, although the costs and benefits of synchrony are unclear. Synchronous hatching is costly to parents in other species because it increases the level of competition between siblings. Increased competition can increase the energy expenditure of the brood and artificially synchronised broods can have higher feeding rates, or poorer growth than asynchronous broods (Hahn 1981, Fujioka 1985, Wiebe and Bortolotti 1994a).

The optimal levels of hatching asynchrony in rosellas may vary seasonally or between individual females. Female American kestrels (*Falco sparverius*) manipulated hatching asynchrony in response to predicted food abundance, suggesting optimal hatching patterns differ between females (Wiebe and Bortolotti 1994b). Hatching asynchrony in rosellas was highly variable and increased over the breeding season. Thus there may be seasonal, or individual advantages to a given level of hatching asynchrony.

To examine the costs and benefits to differing levels of hatching asynchrony in rosellas, experiments are required that manipulate hatching patterns both early and late in the breeding season. The costs of provisioning synchronous broods can be compared with those of provisioning aynchronous broods. If the benefits vary seasonally asynchronous hatching should reduce brood productivity early in the season, but enhance productivity late in the season.

Why do male and female rosellas allocate food differently?

There is little consensus as to the reasons that males and females might allocate food differently within broods in species with biparental care. Potentially parents differ in their ability to discriminate between nestlings, their relatedness to all offspring, their investment in current reproduction (see Slagsvold 1997 for a review). In this study, male and female rosellas differed not only in which chicks they fed most, but in their overall strategies of food allocation. These differences do not seem to be a consequence of males or females differing in their familiarity with the brood or in their ability to discriminate between chicks as suggested by Gottlander (1987). In rosellas both sexes selectively fed small chicks, but under differing circumstances. Thus the costs and benefits of allocating food within the brood must vary in a complex way for males and females.

I attempted to understand which cues parents use to feed chicks by manipulating the hunger of chicks in this study. However neither parent responded in a simple way to chick hunger, and chicks did not change their behaviours as predicted. To understand why parents allocate food in different ways to nestlings, future experiments should manipulate the costs of delivering and distributing food, for each sex separately, without changing the behaviour of nestlings. One way this could be done is by “handicapping” each sex at different times (or in different broods) by attaching small weights to their body (e.g. Wright and Cuthill 1990). A second experiment could reduce the cost of provisioning by providing supplemental food. If males and females have different strategies for distributing food, they should respond differently to increased costs of provisioning. For example, if males distribute food based on short-term changes in chick hunger and females distribute food based on the long-term survival of the brood, patterns of food allocation should only change for females if the costs of provisioning are altered. These designs would also have the advantage of allowing examination of long-term changes in food allocation.

What is the function of begging in rosellas?

Begging in most birds signals nestling hunger. Experimental manipulations have consistently shown that nestlings beg more when they are hungry and that parents increase feeding rates to broods in response to begging (Kilner and Johnstone 1997). However, in this study, begging did not correlate to chick hunger in a straightforward way. Only chicks who were begging were fed, however they did not obtain more food by begging more intensely. Hungry chicks only begged more intensely when the whole brood was hungry. Thus nestling competition appears to be more important than nestling hunger in regulating the level of begging within broods.

My experiments examining the behaviour of hungry chicks may have been confounded by two factors. First, depriving chicks of food without first controlling chick hunger levels, produces only crude changes in chick hunger. This problem also applies to my ‘control’ periods, where I assumed that hunger was relatively low. Nestling hunger can be controlled in a more precise way by first feeding chicks to satiation, and then starving them for a standard period of time (e.g. Price et al. 1996).

A second confounding factor in my manipulations of nestling hunger was that I simultaneously examined the effects of begging and scramble competition on the distribution of food. If the begging and scramble competition interact in a complex way to produce the observed distribution of food, I may not have detected a separate response to each factor. To evaluate the role that begging and scramble competition have in food allocation, it is necessary to manipulate one independently of the other. One way of removing the effects of scramble competition between nestlings is by physically dividing the brood within the nestbox using partitions (e.g. Kilner 1995). Since parents may also respond to the height that nestlings reach (e.g. Teather 1992), I could also alter the relative heights of nestlings within the brood and examine the effect of height, independent of size and hatching rank within broods.

Research to date suggests that food allocation in rosella broods is primarily under parental control and that parents do not use the intensity of begging behaviours to distribute food. This suggests that parents use alternate cues to distribute food. However, in these initial experiments, I was unable to clearly separate whether parental or chick behaviours produced the observed food distribution. Experiments are required that examine the responses of parents and chicks to increased hunger, but where nestling hunger is better controlled, and the effects of competition examined separately. If parents are able to completely control the distribution of food, the benefits of begging may be low for nestlings. In addition, parents may be more likely to rely on physical signals which are not affected by the competitive ability of nestlings (e.g. Kilner 1997).

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