Conflict & Communication:
Consequences Of Female Nest Confinement In Yellow Billed Hornbills

This dissertation is submitted for the degree of Doctor of Philosophy

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Preface

This dissertation is my own work and contains nothing which is the outcome of work done in collaboration with others, except as specified in the text and acknowledgements. The total length of the text does not exceed 60,000 words, including the bibliography and appendices. No part of this dissertation has been submitted to any other university in application for a higher degree.

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Summary

The most striking feature of hornbills (*Bucerotiformes*) is their unusual nesting behaviour. Before laying, a female hornbill enters the nest in a tree cavity. Uniquely among birds, she then seals the nest entrance using her faeces and locally available materials, leaving a narrow gap only 1 cm wide. Through this tiny slit, the female is totally dependent on her mate for between 40 days in the smallest hornbills and up to 130 days in the largest. Once walled in the nest, the female will lay her eggs and shed all of her wing and tail feathers. The male then becomes completely responsible for provisioning his mate and a few weeks later, the chicks. When her feathers have regrown, the female breaks out of the nest, often before the chicks are fully grown. The chicks then reseal the entrance until they too are ready to fledge.

This thesis describes attempts to better understand the nesting behaviour of hornbills. The first chapter introduces hornbill ecology and behaviour and highlights their potential as model systems for studying conflict and communication. Chapter 2 describes the methods used to set up a study population of Southern Yellow-Billed Hornbill (*Tockus leucomelas*) consisting of 47 occupied nest boxes, over 35km^2 in the Southern Kalahari Desert, South Africa.

Chapter 3 summarises behaviour over three breeding seasons from October 2008 to April 2011. Female feather moult followed a precise staggered pattern, unlike other populations. Widespread filial cannibalism by females of both eggs and chicks was observed for the first time. The possible proximate causes of cannibalism are explored. Egg cannibalism allowed females to recoup some of their energetic investment, while cannibalism of chicks served as an efficient mechanism of brood reduction for nests with low paternal feeding rate. Chapter 4 investigates how females communicate need for nesting materials to males. Females altered the rate and structure of their begging calls when experimentally deprived of nest lining and males in turn delivered more nest materials. Chapter 5 examines the factors that determine how long females remain in the nest. Females with larger broods stayed in the nest longer, irrespective of their own or their chicks' condition or male feeding rates. This raises questions about the role of mothers in the nest. Chapter 6 addresses this issue, demonstrating that females controlled sibling competition in the nest. Experimental temporary removal of mothers led to increased intrabrood aggression and more uneven food distribution in the brood, with larger chicks taking a greater share. The final chapter draws these findings together and the potential for future research is discussed.

Acknowledgements

Since someone like me trying to do a PhD was a very silly thing to do, these acknowledgements are not just a list of thanks but an apology to all the people who have been so kind, helpful and patient and without whom I would probably even now be sitting under a bush in the Kalahari, humming away like a demented cicada, chewing on a raw springhare.

First of all I have to thank Nick Davies. Nick is the reason I first became so fascinated by behavioural ecology. Without Nick's inspirational lectures, practicals and field trips I would never have completed my undergraduate degree, let alone hand in a PhD thesis. As a supervisor Nick has been fantastic, gently prodding me in the right direction, encouraging me through both droughts and computer smashing frustration. His patience is astounding and I feel he has taught me more with that quiet, slightly concerned look that he does so well, than any other supervisor could have done with the entire world at their disposal. His infectious joy of the world around us and the way he communicates it so simply and elegantly demonstrates precisely how we can make the world a better place just by trying to understand it a little bit better. It is a great shame that he has not yet had a chance to come out and meet the hornbills. I feel they would get on rather well.

There are many other researchers in Cambridge that have been so kind to me, helping me scientifically and practically. Rose Thorogood has been like an academic big sister to me. Rose has shared an office with me for the last year and a half and has had to put up with me grumbling in my messy corner. Amazingly Rose has achieved the unthinkable, patiently, slowly and with great repetition teaching me to use R. Rose has picked me up when I've been down and given me the confidence to carry on when all I wanted to do was give up. Anyone who witnessed the 2011 Zoology Christmas party will understand that there are no limits to Rose's ability. Claire Spottiswoode has been a great help, with visas, reading drafts importantly being a fellow Hilux enthusiast. Another member of the 'Cambridge Hilux Club' was Justin Welbergen, who also gave me fantastic advice and importantly was a great contact for playing football in Cambridge. I received great help from my advisors Becky Kilner and Rufus Johnstone, as well as other members of staff including Mike Brooke, Hugh Drummond, Giuseppe Boncoraglio, Ana Duarte, Hannah Rowland, Martin Stevens, Sheena Cotter, Camilla Hinde, Carita Lindstedt Martha "Maple" Flower and James Westrip. It was a tight contest between Jolyon Troscianko and Amy Backhouse for the best baking efforts and I value ongoing supplies of cake far too much to pick a winner. Unlike many research groups, the behavioural ecology group deals with a huge range of topics as can be seen from the fascinating subjects studied by my fellow postgrad students; Eleanor Caves, Carmen Panayi, Lina Arenas, Ornela De Gasperin, Kate Marshall, Marj Sorensen, Alexandra Török, Jo Venables, Leila Walker, Martina Boerner, Lucy Browning, Savrina Carrizo and Cassie Stoddard. Talking to any of them about their work was a great way to get enthused about science, even if I struggled to understand the complicated bits.

Having worked with meerkats I still feel part of the extended family that is LARG. My friends there; Stu Sharp, Dieter Lucas, Alex Thornton, Matt Bell, Andrew Bateman, Peter Santema, Kirsty Macleod and Raff Mares were always helpful, both in terms of ideas and appreciation of real ale. To another (now former) LARG member I owe a great debt of thanks. Sinéad 'Shady' English was kind enough to let me be her field assistant while I tried to work out how to research hornbills. As well as teaching me loads about experimental design, analysis and scorpion digging, Shady was tolerant of me taking afternoons off to stare at squawking holes in trees and would even let me disappear off following promising hornbills while I should have been weighing meerkats.

Like everything in Cambridge, this thesis was only possible due to the hard work of secretaries who actually make this place function. I thought that Linda Wheatley's departure would see us all out on the street but Alice Nelson quietly and calmly stepped into the breach.

I have been made so welcome in South Africa, both before and during my PhD. I have to thank Johnny & Sonnette Kotze, the de Bruins and Peter Kotze for letting me run all over their land and even stick nest boxes on their trees. Thanks go to the Van Zyl's Rugby team, for letting a puny Englishman play for them and eventually believing that I was a flanker. Thanks also to the Block Cheetahs football team in all their incarnations for making me feel welcome and teaching me the value of shibobo. Away from Van Zyl's, thanks to Morne du Plessis for giving me a taste of hornbill research and to all my friends in the Bushveld and apologies for not coming to visit, especially Zani Kunz, Gustav Roux, Bruce MacDonald, Edward and Elias. Alan Kemp and John Medelsohn were very helpful and generous in sharing their years of hornbill experience.

The Kuruman River Reserve, it has become a bit of a second home. Thanks to Tim Clutton-Brock and Marta Manser for letting me deface the veldt with Nestboxes. Many people helped me by finding hornbill nests for me, in particular Beke Graw and Mandy Ridley. Mandy has been so kind and helpful, full of sage advice and support, though I must apologise for my part in turning Gannavlacte from a female dominated babbler haven into the home of the 'Team GV' footballing juggernaut. Aside from my specially selected field assistants, other key players were Adam 'Legs' Britton, Thomas Klinner, Benny, Dave Humphries and Kate 'Babbler' du Plessis who contends with Tom Flower for the coveted title of GV's dirtiest player. Commiserations to those who opposed us on the hallowed sand of the REV driveway, with special mentions to Christophe Bousquet Lucy 'Filth' Kirkpatrick, Nicola 'Tucs' Harrisson, Dave Hamilton, Marcus Zottl, Matt 'Judas' Gribble, George 'Mick McCarthy' Woodcock and their most fanatical and dedicated player Simon 'the body' Townsend. Thanks to all the other researchers and volunteers on the reserve who made life in the desert so interesting. Thanks to Rob Sutcliffe, Dave Bell, Jamie 'Jizzle' Samson, Nate Tharavaj, Christele Borgeaud and Megan Price for their varied efforts in running the reserve and also to Sophie Bell and Mellissa Delport for their work at Gannavlacte. Thanks to Beke Graw and all the slender girls, particularly Kat Young for trapping so many hornbills for me.

Without one lady the reserve would be a much poorer place. Alta Cooper provided fantastic food for us all, putting up with obscure tastes and intolerances and was always happy to have a chat. Alta got to know Bunny the hornbill quite well over the years as Bunny would suddenly appear squawking at her own reflection in the kitchen window just when 'Oma Kokosiep' least expected it.

In the field I was blessed with 3 amazing assistants. 'Little' Alex Thompson was instrumental in getting the project going, with his enthusiasm and scientific nous. He has been a great friend since before my PhD, either drinking tea and discussing science or sport in hammocks or spotting me in the gym. Credit lies with Alex for the hornbill that decorates the bottom of each page. Kirsty Scott I thank elsewhere but was by far and away the most 'organised' of my assistants. Mark 'Reachy' Whiteside impressed me from his first interview and didn't let me down with his determination to fieldwork only matched by his determination to get big in the gym. Many thanks are due to Jo Madden for recommending him as well as for great friendship and mentoring over the years. The mantra "what would Madden do?" has proved a useful one when things don't go to plan.

My family have always been so supportive of all my hair brained schemes. My Mum & Dad have been fantastic, driving me to the airport, supporting me financially when times were tight and always being there when I needed them. Uncle Mike has always been full of good advice, not that I've always heeded it. Auntie Reba empathised with her mad nephew who wanted to go off to Africa and play with the animals. I sorry that my travels meant that I didn't get to see her as much as I should have in the last few years before she passed away. My siblings John, Anne and Ian have always been an inspiration. I have to admit that there may have been a little bit of competitiveness underlying my efforts to become another Dr Finnie. Work has kept me away from my family far too much over the last few years, apart of course from last September when ISBE were kind enough to give me a paid excuse to visit Perth.

At home I've always had people to turn to. Thanks to Suzi Hogg for putting up with me and for some great climbing. Jim Siverns, Sam Page and Sean Hammerton (when not on holiday) have always been around to distract me, putting the world to rights over whisky or going up mountains.

Kirsty Scott has changed my life. She has without doubt kept me sane and has damn well made sure that I at least hand in a thesis. I have been a pain to live with and I hope to make it up to her over the rest of our lives.

I need to thank and definitely apologise to Ron, my trusty, mistreated Hilux. I'm sorry that we had to deal with South African mechanics. I hope Ron continues to trundle round the desert for many years to come. Thanks to Both Michiel Jooste and Tom Flower for loaning me their cars when Ron was indisposed.

Lastly I have to mention the hornbills themselves. They are ridiculous birds and it has been a real privilege getting to understand them a little better. While throughout this thesis I describe them as 'exciting models' and an 'interesting system', they are so much more than that. Talking about Indian hornbills, Douglas Dewar described them:

"Hornbills are caricatures of birds, freaks of nature, ludicrous clowns. There is not a single feature about them which is not comical."

He was right. Even in the gruesome act of cannibalism they can't quite appear serious with the poor chick sticking his legs out of his mother's mouth like Terry Thomas' moustache. I am sad that in the thesis I have not been able to describe their territorial interactions, and give to the scientific literature the term 'Chav Walk'. Despite trying to remain objective some of the hornbills gained nicknames, specifically: Bunny, 'The Dude', Oaf, Little Marky, Little Adam, the photogenic 'Captain Super Fantastic', the elusive 'Scarlet Pimperknob' and the ever reliable 'Captain Consistent' and 'The Shit'. Both 'The Dick' and the philandering 'Ed' were less likeable but still provided very valuable data.

I started this PhD because I was fascinated by seeing hornbills in the wild. I certainly would never have finished it had they not proved to be even more fascinating than I could possibly have imagined.

Table of contents

Chapter 1

Introduction

1.1 HORNBILLS

This thesis is about the breeding ecology of hornbills. While the general theme of biological interest is the evolution of family life, it is the remarkable life history of hornbills that makes it possible to address this topic in such an exciting way. Before discussing theoretical questions, it is first necessary to introduce the birds and what makes them so unique.

Hornbills are unusual in many ways. Hornbills form a monophyletic group, the order Bucerotiformes, sharing various morphological traits. The large sickle-like decurved bill quickly distinguishes all 54 species of hornbill. While other birds such as the related hoopoes (Upupidae) and the unrelated but often confused (by the general public at least) toucans (Ramphastidae) also possess downward curved bills, only the hornbills have a casque on top, the ‘horn’ that gives them their name. Casques range in form from simple ridges running the length of the bill such as in Southern Yellow-Billed Hornbill (*Tockus leucomelas*), to extremely elaborate protrusions such as those of the Rhinoceros Hornbill (*Buceros* rhinoceros) and Great Helmeted Hornbills (*Rhinoplax vigil*). Hornbills are the only birds in which the first two neck vertebrae (axis and atlas) are fused together (Kemp 1995). They also have unusual kidneys, being the only birds whose kidneys have two rather than three lobes (Johnson 1979). Both these adaptions may well be linked to the bill structure, the first adding strength to the neck and the second compensating for the difficulty of drinking through such a long, curved bill. All hornbills feature distinctive ‘eyelashes’ that appear to be used as sunshades (Martin & Coetzee 2004).

While hornbill anatomy may be unique, the breeding biology is distinctly odd. All hornbills are hole nesters. Most nest are natural cavities in trees or rock cracks, though cavities created by woodpeckers or barbets will be readily stolen if they become large enough. It is once nesting begins however, that hornbills become unique. After entering the nest, the female will seal the entrance, leaving only a narrow slit, through which she must be supplied with food by her mate. As if this were not confining enough, the female will simultaneously shed all of her flight feathers (remiges) rendering her flightless as well her tail feathers (retrices) . With the female in the nest, the male provides all the food for his mate and the chicks until the females feathers have regrown. Female confinement lasts for at least 40 days in the smallest hornbill species. The longest recorded nest confinement was a Bar-pouched Wreathed Hornbill (*Aceros* undulatus) of 137 days (Kemp 1995). All species of hornbill follow this broad pattern, apart from the two species of ground hornbill. The ground hornbills are very different beasts to most other hornbills, forming their own family, the Bucorvidae.

Ground hornbills separated from other hornbills early in their radiation and were present in fossil records from the Miocene (Olson 1985, Boev & Kovachev 2007). Whether nest sealing evolved after the divergence of ground hornbills or whether they subsequently lost the trait is unclear. It is obvious however that the morphology and ecology of ground hornbills makes nest sealing an unlikely prospect. Ground hornbills are very large birds, weighing up to 4kg and measuring 1m in length. They are the only hornbills that are not exclusive cavity nesters, sometimes occupying large bowls in the crowns of large trees such as baobab or even occasionally stick nests of other birds (Kemp1995). This more flexible nesting strategy may well be driven by necessity. Ground hornbills live in cooperative groups in open savannahs up the Eastern coast of Africa. In such an environment, trees large enough to form cavities big enough to house a ground hornbill are rare. In fact, lack of large mature trees is one of the main factors threatening these species (Kemp & Begg 1996).

Apart from the Bucorvus ground hornbills, all female hornbills will seal themselves into their nests and shed their flight and tail feathers. This behaviour unifies a group of birds that otherwise range massively in behaviour and ecological niche (Kemp 1995). Hornbills are present across most of Africa and South East Asia, spanning all kinds of habitats. They are found in deserts, savannah, highlands, coastal swamps and rainforest. All are omnivorous, though some are true generalists like the small species in the Tockus genus, while others are more specialised such as the frugivorous hornbills of the Asian rainforests. Displays differ, though they are usually amongst the most distinctive in any environment, from the whistling whine of African Grey Hornbill (*Tockus nasatus*), to the almost lion like booming of ground hornbills, not to mention the thunderous crack of jousting Great Helmeted Hornbill. Breeding biology also varies around the theme of sealed nests. The females of some species such as Rufous-necked Hornbill (*Aceros (Aceros) nipalensis*) will remain in the nest until the chicks are ready to fledge, in others like the various species in the *Tockus* genus the female will emerge halfway through chick growth, while in a few species such as Oriental Pied Hornbill (*Buceros bicornis*), females emerge at any stage once their wings have regrown (Kemp 1995). While sealing the female in the nest may seem logical only in monogamous species, several species of hornbill appear to breed in small cooperative groups. In fact, cooperative breeding has been reported for somewhere between 18% and 33% of hornbill species (Kemp 1995), much higher than the average for all birds which is around 2.4% (Stacey & Koenig 1990). Sadly, little is known of how cooperation operates in these species.

1.2 PREVIOUS RESEARCH

Hornbills have long fascinated naturalists. Indeed, some authors believe that the fantastical Tragopans described in Pliny the Elder’s Natural Histories were based on hornbills (Newton 1893, Dewar 1906). The striking appearance of hornbills was not lost on naturalists of the 18th and 19th Centuries, even if they were seen as aberrations by some (Buffon 1793). The description by Douglas Dewar in 1906 provides one of the earliest detailed accounts of hornbill breeding and asks most of the questions that have intrigued anyone who has watched hornbills in the wild, albeit with a flavour of the preconceptions of his time:

> “It is to-day, an established fact that, when the breeding season comes round, the lady hornbill is barricaded up in a hole in the trunk of a tree, and remains thus incarcerated until the eggs are hatched. In order that the female may not starve to death a window is left in her prison, through which the male bird feeds her. This extraordinary habit seems to run through the whole family of hornbills. The hole in which the hen-bird is plastered up is usually situated high in a lofty tree; when she has taken her place in it, both she and her husband proceed to close it up, except for the slit above referred to, by means of earth mixed with bird-droppings, or in some cases with droppings alone.
>
> Here, then, among the hornbills, during the nesting season, is a division of labour as complete as that which prevails among human beings — the male goes forth and brings back food for his family, while the female stays at home and attends to domestic affairs.
>
> How this strange habit arose it is difficult to imagine. Its raison d'etre can scarcely be the protection of the female while sitting on her eggs, for her enormous beak is a weapon calculated to keep all raptorial birds at a respectful distance. It would almost seem as if the female hornbill is by nature a flighty young thing, a gad-about, and that consequently her eggs, despite the admonitions of her husband, used to suffer. She, no doubt, tried to do her duty, but the attractions of the gay world round about her proved irresistible; her spirit was willing, but her flesh was weak; consequently she and her spouse recognized that “durance vile " was the only remedy.
>
> Many weak-minded human beings pursue a similar policy. I once knew a man at Cambridge who could not bring himself to take sufficient exercise to keep his body in health, so he hit upon the plan of starting out with three shillings in his pocket, and taking a cab to the railway station, which cost him two of his shillings; the last he used to spend on a third-class ticket to a station twelve miles out, and, once landed there, he had no option but to walk home.
>
> I wonder whether any one has ever shot a cock horn-bill at a time when his wife is plastered up in her nest. It would be a cruel but interesting experiment. What would the hen bird do when the cock failed to come and feed her? Would she stick to her position and die of starvation? Would she break open the barrier and thus put an end to her self-imposed imprisonment? Or would she sit at the window of her castle and endeavour to attract, by the “sweet melancholy “of her voice,

> some knight-errant of a hornbill? I have never had the opportunity of performing such an experiment, as, although hornbills are fairly numerous in Northern India, they seem very secretive with regard to the position of their nests.”

Indeed throughout the 20th Century, the nesting habits of hornbills have continued to be the central focus of research into hornbill biology. Why do hornbills seal the nest cavity? Is it for protection, control of nest microclimate or as a form of mate guarding? How does the female communicate with outside world? What insurance does the female have if her mate is killed or abandons her?

Sadly though, the sealing of the nest that makes hornbill breeding so fascinating makes the study of hornbill breeding very difficult. Early work on hornbill breeding such as that by Moreau & Moreau (1941) revealed that female hornbills are not ‘incarcerated’ in the nest but lock themselves in, the male merely providing the materials for her to make the nest plug. Actually finding out what occurred in the nest proved much more difficult. Either the nest had to be cut open (Prozesky 1965) or great care taken with dentists mirrors to see inside the nest (Kemp 1976). Such techniques, while capable of providing fascinating snapshots of hornbill life history, could not permit the study of behaviours in the nest. In their 1972 NBC-TV documentary “Secrets of the African Baobab”, Alan and Joan Root pioneered the use of cameras to document life in a hornbill nest. The technology available at the time meant that getting video recordings from inside a hornbill nest was a remarkable achievement. First, 3 cavities in branches previously used as hornbill nests had windows cut into them and covered with blacked out glass. After waiting for 21 months a hornbill moved into one of the nests. Once the eggs had hatched, the Roots built a blacked out hide on the branch, replacing the black glass window with clear glass. Over the course of a whole day, the Roots slowly turned up the lights in the hide with a rheostat until they could use the camera. Even then, the observed behaviour was not entirely natural as the female hornbill spent much of her time trying to seal up what was apparently a gaping hole in the side of her nest, applying sealing to the glass window as fast as the Roots could clean spare panels.

Advances in digital video recording and infra red cameras for the CCTV industry have now provided much easier methods of recording inside the nest. Several studies have also demonstrated that hornbills of all sizes will readily use nestboxes (Reynauld 2006, Klassen et al 2003, DuPlessis et al 2007, Ng et al 2011). These combine to provide an exciting opportunity to glimpse the behaviours of hornbills in the nest from first entry to the fledging of chicks.

1.3 THEORETICAL BACKGROUND

This section provides a brief general overview of the theoretical background for the thesis. More detailed introductions are provided for particular topics in the subsequent chapters.

1.3.1 Intrafamilial conflict

Conflict has long been accepted as a fundamental part of family life. Families are not as once thought, harmonious units striving together for mutual gain. Genetic differences between family members mean that each individual should invest in their own fitness at the expense of their relatives (Trivers 1974). Each offspring may demand more than a fair share of investment, while parents often maximise their fitness returns by spreading investment more evenly between offspring (Mock & Parker 1997). Sibling rivalry may manifest itself by escalated begging (Price & Ydenberg 1995) or by direct aggression (Drummond 2001). Parents can usually resist their offspring’s attempted manipulation. In altricial animals, parents control the supply of food and while offspring may try to manipulate parental provisioning decisions, they have no direct control. Parents can also intervene directly in sibling rivalry. For instance, moorhen (*Gallinula chloropus*) parents will tousle chicks reducing their demand for food (Leonard et al 1988).

Conflict will also exist between parents (Parker et al 2002). Conflict can occur over both the paternity of the offspring and the amount of care provided by each parent. Each parent seeks to maximise both the amount and fitness of offspring produced over the course of their lifetime. Males may increase their reproductive output by breeding with several females and sharing care between broods. Females on the other hand might seek to copulate with several males, either to gain high quality sperm to fertilise her eggs or to persuade several males to help rear her offspring. This is evident from the spectrum of breeding systems seen in the wild. Even within monogamous pairs there is conflict. Parents may disagree over which offspring should receive the most care (Dickens & Hartley 2007) or simply how much care each parent should provide (Hinde & Kilner 2006). All these conflicts lead to compromise by different family members and the result is an evolutionarily stable strategy (ESS). The ESS will vary according to environmental and physiological constraints of the organisms involved. Some family systems appear rife with conflict, such as obligately siblicidal birds (e.g. Anderson 1990), while others seem much more harmonious. Given that conflict resolution will result in a compromised strategy, apparent conflict such as squabbling chicks or indeed apparent lack of conflict may not be a fair reflection of the underlying genetic conflicts.

All studies of intrafamilal conflict must then look beyond superficial squabbles. In order to demonstrate the extent of conflict, investigations must show that when one side gains, the other loses (Mock & Forbes 1992). In most natural systems parents are firmly in charge. While this is obvious in altricial animals where parents provide food to helpless offspring, parents exert even more control. Offspring for instance have no control over their sex or resources deposited in their egg (Kilner & Drummond 2007). This makes it difficult to discover clear evidence of conflict as there are rarely situations in which the offspring can win the conflict.

1.3.2 Communication

An issue closely tied to conflict is that of communication between relatives. Any interaction between individuals involves the transfer of information. Sometimes this transfer is passive, the receiver picking up information that is not deliberately broadcast. In other situations, one individual, the signaller, will actively transmit information to another, the receiver in an effort to influence the behaviour of the receiver. Information can be transmitted in many ways, via acoustic, visual or chemical pathways, taking many elaborate forms, from the bright display of a peacocks tail (Zi et al 2003) to the ocean spanning calls of cetaceans (Payne & McVay 1971). Whenever such information is transmitted several questions arise. At a basic level one can investigate how the information is coded. To understand that however one needs to understand what both the signaller and receiver ‘want’ from the interaction. Is the aim of communication mutualistic or is the signaller trying to exploit the receiver?

Begging is a particularly interesting area for the study of communication. Viewing a brood of begging chicks it is all too apparent that begging is an elaborate behaviour. Begging appears almost universally energetic in most species from birds to mammals and even insects (Milne & Milne 1976). If the interests of parents and offspring coincided completely then selection would favour a begging signal that is both energetically efficient and unlikely to alert eavesdropping predators. However, the begging displays of altricial birds are often exuberant and energetically costly. This has led to the suggestion that begging is so elaborate because it has to be costly in order for it to be honest (Zahavi 1975, Grafen 1990). Since offspring will demand more care than the parental optima, if offspring used a begging call that had no costs, they could exploit a naive parent, signalling for more and more care. If begging is sufficiently costly, however, then the cost imposes honesty on the signaller, with the intensity of the signal reflecting the state of the signaller. Whether the state of the signaller that is reflected in begging is offspring need or quality is still hotly debated (Mock et al 2011 and replies from Johnstone & Kilner 2011, Kolliker 2011, Grodzinski 2011 and Hinde & Godfray 2011). One of the difficulties in understanding begging mechanisms is the problem of quantifying the conflict between the signalling young and their parents.

If the potential control exerted by either party could either be quantified or removed then the nature of the signalling game between parents and offspring could be better understood. Begging for resources when the benefits to both signaller and receiver overlap would allow communication to be investigated in a novel light. Removing one party's advantage in a potential conflict would allow the other party a chance to win, thus demonstrating that conflict does exist.

1.4 HORNBILLS AS MODEL SYSTEMS

Hornbills, with their peculiar breeding system have lots of potential for answering questions about the evolution of family life. The physical separation of the members of the family, initially the male from the female, then the male from the female and the brood and finally between the brood and both parents provides an opportunity to examine some of the conflicts. The nest seal narrows the available communication channels between males and the nest inmates, depriving him of anything but auditory cues. Of course in order to test theories it is important to be able to manipulate the systems involved. Hornbills in their natural nests are not easy to manipulate. Hornbills in nest boxes however are great subjects for behavioural experiments. The inside of the nest can be observed using cameras and the box opened without damaging the nest seal (Chapter 2). This allows us to manipulate the state of the nest inmates or even the nest itself and record the results.

Chapter 3 describes the breeding behaviour of Southern Yellow-Billed Hornbill (*Tockus leucomelas*) in the Southern Kalahari. It highlights new discoveries, including female cannibalism of both eggs and chicks. Filial cannibalism has been the subject of much theoretical study but so far such theories have not been tested in birds.

Chapter 4 investigates communication in a novel context. Females are supplied with bark by their mate in order to line the nest. The bark has little direct benefit to the female and is used to raise the floor of the nest to a depth where chicks can reach the nest entrance when the female departs. Males cannot see into the nest so must rely on indirect cues to assess the need for bark. The influence of both nest depth and female hunger on female begging is investigated.

Chapters 5 and 6 investigate issues of conflict, examining the conflict surrounding the female's role in the nest. Chapter 5 examines the proximate factors that relate to the length of females' stay in the nest. Female Monteiro's Hornbill (*Tockus monteiri*) timed their departure from the nest purely in relation to their own condition (Mills et al 2005). The factors relating to the length of female confinement are complex, relating to both conflict between the male and female and between the mother and her offspring. The ability to monitor all aspects of breeding biology in the nest, including condition of females and chicks allowed us to investigate the trade-offs involved in the timing of maternal departure.

Chapter 6 expands on these findings by experimentally manipulating the conflict occurring between parents and offspring, allowing offspring a rare chance to 'win' the conflict. Females can control food distribution within the nest while they are confined with the chicks. When the female leaves, the chicks reseal the nest and neither parent can control food distribution. By experimentally removing the mother before she would naturally fledge, we can demonstrate how food would be distributed in the nest without parental control.

The final chapter discusses the results, drawing conclusions about the extent of conflict occurring during hornbill breeding. While this thesis deals purely in the conflicts faced by hornbill families, in doing so it provides new practical insights into the inherent conflicts of family life in general.

Chapter 2

General Methods

2.1 STUDY SPECIES

To study the nesting behaviour of hornbills it was important to find a species that was easy to follow, with nests that are easily accessible. Many hornbill species live in forests, nesting high up in tall trees. The 14 species of the *Tockus* genus however are savannah specialists, occurring all across Africa. Working on savannah dwelling species holds several advantages. Trees are generally small, meaning that nests are never very high. Open savannah is also a much easier environment in which to observe animals than dense forest. Southern Yellow-Billed Hornbills (*Tockus leucomelas*) are common across Southern Africa (Figure 2.1). They are generalist foragers, inhabiting a broad range of savannah habitats. They are a bold species, easily habituating to humans and a common sight scavenging at campsites. Like many species in the *Tockus* genus, Southern Yellow-Billed Hornbills deliver food to the nest one item at a time, holding the item in the tip of the bill, making nest provisioning particularly easy to record. While they are generalists, Southern Yellow-Billed Hornbills spend a great deal of their time foraging on the ground, making foraging birds relatively easy to follow and trap. Chapter 3 summarises the basic ecology of the study population.

Figure 2.1 Range of Southern Yellow-Billed Hornbill (yellow shading). Location of study site is marked (●). Map reproduced with permission from IUCN (2012)

2.2 STUDY SITE

The study was conducted in the Southern Kalahari Desert in South Africa's Northern Cape Province. The main study site was the Kuruman River Reserve (26°58'S, 21°50'E), though data were also collected on two neighbouring ranches, Rus en Vrede and Leeupan. A variety of species are studied on the reserve and surrounding ranches, including Meerkats (*Suricata suricatta*), Slender Mongooses (*Galerella sanguinea*), Southern Pied Babbler (*Turdoides bicolor*), Fork Tailed Drongo (*Dicrurus adsimilis*) and Crimson Breasted Shrikes (*Laniarius atrococcineus*). Most of these species are habituated to humans meaning that many animals in the area are particularly tolerant of close observation, including the two resident hornbills species, Southern Yellow-Billed Hornbill and African Grey Hornbill (*Tockus nasatus*). Two other sites were considered. The Daan Viljoen nature reserve in the Khomas Hochland hills near Windhoek, Namibia already had a nest box using population of both Southern Yellow-Billed Hornbill and Monteiro's Hornbill. In recent years however, baboons in the area discovered how to break into nest boxes, meaning that new, more secure boxes would have to be used. The density of boxes at Daan Viljoen was also very high, meaning that hornbills were breeding at a much higher density than natural levels (Klaassen et al 2003). The Allied Private Nature Reserves (APNR) that border Kruger National Park in South Africa have large populations of Southern Yellow-Billed Hornbill, Red-Billed Hornbill and African Grey Hornbill. The APNR is very open to research, hosting projects such as the University of Cape Town's Southern Ground Hornbill Research and Conservation Project and the South African Transboundary Project that investigates large scale elephant migration. The APNR was rejected as a study site since the dense nature of the bushveld habitat as well as the resident megafauna would make observing hornbill nests particularly difficult. Both Daan Viljoen and the APNR would make fantastic sites for comparative studies of hornbill behaviour in very different environments to the Kalahari, albeit with some extra challenges.

2.2.1 Habitat

The study site has an unusual habitat for the Southern Kalahari since it features a stretch of the dry Kuruman River, making it particularly good habitat for hornbills. The River and surrounding terraces (Figure 2.2 a) have many tall Camel Thorn trees (*Acacia erioloba*). The rest of the site (Figure 2.2 b) is more typical Kalahari thornveld, comprising sparsely vegetated dunes and small pans. Grasses (mainly *Schmidtia kalahariensis* and *Stipagrostis* spp.) and small shrubs (*Rhigozum trichotomum*) dominate with occasional bushes and trees

(*A. erioloba*, *A. haematoxylon*, *A. Mellifera*, *Boscia albitrunca* and the invasive *Prosopis grandulosa*).

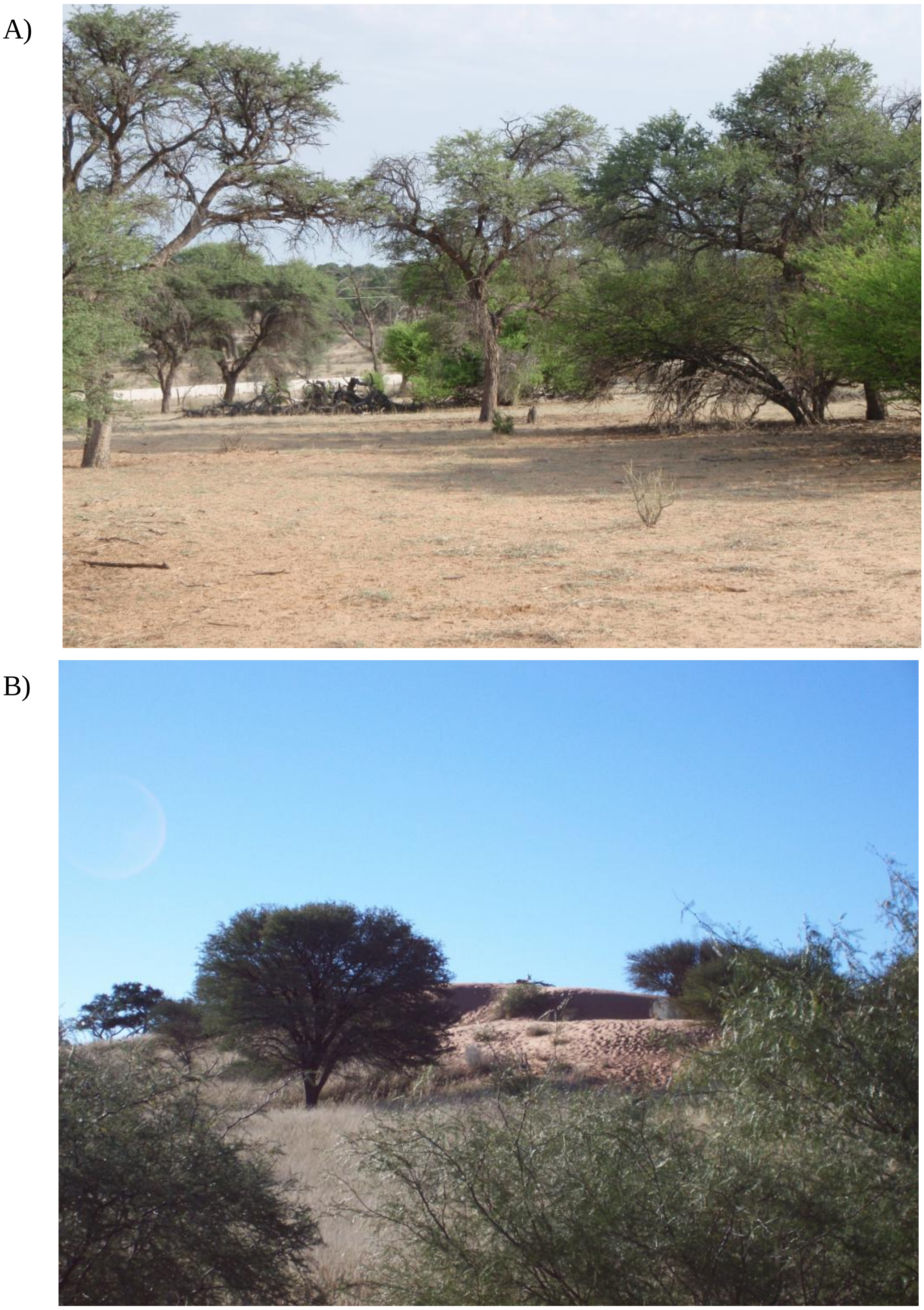

Figure 2.2 Habitats on the Kuruman River Reserve. A) River terrace with large trees. B) Dune grassland.

2.2.3 Climate

The Southern Kalahari is a semi desert environment, receiving on average 250mm of rain per year. The region has two distinct seasons, a cold dry winter, with night time temperature regularly below freezing and a hot wet summer with day time temperature regularly exceeding 40 ^{o}C. Most rain falls during the summer months between October and April in a few large thunderstorms. Two of the breeding seasons during the study (2009-2010 and 2010-2011) had unusual rainfall. Rains started late, towards the end of October but then little more fell until January. Unfortunately, management problems on the reserve led to inaccurate and sporadic recording of rainfall and temperature during the study. Personal notes recorded the days when rain fell. While 2008 had only a maximum of 15 days without rain between the start of the rains and January, 2009 and 2010 were much drier with 48 and 27 days without rain respectively. Rainfall data used in analysis in chapter 3 were acquired using the GES-DISC Interactive Online Visualization and analysis Infrastructure (Giovanni) as part of the NASA's Goddard Earth Sciences (GES) Data and Information Services Center (DISC). These data are accurate to a scale of 0.25^{o} of latitude and longitude so only give a general idea of local rainfall.

2.2.4 Fauna: Potential predators and prey

Most large terrestrial predators are very rare or absent from the study site due to persecution by local ranchers. However many potential predators were seen on the site during the study. Known predators of adult birds (from Kemp 1995) included Secretary Bird (*Sagittarius serpentarius*), Lanner Falcon (*Falco biarmicus*), Bateleur (*Terathopius ecaudatus*), Tawny Eagle (*Aquila rapax*), Wahlberg’s Eagle (*Aquila wahlbergi*), Martial Eagle (*Polemaetus bellicosus*) and Spotted Eagle Owl (*Bubo africanus*). Other potential predators seen at the study site include African Wild Cat (*Felis lybica*), Domestic Cat (*Felis catus)*, Caracal (*Felis caracal*), Black Backed Jackal (*Canis mesomelas*), Cape Fox (*Vulpes chama*), Small Spotted Genet (*Genetta genetta*), Giant Eagle Owl (*Bubo lacteus*), Black Breasted Snake Eagle (*Circaetus gallicus*). Southern Pale Chanting Goshawks (*Melierax caorus*) and Gabar Goshawks (*Micronisus gabar*) are commonly seen chasing and being chased by juvenile hornbills, though it is unlikely they pose any major threat, being largely ignored by adult hornbills. The sealing of hornbill nests makes nest predation very rare in all habitats (Kemp 1995). The study site at least has many potential nest predators. Chacma Baboon (*Papio ursinus*), rarely sighted during extreme dry periods (2 troops were seen in the area during the study) are known to prey on hornbills in nest boxes in Namibia’s Khomas Hochland highlands (John Mendelsohn, personal communication). Two predatory mongoose species are found on the site and are common predators of nests and young birds of many species. However it is unlikely that either could break into a defended hornbill nest. Slender mongooses are mobbed by hornbills when around the nest, though this may be due to the fact that both species compete for the same tree cavities. Yellow mongooses are tolerated, often foraging in close proximity to hornbills. Though the hornbills often foraged with both yellow mongoose and meerkats, there was no evidence of the amazingly strong mutualisms seen between Von der Decken’s Hornbill (*Tockus deckeni*) and dwarf mongoose (*Helogale undulata*) observed in Kenya (Rasa 1981, 1983). Both Cape Cobras (*Naja nivea*) and Mole Snakes (*Pseudaspis cana*) are abundant, though again it is unlikely they could fit into a sealed hornbill nest. The only common predator with a significant chance of success would be the rock monitor (*Varanus albigularis*), though no interactions between hornbills and monitors were observed.

Southern Yellow-Billed Hornbills are generalist foragers and eat a wide range of vertebrate and invertebrate prey as well as vegetable matter and calcium rich detritus such as snail and millipede shells. The commonest prey species taken during the study are summarised in chapter 3.

2.3 NEST BOXES

2.3.1 Location

In total 47 nest boxes were installed (figure 2.3). Fourteen nest boxes were erected in 2008, followed by more in 2009 and 2010. Four of the original nest boxes were erected in vacant territories at the edges of the study site. Of these, 3 were occupied in the first season. The one unoccupied box was later found to be located under an active genet roost. This demonstrated that suitable nest sites were in short supply. In order to maintain natural breeding density, all subsequent boxes were erected over known active hornbill nest sites. Where natural nests were too high to reach with a 2m ladder, the natural cavity was blocked and the box placed lower on the tree. Nestboxes were erected after the breeding season in March and April. Natural nests were located by following foraging hornbills and listening for the loud begging given by nesting females when they are fed by their mate. In cases when nests were not found while the nest was being provisioned, courting pairs were followed. Once a vague territory was discovered pairs could be easily found by listening for their loud territorial calls. If hornbills were not calling, they could be attracted by mimicking their calls, giving a series of staccato ‘tocks’ of increasing tempo. Other researchers were of great help, reporting whenever they saw males provisioning nests or heard hornbill begging calls. Most natural nests occurred close to the Kuruman River where trees were more abundant.

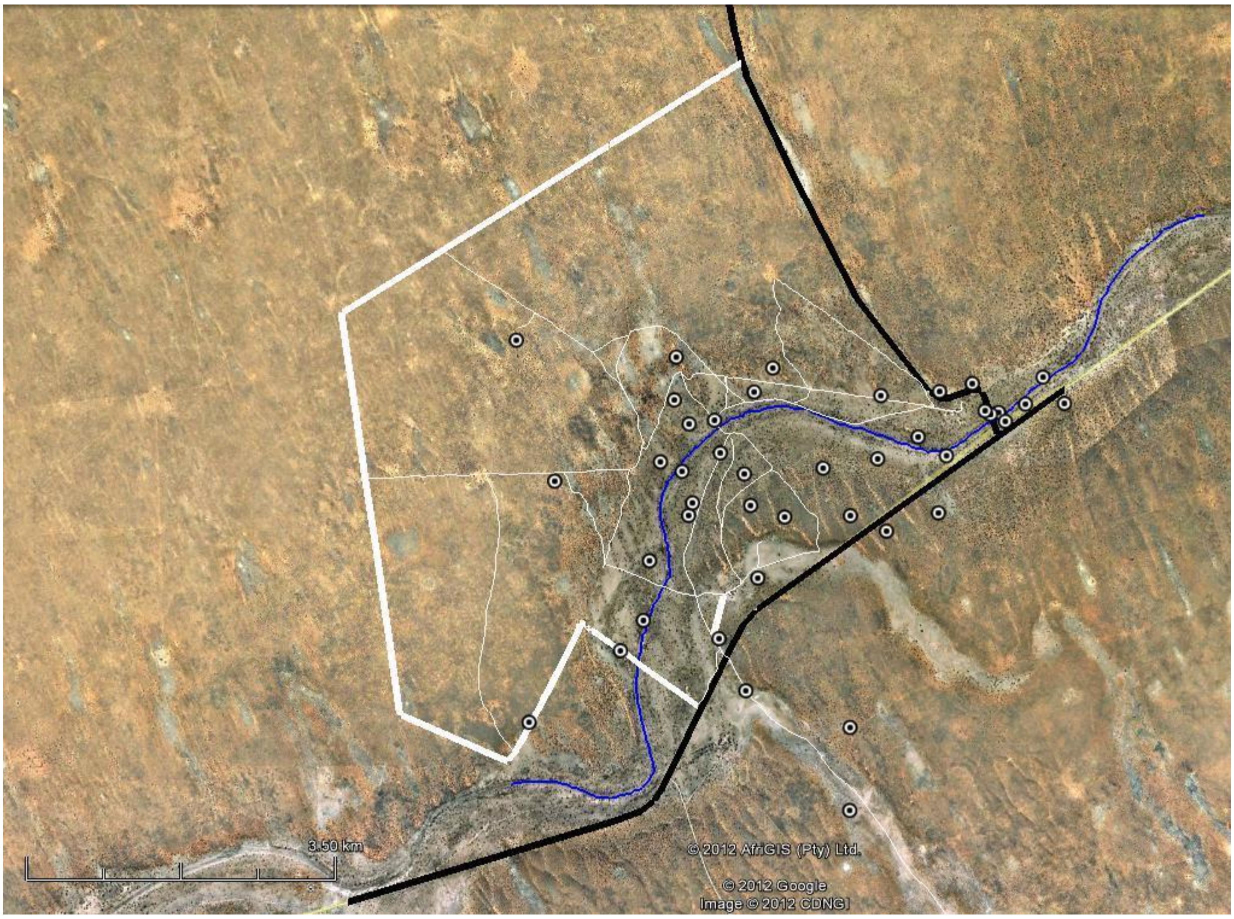

Figure 2.3 Satellite map of the Kuruman River Reserve and adjoining farms. Nest boxes used by hornbills during the study indicated by circles. Reserve bounded to the South and East by public roads (thick black lines) and to the North and West by game fencing (thick white lines). Kuruman River marked by blue line, with surrounding river terraces easily visible.

2.3.2 Design

Nest box dimensions were initially based on boxes used successfully for the larger Monteiro’s Hornbill (Stanback et al. 2002) and for smaller Red-Billed Hornbill (Diop & Treca 1996). Boxes internal cross sections were 220mm x 220mm x 180mm. Box dimensions closely matched the dimensions of natural nest cavities recorded (n = 18), which had an average internal width of 188.61mm (± 9.50 S.E.) and an interquartile range of 156.25mm to 218.75mm. Boxes were constructed from 20mm pine planks, held together by wood glue and nails. The boxes were weatherproofed with several coats of UV resistant varnish either clear or light brown in colour. The lids were made from 7mm plywood painted with green acrylic roof paint to provide a hard wearing weatherproof finish. Lids of nest boxes were held on with wire to allow secure attachment but also allow easy access to the nest when required. Nests were attached to trees by wrapping two wires around the tree and nest box, one above the entrance and one below. After initial observations, perches were added to the front of boxes so that males could easily pass food to the female inside.

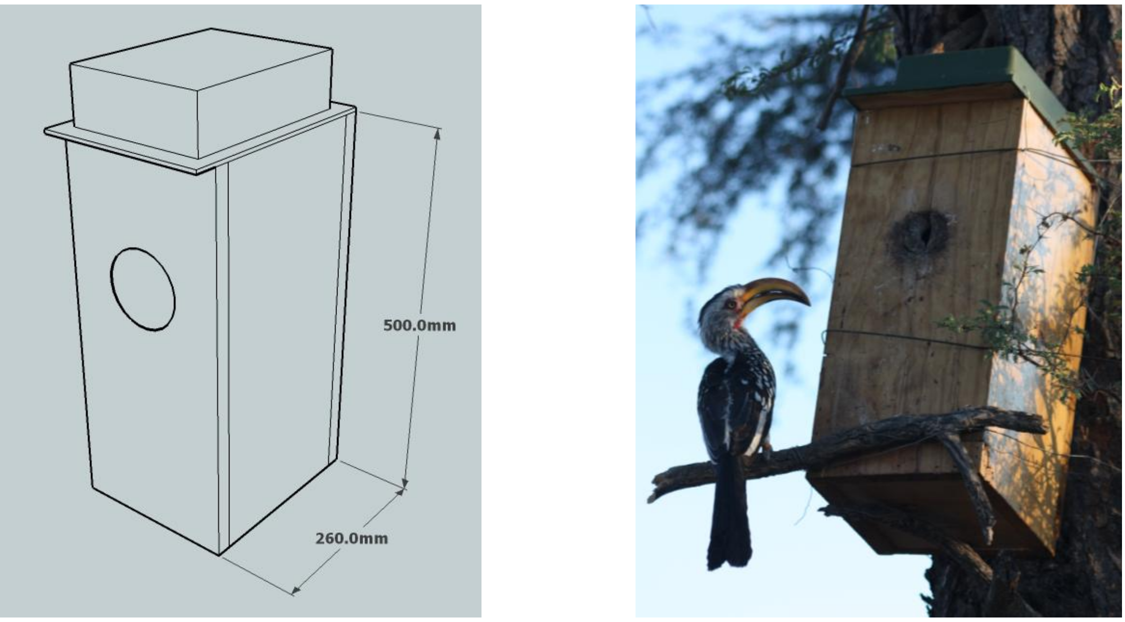

Figure 2.4 Hornbill nest boxes. Left: Technical drawing. Right: Nest box in use with ringed male on perch and female sealed inside.

2.3.3 Breeding Success

In the 2008-2009 season both natural nests (n=8) and nest boxes (n=8) were monitored. Breeding success, measured by the number of chicks fledged did not differ between natural and artificial nests (Two Sample T Test, $T_{13.95} = -0.305$, $P = 0.72$).

2.4 RECORDING BOXES

To minimise costs, each nest box did not have a permanent recording system. Instead each box was fitted with a dummy recording box. Dummy boxes were identical to the real recording boxes, except that they did not contain the recording equipment, allowing the birds to get used to their presence. Both dummy and recording boxes were made from Addisware Saver 2L plastic food boxes. Each nest had a lid of an Addisware box nailed and glued upside down to the roof of the nest with a small (50mm x 30mm) hole cut through the middle of both to allow the camera to record the nest interior. This lid provided a secure attachment point for the recording or dummy boxes, allowing boxes to be swapped in under 5s. Recording boxes measured 220mm long, 165mm wide and 65mm tall. All boxes were lined with corrugated cardboard, to minimise external noise and ensure that no light entered the box. Recording boxes were painted with the same green roof paint as the nest box lids. Strips of Velcro were glued to the inside of the recording boxes while recording equipment had matching strips, allowing flexible recording set ups. Small sections of hose, cut down the middle were glued to the inside of boxes to keep cables in place. Recording boxes were self contained units, containing camera, DVR, microphone, audio recorder and all associated batteries (Figure 2.5). Nests could be recorded with the minimum of disturbance, turning equipment on and fitting within 30s, without disturbing the main nest cavity. Hornbills only interacted with the recording equipment if the box had not been securely fastened, allowing some light to enter. Any cracks in the nest are quickly sealed up by females and incorrectly fitted boxes were treated as new cracks, the female reaching up and applying sealing material where light enters the nest. Any recordings featuring interactions with the recording equipment were discarded.

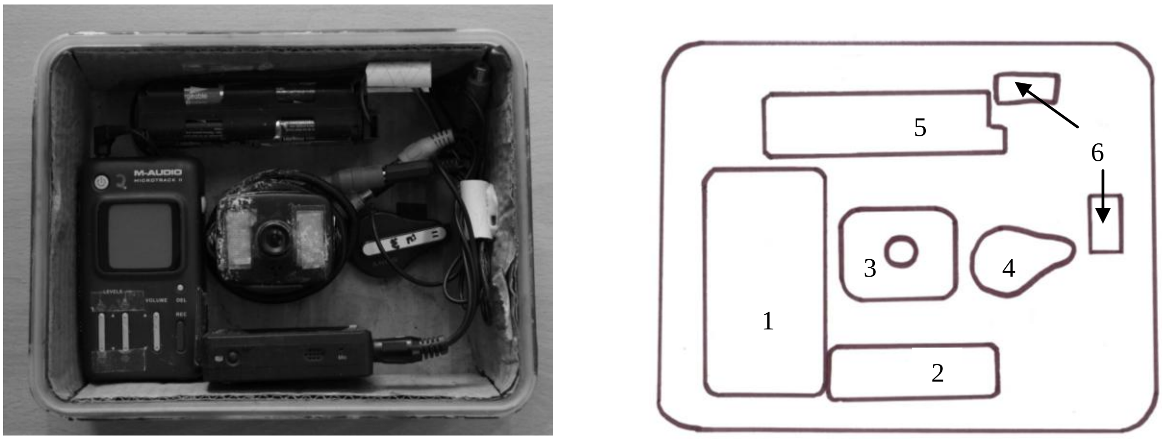

Figure 2.5 Recording box with contents. All items secured with Velcro. Note cardboard lining. 1: Microtrack recorder. Recording level lights blacked out. 2: DVR. 3: Camera with infrared LED light source. Note tape covering LED banks to reduce light levels in nest. 4: Microphone. 5: Battery pack for camera containing 8 rechargeable AA batteries. 6: split hosing used to secure cables.

The use of cameras for both still and video recording is now commonplace in many aspects of zoology. Using cameras allows us to remotely record behaviours that we cannot observe directly, either because of their location such as interactions inside a nest, because direct observation would interfere with the behaviours under observation or simply because the behaviour is so quick the human eye cannot follow it. To capture sealed nesting behaviour of hornbills, the only option is to use cameras.

The first use of photography in the study of animal behaviour was used by Eadweard Muybridge in 1887 to settle a longstanding debate about the gait of galloping horses, using a series of cameras triggered by tripwires (Muybridge 1887). The first use of photography in the study of bird nesting behaviour was by Royama (1959) who recorded the diet of nestling Great Tits (*Parus major*).While still photography allows many insights into animal behaviour, all it provides are quite literally, snapshots. Video recordings can tell a much more complete story. The technology used for closed-circuit television surveillance is perfect for monitoring wild animals. Haftorn (1972, 1978a, 1978b, 1978c) pioneered the use of video recording in the study of wild bird behaviour. At the same time (1972), film makers Alan and Joan Root were using video cameras to record inside of a hornbill nest for their documentary “Secrets Of The African Baobab”. Since the 70’s video recording technology has advanced rapidly. In particular, the development of low cost digital video recording has made field recordings much more practical.

Several factors contributed to the final choice of equipment used in the study. The equipment had to be reasonably low cost, reliable and robust enough to cope with the rigours of the Kalahari environment. To record nest behaviour, both a camera and a recorder were required. All cameras require a light source. While for many applications, natural lighting can be used, this is not an option for recording in the dark interior nest boxes, which requires an artificial light source. Lighting with visible wavelengths could interfere with natural behaviour, while infra red light is not visible to birds. Henry’s Electronics Ltd (Edgware Road, London) manufacture a small robust camera, fitted with infrared LED’s to provide passive illumination. This has been used successfully in other nest box studies (Thorogood et al 2011). The camera was modified by placing several layers of translucent tape over the banks of LED’s. This lowered the light levels in the nest, minimising over exposure. These cameras require a separate power supply. Usually they are powered by a 12V DC supply, either from a lead acid battery or a transformer attached to a mains supply. In the field, neither mains electricity or bulky lead acid batteries were practical. Experimentation demonstrated that the cameras could run off a 10V supply. This meant that 8 AA rechargeable batteries

(1.2V each) could be used in series to supply the unit (supplying 9.6V). Using rechargeable AA batteries gave a degree of flexibility and saved on mass and expense, while being more reliable than lead acid batteries. In theory, with the camera drawing 2Watts of power (manufacturers specifications) and rechargeable AA's typically holding approximately 2500mAh of energy, this system could run for 12 hours at a time. In actual fact the power draw of the cameras appears to be lower than 2 Watts, with some cameras still recording upwards of 15 hours after deployment. The modular design of the recording boxes allowed batteries to be changed quickly and easily when required. If longer recordings were necessary solar panels could be used to supply the power.

To record the output of the CCTV camera, the obvious choice was a digital video recorder (DVR). Two broad types were available. Many studies have used hard drive based recorders such as the Archos system (Ridley & Thompson 2011, Thorogood et al 2011). These require moving internal parts so are not very robust, being sensitive to dust and extremes of temperature. Solid state recorders are much more appropriate for field studies, though have only become an affordable option in the last few years. Solid state DVR's record onto SD memory cards, allowing large volumes of data to be recorded, which is easily transferrable onto computer. Many models are available, for a variety of purposes. For the study, the DVR had to be particularly compact and robust, while being reasonably cheap. To make recording easier, an inbuilt video screen would be an advantage. Thankfully one of the markets for DVR's is extreme sports recording. These DVR's are small and particularly robust, while capable of high resolution recording. DVR's were purchased from Dogcamsport (Callywith Industrial Estate, Bodmin, Cornwall). These provided high capacity and ran on cheap easily rechargeable mobile phone batteries. On their own these could run for 4 to 5 hours. They could also take external power via a USB connection (either 4 AA's in series or commercially available Lithium ion battery packs), allowing them to record for days at a time, though this was rarely required. These DVR's have since been used successfully in other studies such as Spottiswoode & Koorevaar (2011).

The DVR's had the capability to record only when movement was detected. There is so much activity in the nests of hornbills that this proved impractical. Recordings were analysed using VLC media player which allows playback at up to 32x real speed, though videos were generally played at 16x speed allowing accurate transcription of behaviour. This greatly increased the rate at which videos could be analysed.

2.4.2 Audio Recording

Designing a portable, reliable audio recording system that fitted into nest boxes provided its own challenges. Just as the video recording system required both a camera and a recorder, the audio system required a microphone and a recorder. The microphone used was a Sony ECM-T6 tie-clip microphone. While small and inexpensive, this microphone has a good battery life and importantly lacks the bandpass filters of many more expensive microphones. Hornbill begging is extremely broadband and goes beyond the range of human hearing. High end microphones have built in filters that stop any sound beyond this range.

As with video recording, digital recording has recently become accessible for high quality audio work. Several portable digital solid recorders were trialled. The Marantz PDM660 provides high quality recordings but is bulky, with poor battery life. The Microtrack II from M-Audio is much cheaper, smaller and provides very similar recording qualities, which led to its selection as the recorder of choice. Importantly, the recorder used had to be able to record at a sample rate of 48.1 KHz. Many recorders record at 44.1 KHz. This is because most recorders are designed to record the human voice. Humans can hear frequencies of up to 20 KHz. An inherent property of recording sound is that recorders can only record frequencies of up to half their sample rate. For human use, 44.1 KHz is adequate, recording frequencies up to 22 KHz. Hornbills however can emit calls of up to 23 KHz which are cut off unless a higher sample rate is used.

2.5 MASS, MORPHOMETRIC & LIFE HISTORY DATA

A SAFRING permit and permission from Northern Cape Conservation were obtained to ring and handle adult and nestling hornbills, working with traps and nest boxes. The use of nest boxes by hornbills not only allowed collection of internal video but also allowed regular access to nests. This meant that nests could be checked regularly for life history information and for the removal of nest occupants (females, chicks and eggs) to collect morphometric data. During the 2008/2009 season nests were opened more rarely as it was unclear how nesting females would react to disturbance. However the behaviour and success of regularly inspected nests did not differ from that of natural nests. Therefore during the subsequent seasons, nests were checked very regularly to provide exact dates for important life history events. Weights of mothers and chicks were taken as frequently as possible, particularly around important events such as laying, hatching and fledging. Eggs were also measured using digital callipers, while chick tarsi were measured every time a chick was weighed in order to get accurate condition scores. Females and older chicks were kept in large cotton capture bags during handling, while smaller chicks could be handled without bags. Bags used for all handling events were washed regularly. Females were not handled before they had shed their tail feathers. Preliminary attempts to handle females as soon as they entered the nest caused them to shed their tail prematurely, though did not make them more likely to desert.

Females and chicks were ringed while in the nest. Three coloured plastic rings and one metal identity ring were used on each bird. Hornbills took 8mm rings. After the first field season it became apparent that coloured rings were easily removed by the hornbills. The use of tiny amounts of PVC cement greatly reduced ring loss. No ring injuries were recorded out of 144 birds ringed. Males were also ringed using walk in traps. After trials with flap traps and readymade walk in traps, a custom made version was designed (Figure 2.6).

Males could be trapped outside of the nesting period by calling them in with playbacks of territorial calls with baited traps and a model hornbill (Figure 2.6). Trapping was much more successful when conducted while the male was provisioning the nest. Traps could be baited with commercial dry cat food or live scorpions. When the hornbill entered the trap the trigger line was manually pulled from a distance of between 10m and 30m, allowing the trap door to fall shut. The trapper then approached the trap with a sheet over their head to prevent the trapped bird from associating humans with traps. Once at the trap the sheet was thrown over the frame to darken the trap and calm the bird inside. The front door could then be slowly opened and the bird caught by throwing a towel over it, before placing it in a capture bag. Adult birds were always kept in a capture bag while handling to reduce stress. Because of their long neck, hornbills are difficult to hold in a ringers grip. Capture bags allowed birds to be handled, securely cradled in the ringers lap. Captured birds were never kept for more than 10 minutes and any that showed signs of distress were released without taking full measurements. Adult birds could be reliably sexed using a combination of tarsus measurements and inspection of the casque ridge on the upper mandible. Birds were released while the trapper hid beneath a sheet. At no point during trapping or handling did birds see a human. Trapping did not reduce habituation. Males would commonly resume foraging within 20m of observers within 10 minutes of capture.

Figure 2.6. Trap set up. Above: Trap in open position, with trigger string attached. Trap dimensions: 700mm x 700mm x 350mm. Below: Polystyrene dummy hornbill used as an effective lure in traps, made by Alex Thompson.

2.6 BEHAVIOURAL OBSERVATIONS

Direct observations at the nest were conducted using binoculars from a distance of 20-30m. From this distance it was easy to identify birds as well as food items. Yellow-Billed Hornbills only take one item at a time to the nest making identification easier. Calls could also be heard at this distance, including begging which was particularly loud. In cases where direct observation was not possible due to time constraints cameras in the nest were used to establish food delivery, while external cameras allowed identification of individuals visiting the nest.

Before nesting, a number of pairs could be followed at a distance of under 30m without disturbing them. This allowed observation of courtship behaviour. Only pairs habituated to human observation were followed. However since hornbills associate with actively habituated animals on the reserve, most pairs were very tolerant of humans.

Figure 2.7: One of the better habituated hornbills on the reserve, this female hornbill is caught in the act of raiding the bins at the Rus en vrede farmhouse.

Prey items were categorized by length relative to hornbill beak length. ‘Very tiny’ for items just held in the very tip <5mm, ‘Tiny’ up to a quarter of a beak (19mm), ‘Small’ up to a half (38mm), ‘Medium’ up to three quarters (56mm), ‘Large’ up to a complete beak (75mm) and ‘Extra large’ for items larger than a beak length, typically up to 120mm. The biomass of food items were estimated the formula from Rogers et al (1976):

$$B = (0.0305L)^{2.62}$$

Where B is the biomass in grams and L is the length of the prey in mm. This only provides a rough estimation only since the equation is designed to deal with adult terrestrial arthropods.

2.7 EXPERIMENTAL MANIPULATION

Nesting in nest boxes allowed experimental manipulation to be conducted during all stages of breeding. Experiments attempted included removals of both mothers and chicks, playbacks, feeding and removal of nest materials. The exact details of experiments are detailed in the relevant chapters.

2.8 STATISTICAL ANALYSIS

All analyses were conducted using R (R Development Core Team 2011). Parametric tests were conducted when possible. Where necessary, data were transformed to achieve normality of error, using logarithmic or square-root transformations. For analysis involving multiple variables, linear mixed effect models were applied (LME) using lme function from the nlme package. These allow the addition of random terms which can account for repeated observations from the same individual. Models were simplified using a stepwise approach (Crawley 2002). Maximal models were fitted including all terms and interactions of biological interest. The significance of terms was assessed using likelihood ratio tests comparing models with and without each term. Terms were sequentially removed according to their level of significance until a minimal model was reached in which the removal of any terms significantly decreased the fit of the model. Specific statistical methods used in each chapter are explained in the relevant methods sections. Where averages are presented in the text they represent mean ± S.E. unless otherwise stated.

Chapter 3

General Ecology Of Hornbills In The Kalahari

3.1 ABSTRACT

The unique breeding biology of hornbills has captured the attention of naturalists for many years. Female hornbills seal themselves in to the nest at the start of breeding, making a plug out of faeces and locally available materials. The sealing of the nest has made detailed investigation of hornbill breeding biology particularly difficult. The use nest boxes and infra red cameras in this study have allowed new insights into the biology of Southern Yellow-Billed Hornbill. This chapter aims to set the scene for the rest of the thesis by describing interesting aspects of hornbill breeding. Pre-nesting behaviours were observed while pairs were followed in an attempt to find their nest trees. The extent of courtship feeding and mate guarding was documented along with the potential for extra pair copulations and a previously unrecorded use of colourful flowers as flags in intrapair display. Nesting behaviour is then described including details of the timing and success of nesting with regard to male provisioning and breeding female condition. Males provided incarcerated females not only with food but nest materials and pieces of shell and millipede exoskeleton. Detailed observation of wing moult showed a novel pattern for hornbills. Wing feathers (remiges) were shed only after females had finished laying. This meant that females were forced to remain in the nest longer but gave them more time to assess the males' provisioning ability before committing to breeding. Widespread filial cannibalism was observed, accounting for the majority of chick fatalities. Causes of nesting failure were documented. No nests were predated in the 3 years of study. Female condition was recorded throughout nesting. Females generally lost little condition during egg laying and incubation, though condition fell sharply after chicks had hatched. Internal cameras revealed that females did eat after the chicks have hatched and do not starve themselves as previously thought. Females also contributed chick care after they have left the nest.

3.2 INTRODUCTION

To understand the behaviour of any animal, it is vital to have a basic understanding of its ecology (Lack 1968). Careful and detailed observations of even common, seemingly well known animals such as sticklebacks (*Gasterosteus aculeatus*) and herring gulls (*Larus argentatus*) can provide great insights by placing their behaviours into an ecological context (Tinbergen 1952, 1953). The aim of the thesis was to understand the breeding biology of a population of Southern Yellow-Billed Hornbills. During the study, hundreds of hours were spent watching hornbills, both outside the nest and, using infra red cameras, inside the nest. This Chapter is not a test of a specific hypothesis but a description of the breeding behaviour of the study population. In most theses, the ecology of the species is described briefly, with many references to previous studies. The Southern Yellow-Billed Hornbill, while better described than many hornbills, has still received only one detailed, non destructive study (Kemp 1976), on a population thousands of miles away in a very different environment. The use of infra red cameras and openable nest boxes has allowed a much less invasive study of breeding biology than previous attempts (Prozesky 1965). The open habitat and relative habituation of the study population has also provided the opportunity for detailed observations of behaviour outside the nest.

While life history and nest provisioning data were collected in a structured manner, a range of anecdotal observations are included, describing behaviours not previously observed. The data are presented in a roughly chronological order, beginning at the onset of breeding and concluding with the fledging of chicks. This descriptive chapter raises questions that examined with quantitative data and experimental tests in the subsequent chapters.

3.3. NON BREEDING BEHAVIOUR

The non breeding behaviour of the population is really outside the scope of this study but is fascinating in its own right. Hornbills have complex interactions with many species (Rainey et al 2004, Rasa 1983) and this population is no different. Hornbills kelptoparisitised many other species, including Meerkats (*Suricata suricatta*), Yellow Mongoose (*Cynictis penicillata*), Slender Mongoose (*Herpestes sanguineus*), Southern Pied Babbler (*Turdoides bicolour*) Glossy Starling (*Lamprotomis nitens*), Burchell’s Starling (*Lamprotomis australis*) and Grey Hornbill (*Tockus nasatus*). They had a wide range of food, both vegetable and animal. Observed prey is summarized in Table 3.1. Interspecific interactions also included competition for nest cavities. Yellow-Billed Hornbills were dominant over Grey Hornbill (*Tockus nasatus*), Red-Billed Woohoopoe (*Phoeniculus purpureus*) and Slender Mongoose. One pair of hornbills were observed picking up stones and dropping them on to a Slender Mongoose that was roosting in their nest cavity (Beke Graw personal observation).

Outside of the breeding season, territoriality is weak with birds coming together in foraging flocks often with other species such as Glossy and Burchell’s starlings. Pair bonds were seemingly maintained with pairs usually visiting their nests on a daily basis.

Table 3.1: Recorded prey species of Southern Yellow-Billed Hornbill on the Kuruman River Reserve. (**) Denotes prey that was common to all nests in at least 1 breeding season. (+) Denotes prey that was observed in fewer than 5 nests.

Plants

Common Name	**Scientific Name**
Raisin Bush **	*Grevia flava*
Shepherd’s Bush	*Boscia albitrunca*
Prickly Pear +	*Opuntia* spp

Arthropods

Common Name	**Scientific Name**
Burrowing Scorpion	*Opistophthalmus glabifrons*
Thick Tailed Scorpion	*Parabuthus capensis*
Thick Tailed Scorpion	*Parabuthus transvaalicus*
Widow Spider	*Latrodectus spp.*
Mayfly **	*Ephemeroptera spp.*
Termite **	*Isoptera spp.*
Flower Mantid	*Harpagoantis tricolour*
Bark Mantid	*Tarachodes spp.*
Giant Mantid	*Sphodromantis gastric*
Dune Cricket	*Schizodactylidae spp.*
Corn Cricket **	*Bradyporidae spp.*
Acacia Katydid	*Terpnistria zebrata*
Grasshopper **	*Suborder: Caelifera*
Ant Wolf (Dispersal phase)**	*Holoptilus spp.*
Millipede	*Spirostreptrornorpha spp.*
Cicada **	Suborder: *Auchenorrhyncha*
Dung Beetle	*Scarabaeus spp.*
Ground Beetle **	*Anthis spp.*
African Silk Moth **	*Gonometa postica*

Vertebrates

Common Name	**Scientific Name**
Kalahari Tent Tortoise	*Psammobates oculfer*
Common barking gecko	*Ptenopus garrulous maculatus*
Ground Agama	*Agama a. aculeata*
Bushveld Lizard	*Heliobolus lugubris*
Kalahari Tree Skink	*Mabuya spilogaster*
Bat +	*Order: Chiroptera*
Gerbil +	*Gerbilliscus sp.*
Brant’s Whistling Rat +	*Parotomys brantsii*
Violet Eared Waxbill +	*Uraeginthus granatinus*
Sociable Weaver +	*Philetairus socius*
White-Browed Sparrow Weaver +	*Ploccepasser mahali*
Southern Pied Babbler (eggs) +	*Turdoides bicolour*

3.4 PRE NESTING BEHAVIOUR & COURTSHIP

The pre nesting behaviour of hornbills is the best described aspect of their behaviour (Diop & Treca 1996, Kinnaird & O'Brien 1999, Poulsen 1970). Obviously, nesting is difficult to observe as females seal the nest entrance, while outside of the breeding season most hornbills can be surprisingly elusive and unobtrusive. When preparing to breed however, hornbills are universally loud, unsubtle and generally easy to observe. The pre nesting phase is characterised by increased territoriality, closer association between pairs, courtship feeding, nest preparation and frequent mating.

While the main aims of the study were to document behaviour once the female is sealed in the nest, some pre nesting observations were collected. Many of these observations were collected while trying to locate new breeding pairs and find their nests. As such, much of the data presented in this section is anecdotal in nature. Specific behavioural focals were also conducted as described in Chapter 2 and were the source of any numerical data presented.

3.4.1 Onset & duration

Pre-nesting behaviour commences as pairs begin to forage as a pair. Outside of the breeding season, during the winter from May until early September, pairs forage with their offspring from the previous year and commonly group together in foraging flocks, often with other species such as Glossy Starling. Pairs start to become more territorial and offspring disperse long before the start of breeding. In each season, by the start of October, most pairs were getting ready to breed. Presumably this is triggered by changes in day length (Dawson et al 2001), coinciding with rising temperatures and the flowering of camel thorn trees.

While the start of pre-nesting behaviour seems to be fairly regular, the duration can be highly variable. While most pairs will move to nesting soon after the summer rains begin, some wait until much later in the season. Pairs that do not breed straight away will maintain pre-nesting behaviours throughout the breeding season and pairs that have attempted to nest but failed will maintain territoriality, courtship feeding and nest maintenance until autumn returns.

3.4.2 Courtship feeding & foraging behaviour

Males feed females during the breeding season, emitting quiet feeding calls to alert the female when they discover food. Females respond by begging, though rarely approach the male, usually waiting to be fed. When fed, females give a loud harsh acceptance screech. Both male feeding calls and female begging and acceptance screeches are similar to the calls they use once nesting. Females never feed males. Occasionally however, females will pass food back to the male with a feeding call, though the male will always present it again. Courtship feeding consisted of the full range of hornbill prey; invertebrates, small mammals, reptiles and eggs (of birds and reptiles) were presented. Males also provided non edible material including tree bark, camel thorn seed pods, millipedes, and ungulate dung. If accepted, these were taken straight away to the nest by the female and used for preparation of the nest lining or sealing. Males would occasionally take courtship feeds all the way back to the nest and call to the female, even putting their head inside the nest while waiting.

Courtship feeding was a common feature of pre nesting behaviour. During focal watches of foraging behaviour (n=10 pairs, average focal duration: 26.51 minutes ± 3.78) males fed 45.66% (± 11.02) of the food items that they found. This contributed a significant amount to female diet, with on average 50.51% ± 14.52 of female diet (by mass) being provided by their mate.

An intriguing aside is that males would sometimes present brightly coloured flowers. Both the yellow flowers of Devil thorn (*Tribulus z. zeyheri*) and the red flowers of mistletoe (*Tapinanthus oleifolius*) were offered with vigorous calling. While they were sometimes accepted, they were never eaten or used in nest preparation. Indeed the ground below some nests were strewn with mistletoe flowers during courtship. The colour of the flowers may be important as they match the yellow of hornbill bills and the red of their cheek patches. White flowers such as blackthorn (*Acacia mellifera*) or drie doring (*Rhigozum trichotomum*) and purple flowers such as katstert (*Hermbstaedtia fleckii*) were never presented. No other hornbill species or populations have been observed presenting flowers (Kemp 1995).

Many species of bird will display with objects held in the bill. Commonly such objects are used in nest construction such as the "*Halmbalz"* or "stem display" of the estrildid finches (Payne 2010) or the "Weed-trick" of Great Crested Grebes (Huxley 1914). Sometimes, objects with no apparent use are held for display. The use of flowers and other purely decorative 'flags' in courtship display is common in some groups such as fairy wrens (Hindwood 1948) and Bower birds (Borgia et al 1987). The flags are often brightly coloured and may serve to amplify features of the male display (Kelly & Endler 2012) like the effect of colour rings on the success of male zebra finches (Burley et al 1982, but see also Pariser et al 2010). Such displays are not conducted within established pairs, unlike in the Southern Yellow-Billed Hornbills. Both the Green Woodhoopoe (Radford & duPessis 2004) and the Violet Woodhoopoe (duPlessis et al 2007) from the closely related Upupidae pass flowers, pieces of bark and lichen between individuals during territorial displays, though never during courtship. However, presentation of flags has not been observed within monogamous pairs in any species.

The incarceration of female hornbills precludes mating from when the female enters the nest. Since females do not lay immediately upon entering the nest, Stanback et al (2002) suggested that hornbills must have unusually long periods of sperm storage, potentially providing extensive opportunities for extra pair mating. *Tockus* hornbills however typically begin laying only up to 11 days after entering the nest (Kemp 1995), which does not seem to be an unusually long period for sperm storage compared to other birds (Birkhead & Møller 1992). Stanback et al (2002) indeed found no evidence for extra pair paternity (EPP) in the closely related Monteiro's hornbill. They have suggested that the lack of EPP may well be due to the unique situation a female hornbill finds herself in, completely dependent on male care for weeks while she is flightless in the nest. In this case, selection for direct benefits from the pair mate could well override any possible genetic benefits derived from extra pair copulation (EPC) (Weatherhead et al 1994). This would predict that pairs should be not only genetically but behaviourally monogamous as females engaging in EPC run the risk of desertion by their pair mate. While following pairs of Southern Yellow-Billed Hornbills in the breeding season however, several females flew off with extra pair males, leaving the pair male behind (approximately 5-10 instances in c. 200 hours of observations). When females do switch partners they flew a long distance (over 1km) but return within the same day. No extra pair copulations have been observed, though this may be due in part to the difficulty of following eloping females. It would be interesting to test the levels of EPP in a population of hornbills where females certainly spend time away from their social mate. This has been shown to cause behavioural changes in males of species with high rates of EPC. Male reed buntings (*Emberiza schoeniclus*) provide less care to nests where they have lower paternity (Dixon et al 1994). The breeding system could constrain males to care despite female infidelity. Without male care, the female cannot raise a brood as she is trapped in the nest. Only one male (out of 67 breeding attempts) deserted his female and gained a new mate during breeding in the course of the study. The male and his new mate failed to breed however by the end of the season as his nest was still occupied by the old female. Males with females already in the nest will follow neighbouring pairs that have not yet nested. Whether this is prospecting for EPC or territory defence is unclear. While foraging in pairs before nesting there appears little evidence for mate guarding with males and females initiating a similar number of flights (males initiated 49.13% ± 13.58 of flights where both partners moved in 10 focals on separate pairs). High levels of courtship feeding (Tobias & Seddon 2002) and vocal duetting (Levin 1996) have been suggested as possible alternatives to mate guarding as strategies of paternal assurance. While males do courtship feed females, duetting in hornbills does not fit the established model for vocal mate guarding. Males initiate all bouts of duetting, with the female joining as the display reaches its peak. If males were guarding females they should join in with female calls rather than starting the bouts themselves.

All copulation bouts observed (n=9) were between social mates and occurred within 100m of the nest. This contrasts with observations in Kemp (1995) that states that copulations occur away from the nest.

3.4.3 Nest preparation

All natural nests (n = 42) were in cavities in Camel Thorn trees (*Acacia erioloba*). While two other trees grow on the study site, neither Shepherd’s Bush (*Boscia albitrunca*) nor Grey Camel Thorn (*Acacia haemotoxylon*) grow large enough to form cavities big enough for hornbills.

Males appear to hold the territories. None of the colour ringed males observed in multiple seasons (n = 9) bred in different territories. Females could move between territories (2 out of 8 individuals that bred in multiple years), while females never remained on a territory when the male changed (n=8), 5 males maintained their territory with different females in different years. Females did almost all nest preparation, lining and sealing the nest. The male contribution was purely to provide materials to the female. Such materials included bark and camel thorn seed pods which were used to line the nest as well as ungulate dung which females used in making the nest plug. Unlike other populations no mud was available to seal the nest (Kemp 1995). No particular kind of dung was preferred in nest preparation, with the most locally abundant type being used. Dung from sheep (*Ovis aries*), cattle (*Bos taurus*), Eland (*Taurotragus oryx*) and Springbok (*Antidorcas marsupialis*) were all commonly used.

Males also provided females with ‘shongololo’ millipedes (*Spirostreptrornorpha* sp) that are never eaten but used are used to seal the nest entrance. John Mendelsohn (personal communication) has observed that Monteiro’s hornbills line their nests with millipedes, and speculated that their toxicity may help with nest hygiene. Millipedes were never used as nest lining in this population. Consistent with other populations of Southern Yellow-Billed Hornbill (Kemp 1995), leaves were never used in nest lining. The 2010-2011 season featured a great abundance of African silk moths (*Gonometa postica*) breeding in the local area. The caterpillars and pupae were superabundant on camel thorn trees and provided a large part of the diet. The hairy caterpillars required a long handling time to become edible. Hornbills would have to drag them back and form across branches for over two minutes before eating them. More commonly males would give them to females who would take them straight to the nest and smear them against the sides of the entrance to build up the nest plug. When preparing the nest females would commonly enter and leave the nest cavity while being provisioned by their mate. Preparation started with clearing the cavity. Old nest plugs were completely cleaned away and the remains of dead chicks from previous years removed. If the same female reused a nest from the previous year (n=9), most of the nest lining would be left in the nest. Only one repeating female cleaned out her nest completely when reusing it. If however a new female had taken residence (n= 15), the nest lining was completely removed and deposited just outside the nest entrance. While preparing the nest, females will seal up any cracks in the nest cavity as well as most cracks and small holes in the rest of the nest tree. Nest trees were used by other species such as Cape sparrow (*Passer melanurus*), Acacia Pied Barbet (*Tricholaema leucomelas*), Red-Billed Woodhoopoe (*Phoeniculus purpureus*) and Lilac Breasted Roller (*Coracias caudata*), so the sealing behaviour does not appear to be prevent other animals using the same nest tree. Sealing material is applied to the nest entrance from inside and outside, sometimes the nest entrance narrowing to 30mm before the female finally enters. The potential benefits of sealing the nest are discussed at the end of this chapter.

3.5 NESTING

The timing of events and female condition in the nest are summarised in Figure 3.1:

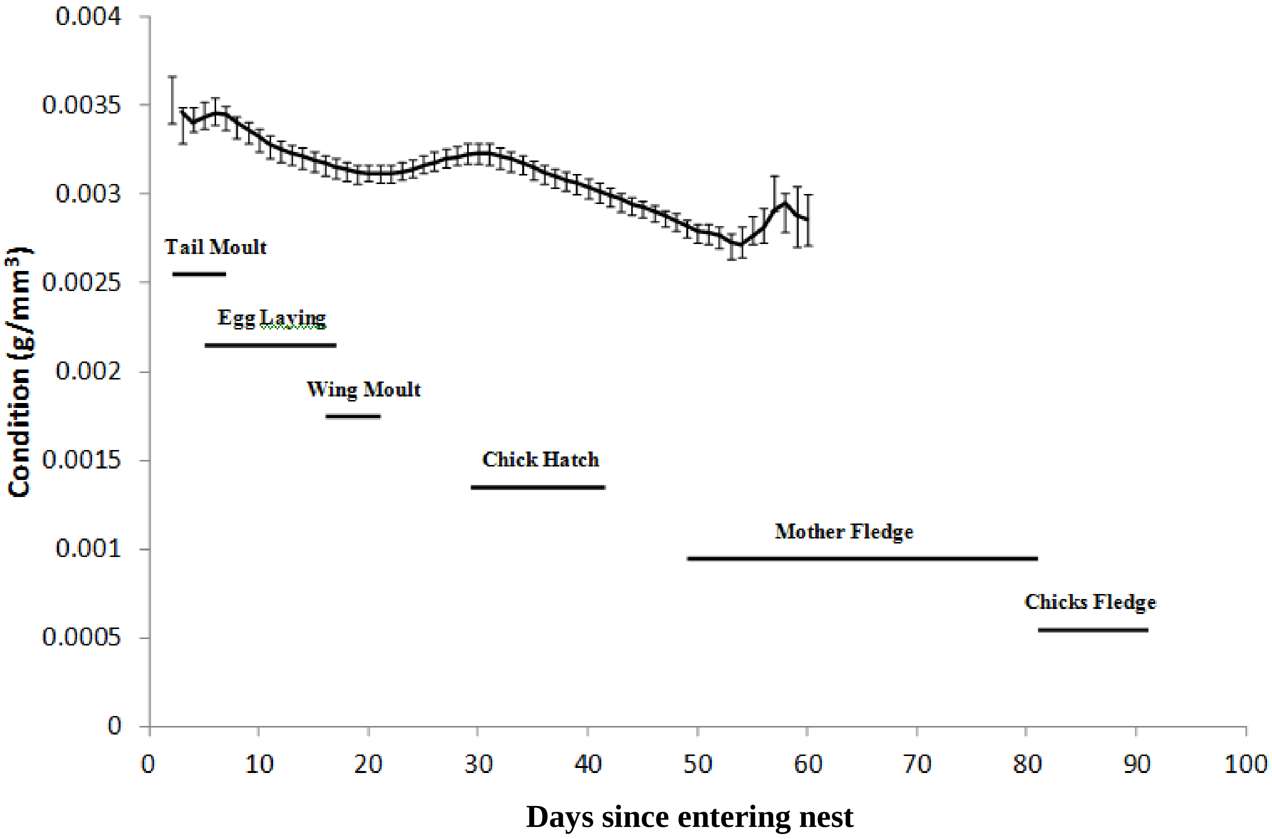

Figure 3.1: Average female condition (mass/tarsus), alongside the timing of nesting events. Horizontal bars represent the interquartile range of timings. Condition scores taken from 41 breeding attempts (from 36 different females) in 2 seasons.

3.5.1 Nest entry and pre laying period

The onset of nesting is strongly linked to rainfall. Across the three seasons, 67 breeding attempts were documented. None of these bred before the first significant (>1mm) rainfall of the year. Soon after rains began, females would enter the nest. All breeding attempts began nesting within 20 days of a significant rainfall. Of 67 nesting attempts across 3 years, only 6 occurred before the first rains of over 10mm in the season.

Figure 3.2 Female hornbill sealed inside nest

Once in the nest, females begin to moult their tail and wing feathers (retrices and remiges). However the timing and sequence of this moult is different to all previously described hornbill populations. Tail feather moult begins soon after entering the nest (4.8 days ± 0.39 from 44 recorded nests). Wing feathers are never moulted at this time, being shed only after laying is complete. This contradicts previous studies which found both wing and tail feathers were shed simultaneously around the time that the first egg was laid (Kemp 1995). Unlike Prozesky (1965), no females shed their claws in the nest. When first in the nest, females spend most of their time applying more material to the nest plug, building up a considerable dome of material inside the entrance (Figure 3.2).

Females use their bills as trowels to smear the sealing material on and then drum with the side of the beak consolidating the material much as one would do with soil or hardcore using a tamping tool or rammer (CD Video 3.1). During this period males visit the nest regularly, supplying nesting material, food and sources of calcium such as weathered millipede exoskeleton (Borell 2004) and pieces of bone and tortoise scutes.

Females can continue to assess conditions (male ability, environment or predator threat) during the pre laying period. Out of 18 recorded nests that females abandoned, 8 of these were deserted before any eggs had been laid (Figure 3. 16).

3.5.2 Egg laying

Females typically began laying after 6 days in the nest (mean = 6.58 ± 0.49, n = 53 breeding attempts), one nest starting on the day of entry and all but 2 nests laying within 12 days. This reinforces the conclusion that nest confinement does not require particularly long periods of sperm storage. Clutch sizes ranged from 1 to 5 eggs (mean = 3.78 ± 0.12, n = 60 clutches), with 4 being the most common (Figure 3.3).

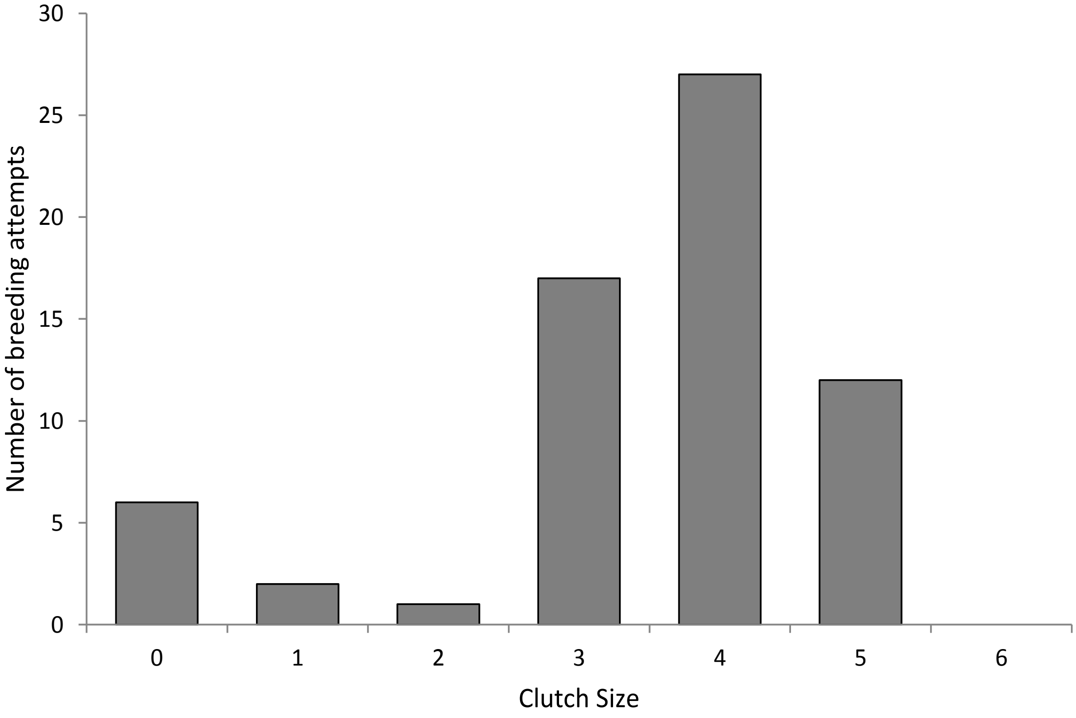

Figure 3.3: Histogram of clutch sizes. Modal clutch size = 4. n = 65 breeding attempts

Clutch size was unrelated to female condition (Figure 3.4) or male feeding rate (Figure 3.5). Clutch size did appear to vary between seasons (Figure 3.6). Much of this variation was due to females that abandoned the broods after laying an incomplete clutch. The apparent increase in early abandoning females could well be due to observation bias. As more nests were discovered each season, the likelihood of recording quickly aborted breeding attempts increased. In the first field season, only the easier to find, more active nests could be recorded but by the third season, nests were recorded irrespective of their status. However looking at histograms of each breeding season it seems that the modal clutch size did drop by an egg each year, from 5 in 2008-2009 to 4 in 2009-2010 and then 3 in 2010-2011 (Figure 3.6).

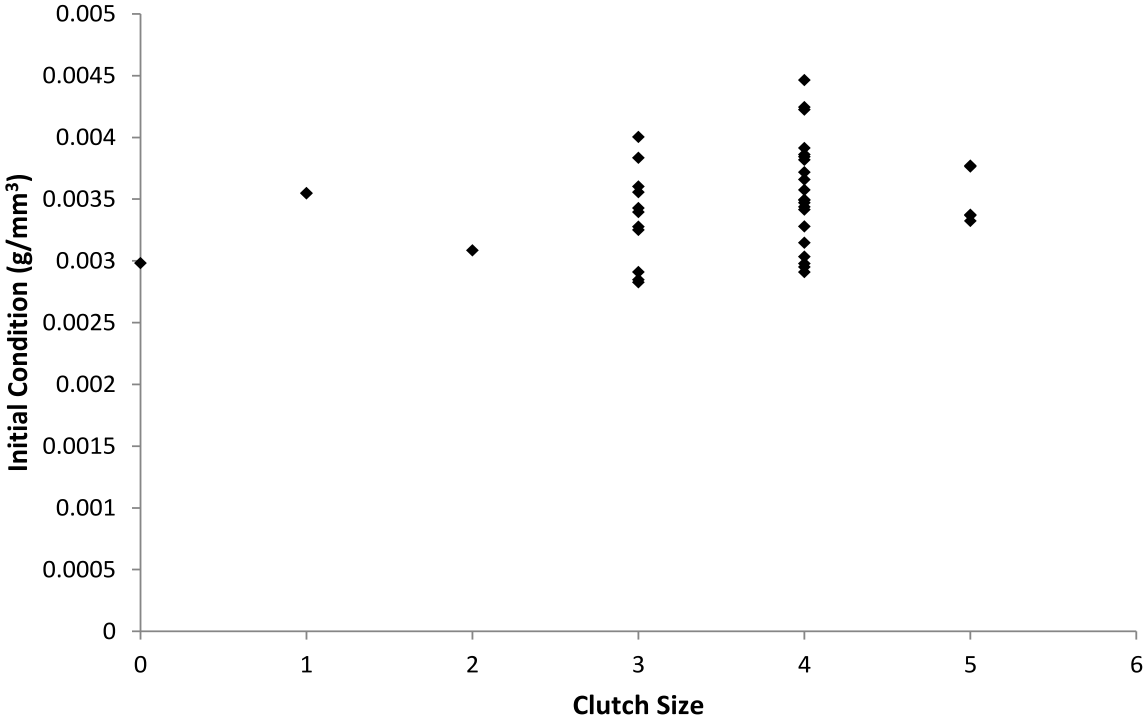

Figure 3.4: Clutch size was not related to female condition before laying. LME: Provisioning rate, $F_{1,6}$= 2.27, p = 0.18, random effects: Female ID & Season

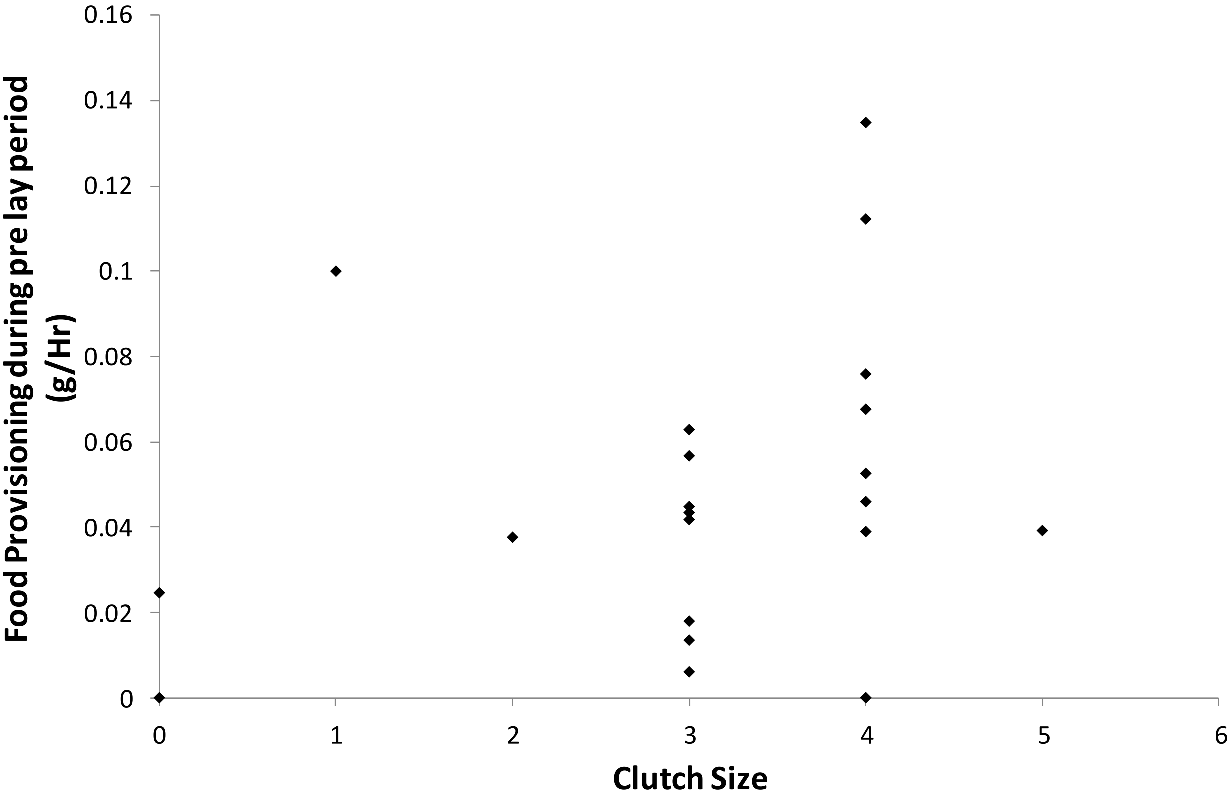

Figure 3.5: Clutch size was not related to male provisioning rates before laying. LME: Provisioning rate, $F_{1,5}$= 0.0021 , p = 0.97, random effects: Female ID & Season

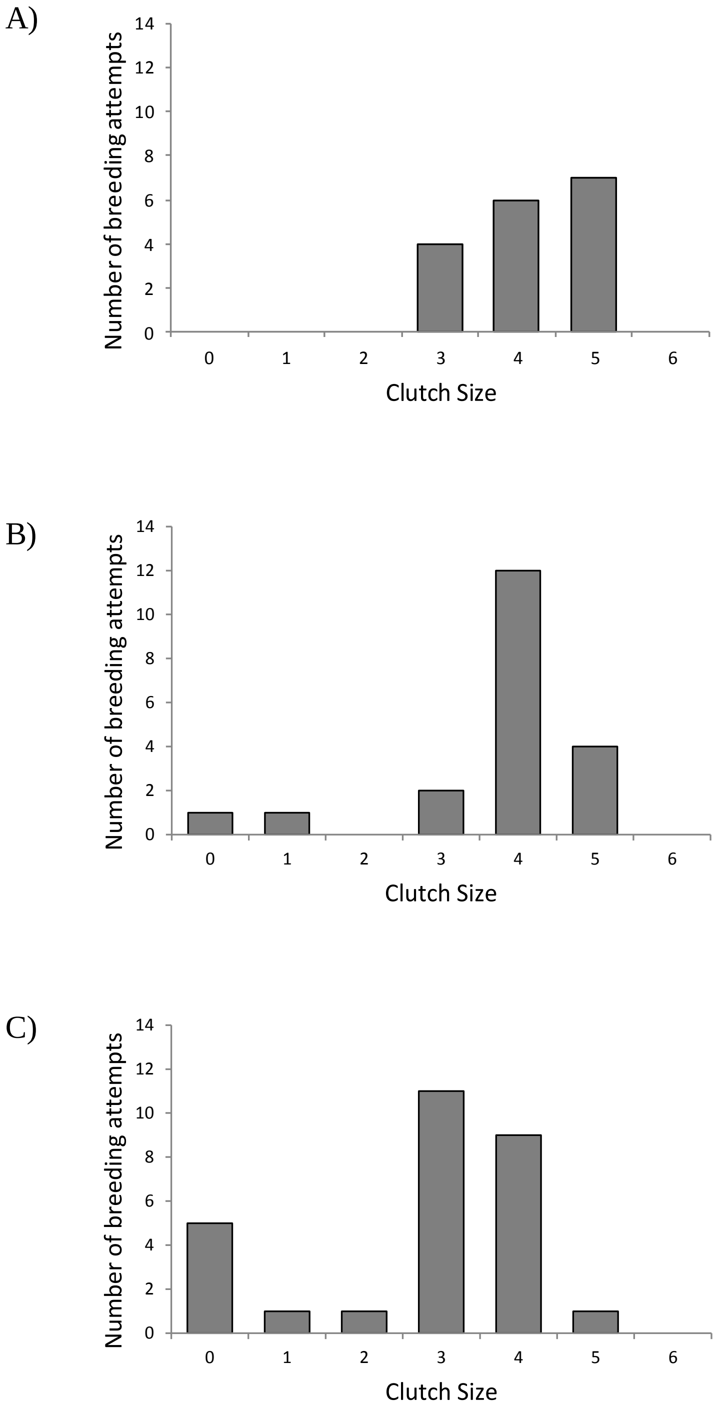

Figure 3.6: Histograms of clutch sizes in the 3 breeding seasons. A: 2008-2009 (n=17), B: 2009-2010 (n=20), C: 2010-2011 (n=30). No statistical analysis conducted as progressive nest discovery may cause observation bias with more unsuccessful nests found in later season.

While clutch size did not vary with female condition and male food delivery, we may be seeing an incomplete story. The types of food delivered may well be of different energetic value. For instance, African silk moth caterpillars (*Gonometa* postica) made up a significant portion of food deliveries in 2010-2011 (15.7%) but were rarely delivered in 2008-2009 (3.9%) or 2009-2010 (11.0%). The same is true of shepherds bush berries. These were abundant in the environment in all three seasons but were only used as food in 2010-2011, perhaps reflecting a lack of other foodstuffs.

The non calorific content of food may be important in determining clutch size. Males delivered small calcium rich items such as egg shell, small bones and weathered millipede exoskeleton (Figure 3.8). Unusually for an arthropod, millipede exoskeleton is not just chitinous but is also rich in calcium salts (Borrell 2004). Examination of internal videos showed that females eat these items rather than use them in nest sealing. Other birds enrich their calcium intake when preparing to lay (Graveland & Berends 1997). In 2008-2009, male supplementation of shell was not seen in pre laying focals but was prevalent in 2009-2010 (0.63 items per hour ± 0.27) and 2010-2011 (1.08 items per hour ± 0.42). In the two seasons when shell made up a portion of pre laying females' diets, the shell delivery rate was not however related with clutch size (Figure 3.7).

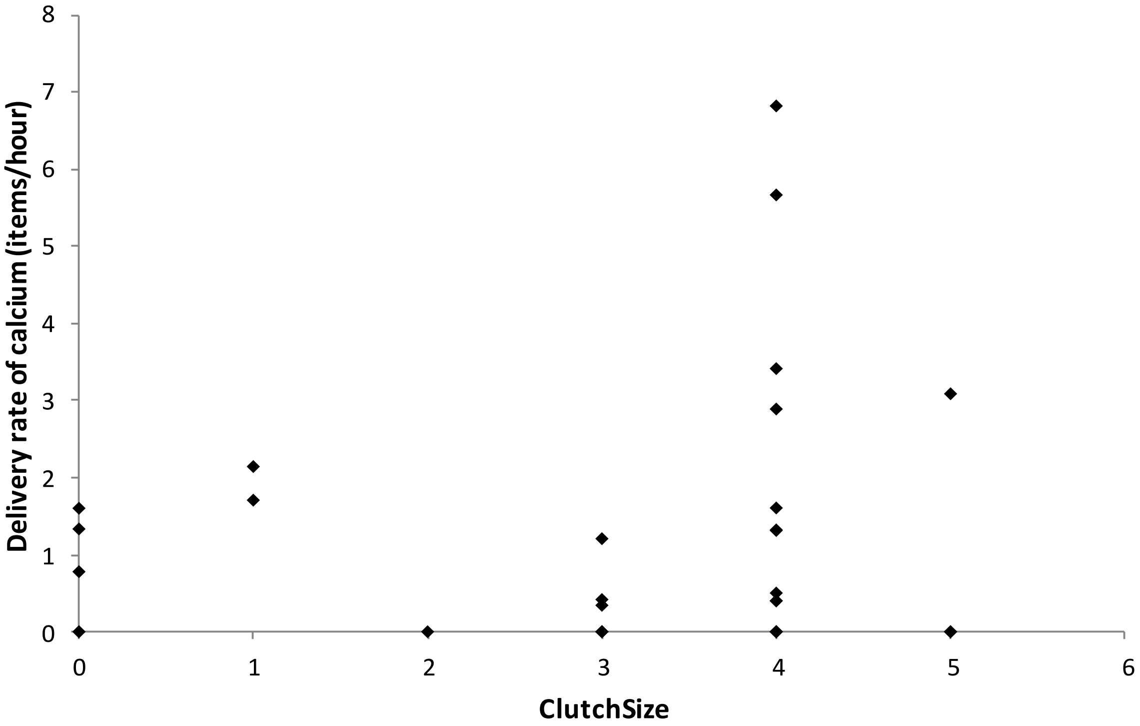

Figure 3.7: Delivery of calcium salts was unrelated to clutch size (n=29 individuals). LME: Rate of calcium delivery, $F_{1,6}$= 0.0019, p = 0.97, random effects: Female ID & Season

Figure 3.8: Male hornbill delivering weathered millipede exoskeleton. Weathered exoskeletons were easy to distinguish from live millipedes due to colour. Live millipedes are a dark red-brown colour but the carapace weathers to almost pure white after death.

Providing items that supply only calcium salts may be a strategy employed when items that are both calorifically and calcium rich are rare. Since hornbills eat food items whole, vertebrate prey will provide calcium from the bones. Unlike Prozesky (1962), the hornbills in the current study never produced pellets so bones must have been digested. Calcium rich items were delivered at a much higher rate in the period before laying (up to 5 days from entering) than in the 10 days before chicks hatch (Figure 3.9), supporting the idea that such items are more useful while preparing to lay.

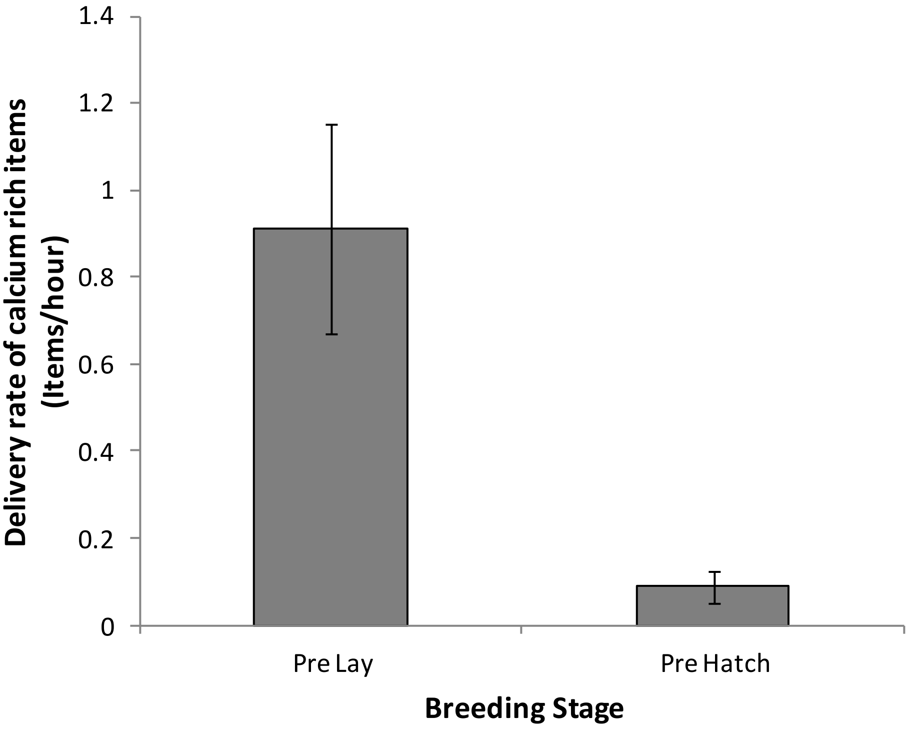

Figure 3.9: Millipede shell fragments and other calcium rich items are delivered at a much higher rate in the 5 days prior to laying (n=41) than in the 5 days prior to hatching (n=23). LME: Stage of breeding, $F_{1,27}$ =6.91, p = 0.014, random effect: Female ID (n=36 individuals).

All eggs were weighed and measured in the 2009-2010 and 2010-2011 seasons (n = 152). Eggs weighed on average 15.13g (± 0.13), ranging from 11.68g to 19.74g. Eggs from the current study were slightly larger than records from the Transvaal (Kemp 1995), measuring 38.30mm (±0.16) long (range 32.66mm to 43.15, n=152 eggs from 44 clutches) by 27.01 (±0.10) wide (range 24.21 to 37.10, n=152 eggs from 44 clutches).

Eggs were typically laid every other day, though the interval was greater between later eggs. The interval between 1st and 2nd eggs was on average 2.35 days (±1.1, n = 55), between 2nd and 3rd eggs was 2.91 (± 0.21, n = 54). The interval between 3rd and 4th eggs was 3.45 (± 0.31, n = 37), and between 4th and 5th eggs was 3.80 days (± 0.71, n = 10).

3.5.4 Wing Moult

Out of 40 breeding attempts where moult was closely monitored (in the 2009-2010 and 2010-2011 seasons), no females continued laying after shedding their wings. On average wing moult began 4.41 days (± 0.43) after the last egg was laid. Some birds began moult on the same day as laying the last egg and some waited up to 12 days after laying (figure 1). All records for hornbill moult (Kemp 1995) show tail and wing moult occurring simultaneously. In many cases the difficulty of recording the dates different feathers are dropped in cavity nests may well account for this discrepancy. It is relatively easy to see when one feather has been dropped, though it is difficult to see where it came from. Several studies however have been detailed enough (either by using nest boxes or through particular dedication) to detect the exact timing of tail and wing moult. These include Alan Kemp’s (1976) studies on various *Tockus* hornbills and the studies of Monteiro’s hornbill in the Daan Viljoen reserve in Namibia (Klassen et al 2003). These also suggest that wings and tail are shed simultaneously around the start of laying. It seems that the Kuruman River Reserve population of Southern Yellow-Billed Hornbill has an unusual moulting strategy. This potentially delays when the female can leave the nest. The dramatic implications of this are discussed in chapter 5.

3.5.5 Incubation

Incubation typically lasts 25 days (mean = 24.89 ± 0.09, mode = 25, n = 126 eggs in 52 clutches), similar to the 24 days reported by Kemp (1995). During incubation, females continue to receive food and nest materials from the male. While in the nest females continue to apply sealing to the nest entrance and any cracks in the nest. Nest sealing is a gradual process, continuing even once the chicks have hatched. Indeed one female continued sealing until the nest became completely closed and remained so for 4 whole days. The male nest visitation rate declines through incubation. There is an especially marked decline in the delivery of nest material. This is discussed in detail in chapter 4.

3.5.6 Hatching

Eggs hatch around 31 days (± 0.40) after females enter the nest. Incubation typically lasts 25 days (mean = 24.89 ± 0.09, mode = 25, n = 126 eggs in 52 clutches). Hatching was preceded by at least one day when the chick could be heard cheeping inside the egg. In total 51of the 65 breeding attempts managed to hatch at least one chick. Approximately a quarter of incubated eggs failed to hatch (33 of 141, 23.4%). These were not pushed out to the edges of the nests so were presumably infertile. Unhatched eggs remained in the nest and were only removed when the nest was prepared at the start of the following season.

The most common brood size at hatching was 4 chicks, matching the modal clutch size. Only two out of the 53 females who stayed in long enough to shed their wings failed to hatch any eggs. In both cases the females had cannibalised their clutch. Interestingly these females were the two who waited over 12 days to begin laying.

Chicks hatched with an average mass (n=108) of 10.21g (±0.21) and tarsi (n=77) measuring 9.87mm (±0.09). Hatching asynchrony was similar to laying asynchrony with 2 days between eggs. This resulted in large size differences between chicks. By the time junior chick hatched in a large brood, its eldest sibling would already be several times its size (Figure 3.10).

Figure 3.10: Typical brood of chicks on the day the youngest chick hatches. Here, the oldest chick, now 9 days old weighs 39.04g and has a tarsus of 20.94mm. The recently hatched chick weighs only 8.59g with a tarsus of 10.26mm. The elder two chicks display prominent air sacs.

3.6 FILIAL CANNIBALISM

3.6.1 Theoretical background

One striking aspect of female behaviour while nesting was the cannibalism of both eggs and young chicks. For many years, filial cannibalism, the act of eating ones relatives was regarded as an aberrant behaviour, caused by environmental or observer generated stress. At first glance, the idea of eating one's own would seem counterintuitive to natural selection. Filial cannibalism has however been reported for many species (Polis 1981). Rohwer (1978) expanded the ideas of parent offspring conflict to suggest that filial cannibalism could, in some circumstances be an adaptive parental strategy. While offspring represent an energetic investment, parents can recoup some of that investment by eating the offspring. Filial cannibalism could be a useful tool to parents in manipulating both their own lifetime reproductive success and the success of surviving offspring in their current brood. Cannibalism of one's own offspring is now regarded as a common adaptive strategy in many taxa such as teleost fish (Manica 2002), reptiles (Lourdais et al 2004) and insects (Thomas & Manica 2003).

While filial cannibalism has been reported in birds and mammals, most occurrences seem to be distant relatives consuming young that are not their own (Mumme et al 1983, Gilchrist 2006) to manipulate their own reproductive success. Relatively few cases of parental filial cannibalism have been reported in birds and most of those have been so rare that the proximate cause, be it an adaptive strategy or a response to disturbance, cannot be determined (Chan et al 2007, Gilbert et al 2005). For the purposes of this discussion I will refer to filial cannibalism as the act of parents eating their own young, rather than intraspecific predation by distantly related individuals.

Several proximate causes have been proposed for filial cannibalism. Cannibalism may be a maladaptive behaviour in response to anthropogenic disturbance. Chardine & Morris (1983) attributed male herring gulls eating their entire clutches to disturbance, though only 2 individuals cannibalised out of 115 nests observed with equal intensity. While the possible effects of disturbance should never be discounted in behavioural studies, there are also adaptive proximate causes of cannibalism. These explain two broad categories (Manica 2002); total filial cannibalism (eating one's entire brood) and partial filial cannibalism (eating part of the brood).

Total filial cannibalism only benefits the parent. Offspring gain no direct benefit, while the parent gains the energy locked up in the offspring. Parents can then use this energy to increase their lifetime reproductive success. The act of total filial cannibalism can be seen as an efficient form of terminating care when the costs of caring for the brood outweigh the benefits (Clutton-Brock 1991). Cannibalism allows parents to recoup some of the costs that would otherwise be wasted by abandoning the brood. Parents with small broods (that will yield few offspring) as well as those in poor condition or with mates in poor condition should be more likely to cannibalise, especially if the chances of subsequent breeding are high.

Partial filial cannibalism is more complex. While parents can recoup some energy from eating some of their brood, the surviving offspring can also benefit. This can be manifested in a variety of ways. If young are diseased (with little chance of survival) or dead, they pose a risk to the nest either through infection of generating scent cues for predators. In such cases they should be removed and if it is safe for parents to eat them then cannibalism is an efficient method of disposal (Polis 1981). Brood reduction is common in many species and is seen as a way of adapting brood size when environmental conditions are changeable (Lack 1968). When conditions are poor it will be better to invest in only a portion of the brood so that a few healthy offspring survive rather than all offspring receiving equal but insufficient food (Magrath 1989). In this respect, parents' interests differ from that of individual offspring (Trivers 1972). Rohwer (1978) suggested that filial cannibalism may merely be an extension of this. Not only will a reduced brood survive better, the energy recouped by the parent may allow it to provide better care for the surviving offspring (Manica 2002). Parents could also adjust sex ratio of the brood to maximise the breeding success of the offspring (Klug & Bonsall 2007). The predictions for partial filial cannibalism differ from that of total filial cannibalism (Manica 2002). Larger broods should experience greater levels of cannibalism as parents remove more offspring with small chance of survival. Later hatched chicks should be more at risk from cannibalism as by the time they hatch, their elder sibling will already have received parental investment.

The theoretical background for filial cannibalism has now been firmly established, with many examples coming from teleost fish. Thorough investigations into filial cannibalism in other vertebrate taxa remain rare. Given the now apparent widespread nature of filial cannibalism, it would be valuable to understand how cannibalism works in species with different life histories.

During preliminary studies on Southern Yellow-Billed Hornbill, it became apparent that chicks and eggs were going missing from sealed nests. The following section aims to present a detailed investigation of the extent nature and proximate causes of filial cannibalism in Southern Yellow-Billed Hornbill.

3.6.2 Evidence for filial cannibalism in hornbills: Cannibalism of eggs

Evidence for filial cannibalism was obtained for cannibalism both of eggs and chicks. No experimental manipulation was conducted but cannibalism was observed in a variety of contexts.

During incubation and in one case even before all eggs have been laid, females will sometimes cannibalise eggs (n = 16 eggs in 12 breeding attempts out of 59 attempts that laid eggs). While no egg cannibalism was caught on camera, there is reasonable evidence that females were eating eggs. One female was caught relatively red handed. On this occasion, a nest was visited twice within the space of twenty minutes in order to take an extra morphometric measurement. Between visits an egg had disappeared and the female had yolk dripping from the sides of her mouth. Even in cases where eggs simply disappeared there is good reason to suspect similar cannibalism. When eggs hatch, females will remove all pieces of eggshell, leaving them on the floor outside the nest. After all the egg disappearances, no eggshell could be seen in or out of the nest. The eggs are too large to fit out of the sealed nest intact so could not have been throw out of the nest or handed to the male.

Three females ate eggs in successive seasons. This accounts for half of all egg cannibalism. One of the three females bred in a different nest with a different partner in two seasons. None of the other 6 females were recorded in more than one season, so unfortunately their cannibalistic tendencies could not be assessed. A longer study would be worthwhile to determine if some females are consistent egg eaters.

The timing of egg cannibalism was highly variable from 12 days after the female entered the nest to 42. Eggs had been incubated for an average of 10.63 days (± 1.59), ranging from 2 days of incubation to 21 days. More first laid eggs were eaten (n = 5) than any other size class, though of course these eggs were more common (Table 3.2). Laying order did not influence the chances of an egg being eaten.

Egg laying order	Number of eggs laid	Number of eggs eaten
1	60	5
2	54	4
3	53	3
4	36	3
5	10	1

Table 3.2: The order eggs were laid in did not appear to influence the chances of cannibalism. Fisher's exact test: $\chi^2_4 = 0.40$, $P = 0.97$

Only two cases of total cannibalism occurred at the egg stage. One was of a brood of only 1 egg and one was of a brood of 3. Both these females had moulted their flight feathers. None of the 4 females that laid but abandoned before moulting their wings ate any eggs at all. Both of the 2 females who ate their whole broods took a long time to lay their eggs and moult in the first place. This suggests that total cannibalism of eggs may only apply to females that terminate breeding after moulting and have to wait until their wings are developed enough for them to leave the nest. Cracked eggs (n = 3) were not eaten and neither were the 28 eggs that failed to hatch, so the cannibalism does not appear to be a way of disposing of damaged or infertile eggs (Stanback & Koenig 1992).

Partial cannibalism was also relatively rare, occurring in 9 out of the 59 clutches laid. There appeared to be no relationship between clutch size and the likelihood of eggs being eaten (Table 3.3). This suggests that egg cannibalism may be more important for adjusting parental condition than in brood reduction. Cannibalising eggs as a means of brood reduction would not be efficient in hornbills as food availability can change quickly with rainfall. It would be more efficient to wait until the chicks hatch, especially as the females cannot leave the nest until their flight feathers have regrown (Chapter 5). All this seems to indicate that egg cannibalism may be a mechanism of increasing female condition. Given the variability of the timing of egg cannibalism it was impossible to do a fair analysis of female condition against the likelihood of cannibalism as female condition changes throughout incubation. A detailed experimental study involving artificially provisioning females could be used to investigate the role of condition on egg cannibalism.

Clutch Size	Number of clutches laid	Number of clutches that experienced cannibalism
2	1	0
3	16	4
4	27	3
5	12	2

Table 3.3: Clutch size did not influence the likelihood of partial filial cannibalism of eggs. Fisher's exact test: $\chi^2_3 = 0.40$, P = 0.54

3.6.3 Evidence for filial cannibalism in hornbills: Cannibalism of chicks

An unexpected feature of the hatching period was the disappearance of young chicks. Sixty three chicks of up to 13 days old vanished from the nest, out of 157 chicks hatched. Unlike eggs, young chicks are small enough to be forced through the nest entrance. This left several possible explanations for the disappearance of chicks. One was that the chicks had died and been passed out of the nest by the female and taken away by either the male or scavengers on the ground below. The other possible fate was cannibalism by the mother, either after the chick had died of starvation or disease or while still alive. There is good evidence that cannibalism is the fate of the vanishing chicks. Firstly, chicks commonly disappeared on the day they hatched (n=20). This does not fit with the idea of chicks dying then being removed. Secondly, chicks that starved to death, slowly losing condition were often left in the nest, gradually being eaten by scavenging arthropods. Apparently healthy chicks were also disappearing, sometimes between visits 30 minutes apart (n=3). This prompted the use of all day video recordings in nests with young chicks. Two instances of cannibalism were recorded. One of a live chick and one of a chick that had seemingly died (or at least become immobile) a few hours before (CD Videos 3.2 & 3.3). In both cases the female picks up the chick and manipulates it in the bill for around 2 minutes before eating it. The live chick was not killed by the mother prior to consumption. This appears to be similar to the actions of Roadrunner (*Geococcyx californianus*) parents that will pick up nestlings and eat any that appeared lethargic (Ohmart 1973). Females feeding chicks to their siblings cannot be discounted. However it seems highly unlikely in most cases as usually when chicks disappeared there were no siblings in the nest large enough to swallow another chick.

Chicks were cannibalised between 0 and 13 days after hatching, with a mean age of 2.90 days (± 0.34). The age at cannibalism was not normally distributed with the 23 chicks disappearing on the day they hatched, 20 of which before they were even seen by observers (Figure 3.11).

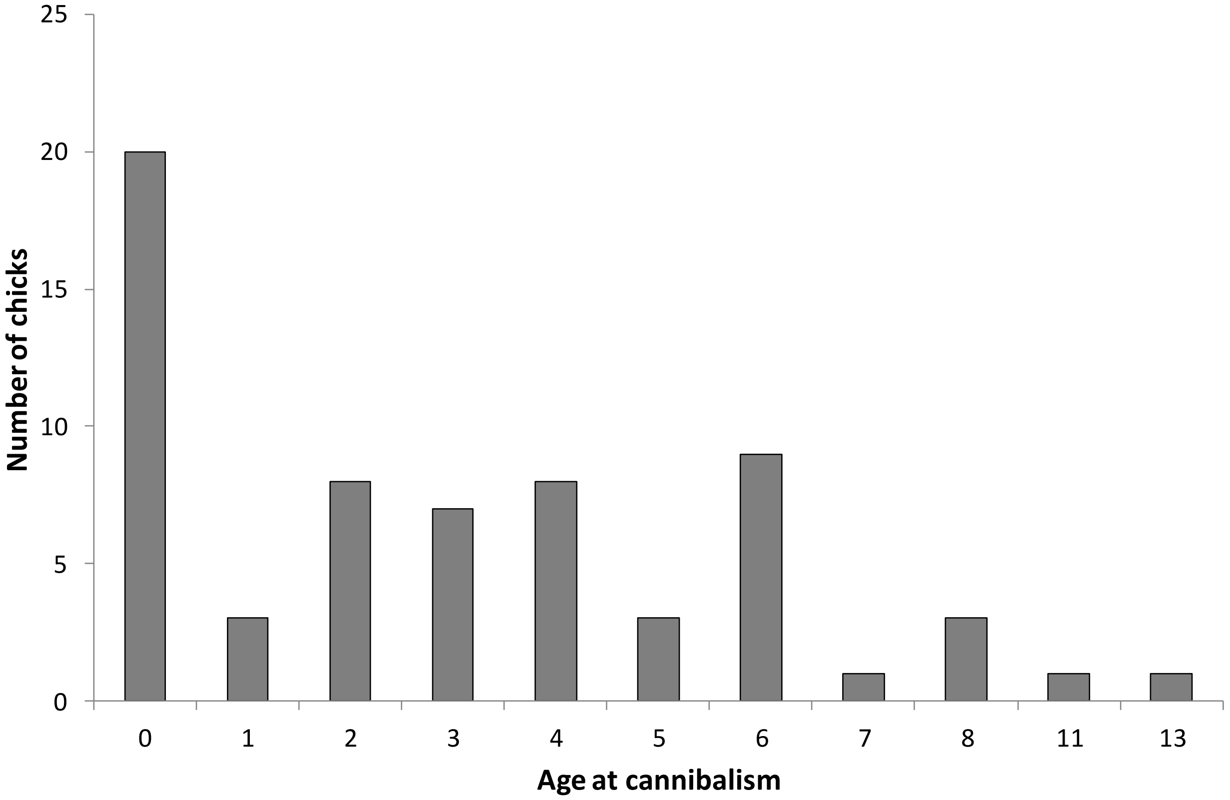

Figure 3.11: Distribution of chick age at death of cannibalised chicks (n= 63)

Total brood cannibalism occurred on 3 occasions. On 2 occasions, only 1 chick hatched and was eaten on the day it hatched and the mother abandoned soon after. The third instance was a brood of 3 chicks. Each chick disappeared on the day it hatched, with the female abandoning on the day it ate the last chick. This female's mate had formed a pair with a new female and was feeding the nest only sporadically.

Partial cannibalism occurred in 33 of the 49 remaining nests that hatched chicks. Cannibalism was so prevalent that there was no effect of brood size on the likelihood of cannibalism occurring (Table 3.4).

Brood size	Number of brood hatched	Number of broods that experienced partial cannibalism
2	11	6
3	10	9
4	21	16
5	4	3

Table 3.4: Brood size did not influence the likelihood of partial filial cannibalism of chicks. Fisher's exact test: $\chi^2_3 = 0.40$, $P = 0.36$

Later hatched chicks were however at greater risk of cannibalism. While sample sizes obviously decreased for later hatched chicks, there remained a significant difference in the likelihood of cannibalism (Table 3.5 & Figure 3.12)

Chick hatch order	Total chicks	Number of chicks cannibalised
1	51	12
2	45	15
3	34	16
4	24	17
5	3	3

Table 3.5: Later hatched chicks were more likely to be eaten than earlier ones. Fisher's exact test: $\chi^2_4 = 0.40$, P <0.001

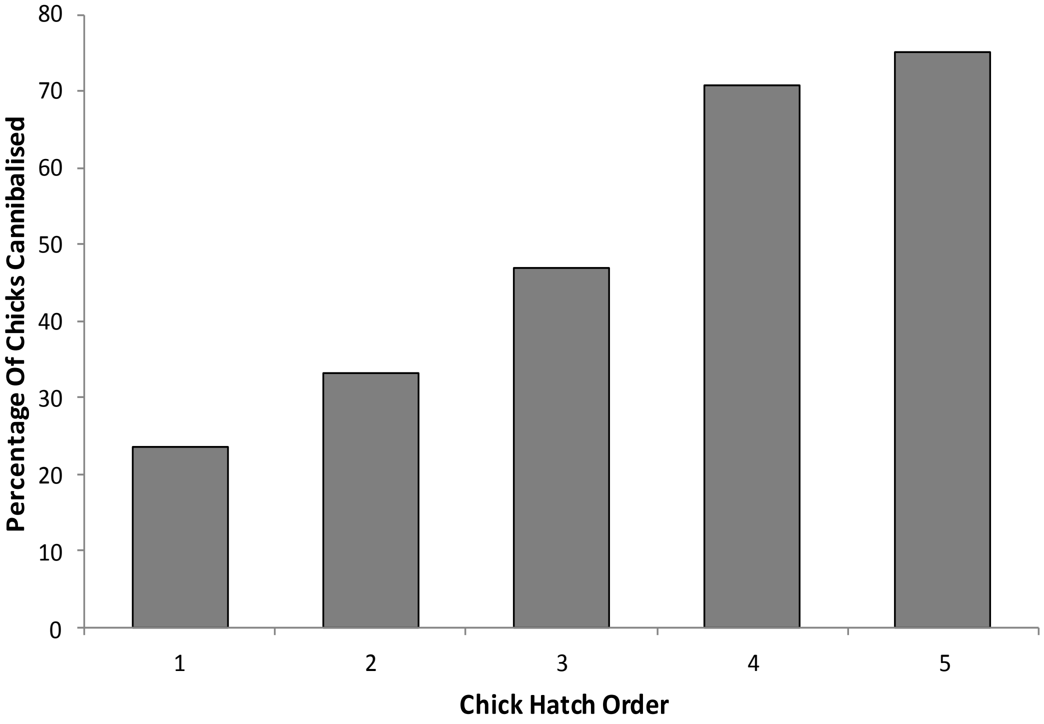

Figure 3.12: Later hatched chicks were more likely to be eaten than earlier ones. Bars represent percentages derived from table 3.5

Brood reduction would predict that larger broods experience higher levels of filial cannibalism, if all nests received the same levels of resources. Of course all nests do not receive equal provisions, so larger broods could cope without brood reduction if they had sufficient food. In order to test the possibility of brood reduction in response to changes in feeding rate nests were monitored to determine if females ate chicks as they hatched. This removed the chances that cannibalism was due to removal of weak or starving chicks. It also meant that disappeared chicks could definitely not be fed to older siblings, which would not yet be large enough to consume them. The male feeding rate to nests was measured in the first 7 days of nesting and then again in the final 7 days before hatching began. For the purpose of this analysis I only used one breeding attempt from each female that was recorded multiple seasons, avoiding pseudoreplication. Females that ate chicks experienced a lower increase in feeding rate than females that did not eat chicks (Figure 3.13).

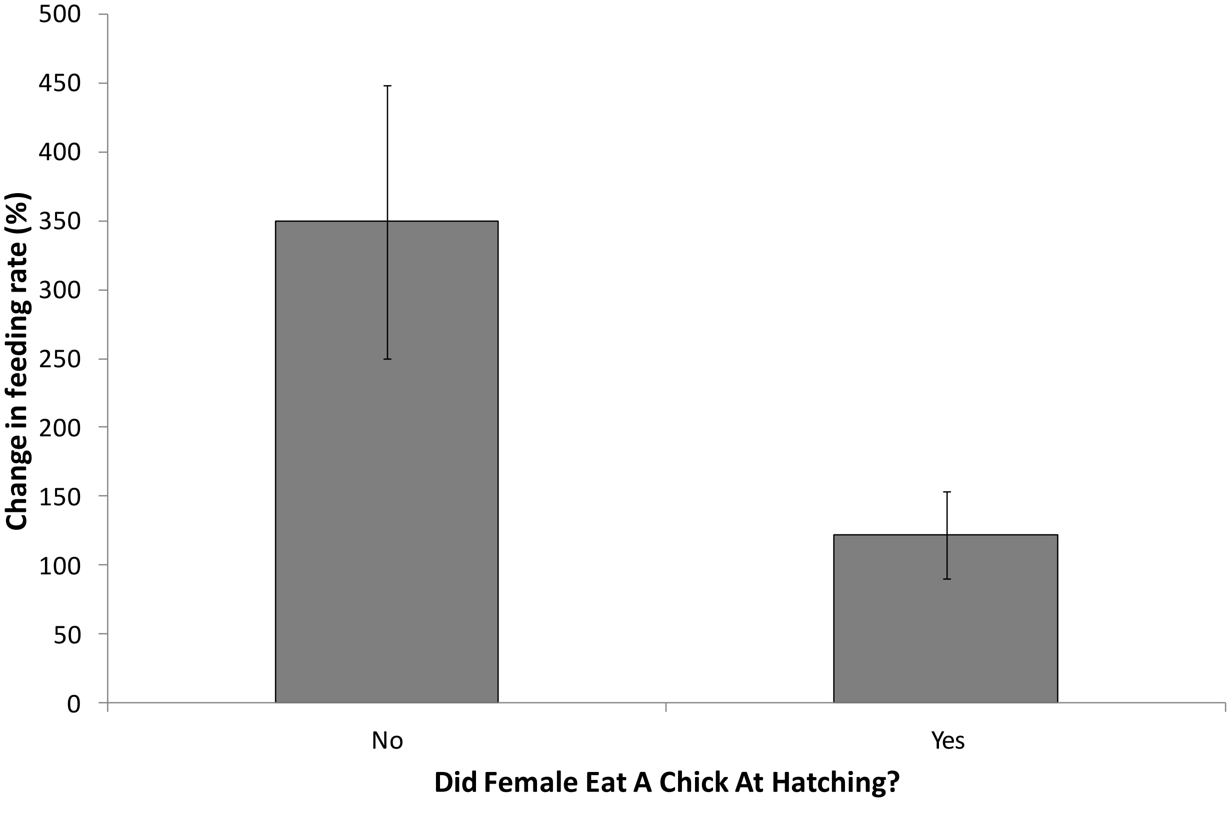

Figure 3.13: Females that ate chicks as they hatched (n=9) experienced a lower increase in feeding rate during incubation than females that did not (n=14) eat chicks. T-test $T_{13.77}$ = 1.83, P = 0.04.

Hornbill chicks have to reseal the nest cavity and be able to take food from the nest entrance once their mother leaves. This puts a large constraint on the viability of hornbill chicks. A brood of small chicks would all die once their mother has left as they simply could not feed or defend themselves. It is much better to ensure that a few chicks can reach the nest entrance and ensure some reproductive success.

3.6.4 Discussion

Cannibalism of eggs in the study population of hornbills was not frequent but certainly not insignificant. Cannibalism of chicks was however very common. Commonplace filial cannibalism has not been observed to this extent in any other bird. Chan et al 2007 observed two instances of infanticide-cannibalism in the Oriental Pied Hornbill (*Anthracoceros albirostris*). On both occasions a fourth hatched chick in a brood of 4 disappeared. On one occasion, the female was caught on camera killing the chick and feeding it to a sibling. Chye et al (2009) describe further infanticide cannibalism in the Oriental Pied Hornbill in both the wild and captivity including 3 chicks killed by heavy rainfall being eaten by the mother. The findings of the current study reinforce the work on the phylogenetically distant Oriental Pied Hornbill (Kemp 1995) and suggest that cannibalism may well be a widespread trait in hornbills, unknown purely because of a lack of nest video recording. Southern Ground Hornbill (*Bucorvus leadbeateri*) are not known to cannibalise offspring but always hatch 2 offspring, the younger of which never survives, usually dying from starvation within a few days of hatching (Kemp 1995). Ground Hornbills are unusual among other hornbills as they are cooperative breeders that do not seal the nest cavity or moult during breeding.

That routine cannibalism should have evolved in the hornbills rather than other bird species can perhaps be explained by their breeding ecology. Firstly, hornbills are long lived; records show Southern Yellow-Billed Hornbill surviving for at least 20 years in captivity. (Strehlow 2001). Secondly, the sealing of females makes maternal investment decisions a particular gamble. Females have to decide on clutch size at the start of breeding, just after the rainy season has begun, with no knowledge of future weather and food availability. Female hornbills also lack the ability of most pair breeding birds to compensate for low feeding rates by their mate (Johnstone & Hinde 2006). This puts female hornbills in a unique gambling situation. Dall & Johnstone (2002) demonstrated theoretically that when faced with uncertainty over resource availability animals can mitigate risks either through gaining as much information as possible to reduce uncertainty or by insuring against it. Filial cannibalism in hornbills can be seen as a way of insuring against the uncertainty of future resource availability when females make decisions over maternal investment. Female hornbills seem to maximise the volume of information they receive before committing to breeding by delaying their wing moult until they have finished laying. Cannibalism then provides insurance against further changes.

At one end of the scale, females can choose to abandon their breeding attempt, recouping a large amount of their energetic expenditure by total filial cannibalism of eggs. This proved relatively rare, but would be a vital strategy for a female should her mate be killed during breeding. Much more common was partial filial cannibalism, this, like classical brood reduction, seems to be a way of fine tuning maternal investment to maximise the reproductive success of the brood. Hornbills could prove a useful species for investigating the trade-off implicit in filial cannibalism. They are amenable to nest box studies allowing video recordings and cross fostering and could be trained to use feeders. The poor chances of later hatched hornbill chicks could also be put to use by conservationists. Otherwise doomed second hatched Southern Ground Hornbill chicks from Kruger National Park, South Africa have been successfully harvested and reared, ready for captive breeding and reintroduction at the Mabula Ground Hornbill Research & Conservation Project (Kemp et al 2007). Similar strategies could be used for other threatened species with chicks that would otherwise not survive.

3.7 POST HATCHING BEHAVIOUR

While chicks and mothers overlapped in the nest, males delivered (n=17) approximately 8.85g of food per hour (±1.41). Males continued to deliver only one item per visit. Females took food from the nest entrance and then distributed it among the brood. Typically females ate 34.31% (± 8.29) of food delivered, passing the rest on to the chicks. Females never divided items between chicks. If an item was too large for any of the chicks to eat, usually the female would consume it herself after offering it to each chick. Between the hatching of chicks and departure from the nest, females lost on average 18.39% (± 1.26) of their body weight (n=36).

Females departed after 53.27 days (±0.76) in the nest when chicks were around 20.27 (± 0.33) days old. Chicks then resealed the nest, with no help from the parents, though often were not as proficient as their mothers (Figure 3.14). After mothers left the nest, chick behaviour changed dramatically. This is described in Chapter 6.

After leaving the nest, females helped males with provisioning. The extent of help varied from female to female. On average when females helped feeding (n=10 out of 15 pair focals), they provided 37.74% of items (±4.22), though 5 females gave no feeds at all. One female adopted a unique technique, waiting in the nest tree, taking food from the male and passing it to the chicks sealed in the nest. This is much more similar to the behaviour of breeding female woodhoopoes (du Plessis et al 2007). Coincidentally, a group of Red-Billed Woodhoopoe would use the same tree as this female, the only nest tree in which both species bred.

Most successful breeding attempts fledged only 1 chick (n=18), the largest number of fledged chicks was 4, achieved by only 2 nests (Figure 3.15). Chicks fledged at an average age of 52.52 days (±0.60). There was considerable variation in chick age at fledging from 46 to 72 days old. Chicks from the same brood did not always fledge simultaneously. Of the 13 nests that fledged 2 chicks, only 2 nests fledged both chicks on the same day. For the others the second chick fledged between 3 and 10 days after its older sibling (mean = 5.89 ± 0.86). In larger broods (n=5), junior chicks stayed in for up to 14 days after the first fledged young. Parents left fledged chicks in nearby trees while feeding the nest. To encourage chicks to fledge parents would perch outside the nest giving feeding calls but not passing food.

Figure 3.14: Nest sealed by chicks after mother departed.

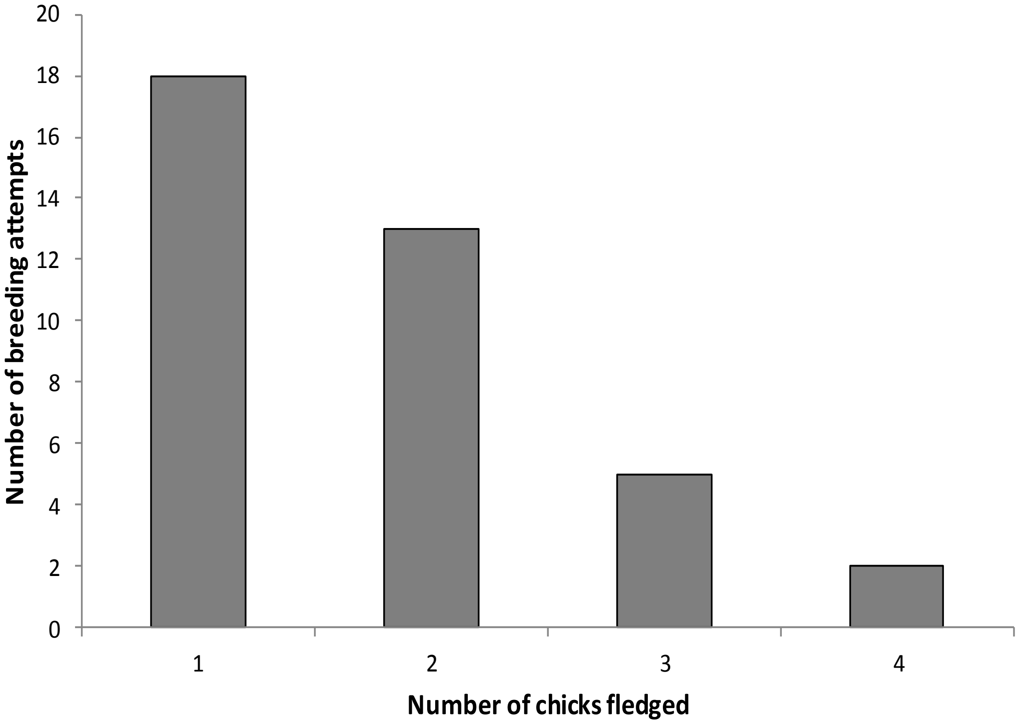

Figure 3.15: Histogram of number of chicks fledged per breeding attempt. Most nests only fledged one chick.

3.8 CONCLUSIONS

Observing behaviour in the nest has demonstrated that hornbill breeding is a more complicated process than previously thought. The complications of sealing the nest demand close cooperation between male and female. While the female relies on the male for food, the male has no direct control over investment decisions within the nest. The following chapters explore the intricacies of hornbill breeding in greater detail. The next chapter deals with communication between confined females and their mates. Males deliver a variety of substances to the nest other than food and how the need for such material is explored. Chapters 5 and 6 deal with intrafamilial conflict and how the duration of female confinement can influence conflicts between parents and offspring.

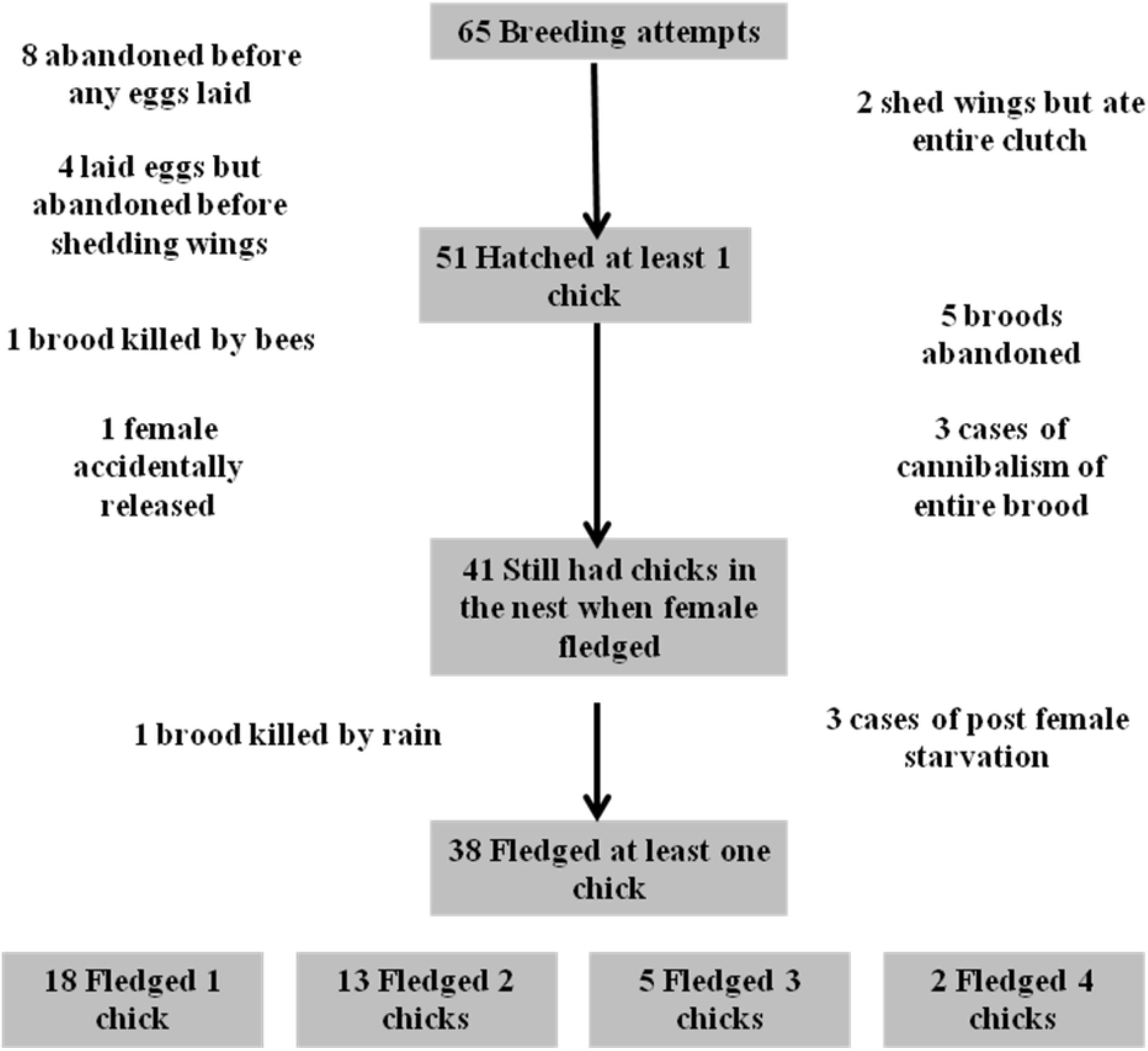

Figure 3.16: Summary of all breeding attempts followed during the 3 study seasons

Chapter 4

Confined Female Hornbills Can Communicate Need For Food And Nest Materials By Modulating Begging Calls

4.1 ABSTRACT

Most begging studies focus on altricial offspring soliciting food from parents. Here a novel system provides an opportunity to investigate begging outside the normal context. Female Southern Yellow-Billed Hornbills (*Tockus leucomelas*) seal themselves into the nest cavity at the start of breeding. Hornbill nests are lined with bark that raises the floor of the nest so chicks can reach the nest entrance when their mother leaves the nest when they are around 20 days old. The male hornbill must therefore supply both food and nesting materials to the female through the tiny nest entrance. Males cannot see into the nest so must rely on cues from female begging to make provisioning decisions. Observations of natural behaviour showed that nest material was plentiful in the environment but was only provisioned early in the nesting period. Experimental removal of nest lining demonstrated that female hornbills modified their begging in response to their need for nest materials. Females gave more and longer begging calls but did not change the pitch of begging. Male hornbills adjusted their provisioning behaviour to nests artificially deprived of nest materials, providing more bark but not changing the delivery of food. Natural variation in female hunger was used to investigate how begging is influenced by short term need for food. Females begged with longer calls when deprived for longer but also changed the pitch of their begging. This chapter demonstrates that female hornbills can beg for both food and nest materials. The potential for future work on this system is discussed.

4. 2 INTRODUCTION

Food solicitation calls produced by nutritionally dependent offspring are taxonomically diverse and well studied (Kilner & Johnstone 1997). Indeed offspring begging has become an important framework for the study of both communication and intra familial conflict (Godfray 1995, Mock & Parker 1997). Most studies take advantage of offspring begging since it is such an amenable, easily manipulated system. Begging outside of the classical parent offspring system is however, not at all rare. Adult individuals of many species give calls structurally analogous to the begging of nutritionally dependent offspring (e.g. Robbins 2000, Brown et al 2004, Lawton & Lawton 1985). Breeding females in particular are known to solicit food from their mates (Otter et al 2007) or subordinates (Radford 2004). Several broad explanations for adult begging have been suggested (Ellis et al 2009), only one of which is analogous to the hungry begging of needy chicks. Females may beg, like offspring as a means of soliciting food (Otter et al 2007). However female begging has also been suggested as a form of fertility advertisement, between mates, within social groups or to extra pair males (Tobias & Seddon 2002) and may also serve to communicate social interactions in group living species (Heinrich et al 1993) Many of these reasons are not mutually exclusive (Ellis et al 2009) and it can be difficult to differentiate between them.

Another little known application of begging is that of individuals of any age begging for types of care other than food. Organisms need resources other than food to survive, so perhaps it should not come as a surprise that need for these resources can be communicated. Nestlings (Evans 1994) and even eggs (Evans et al 1994) beg for warmth from brooding adults. Chimpanzees (*Pan troglodytes*) will provide conspecifics with tools and food upon request (Yamamoto et al 2009). Such unusual examples of begging, while probably widespread are little studied as they fall outside the domain of the theoretical models based on nutritionally dependent offspring.

This chapter presents data from an unusual system. Hornbills of the family Bucerotidae nest in cavities in trees or cliffs. Before laying, the female seals herself in, using cement made of soil, organic material and her own faeces, leaving only a small gap through which she can be provisioned by her mate. The female will then moult her flight feathers, becoming entirely nutritionally dependent on her mate until she has regrown her feathers and is ready to leave the nest. Many birds employ also a gynaeparental incubation strategy, in which males feed the incubating female who supplements the feeding with bouts of foraging. Indeed, females of some species such as several species of Raptor refrain from foraging entirely during incubation (Newton 1979). The incarceration and complete moult of female hornbills however makes them uniquely dependent. As the male brings food, the female begs with a loud harsh call similar to older chicks (Kemp 1995). Females beg to males both during courtship before confinement and once sealed inside the nest. While female begging could serve many purposes during courtship, once confined in the nest, it is unlikely to display anything but need.

Male hornbills not only deliver food to their mates but also materials to line the nest. Nest material is needed since natural cavities of sufficient diameter to accommodate a female and her brood are often also very deep. The floor of the nest must therefore be raised to a level where the chicks can reach the nest entrance when their mother departs. If chicks cannot reach the nest entrance when the mother has left then they are at risk from predation, being neither able to seal or physically defend the nest entrance. Chicks that cannot reach the nest entrance are also unable to take food from their parents and will quickly starve (Personal observation). Nests are commonly lined with a variety of materials, provisioned by both male and female before the female enters the nest. Many species of hornbill rely heavily on seasonal rainfall and will breed quickly following the first rains (Kemp 1995), often before the nest is fully lined. Males therefore continue to provide lining materials once the female is incarcerated. As confinement continues and the nest fills with lining, female demand for materials decreases. Males need to be able to gain some information about the state of the nest, to tailor their efforts so that they can efficiently deliver only items that are needed. Unlike most birds, male hornbills cannot easily see into the nest. Hornbill vision is restricted by the large bill (Martin & Coetzee 2004) and the sealed nest entrance is very narrow, so that when at the nest entrance, males would block any light entering the nest. This means that male hornbills cannot directly assess the depth of the nest. To provision the correct amount of nesting materials, males must rely on indirect cues relating to the state of the nest cavity. Delivery of nest lining could be tailored against the amount of time the female has been in the nest, providing nest materials only early on then stopping after a certain time. A potentially more accurate method would be communication from the female, providing the male with information about what is needed via begging calls.

This chapter aims to investigate how incarcerated females hornbills communicate with their mates. Observations of foraging males were used to quantify the abundance of food and nest lining materials close to the nest. If nest lining materials are rare and difficult to find close to the nest then any variation in delivery could be due to foraging constraints rather than a response to demand. Natural variation in nest material delivery was used to investigate how males change their delivery of nest materials and if this fits with the theory that delivery declines as the nests fill with lining. Experimental manipulation of nest depth was then used to determine if females change their begging in response to need for nest materials and if males in turn respond by changing their provisioning behaviour. Observations of natural behaviour were used to investigate how hunger influences female begging and if begging is modulated differently in response to the need for food and nest materials.

4.3 MATERIALS & METHODS

4.3.1 Study site and equipment

The study was conducted on ranchland in the southern Kalahari Desert (26°58’S, 21°50’E). The study population comprised of colour ringed Southern Yellow-billed Hornbill pairs nesting in 36 artificial nest boxes. Studies were conducted between 2009 and 2011, encompassing two breeding seasons with nesting occurring between October and March. Nest boxes were fitted with internal audio and video recording equipment. Audio recordings were collected using Sony ECM-T6 tie-clip microphone connected to a M Audio Microtrack II audio recorder. Recordings were collected at 48KHz. Videos were recorded using a 117 series CCTV camera with infra red LED’s (Henrys CCTV, Edgware Road, London), connected to recorders, either Mini DVR 1 or Mini DVR 2 (www.dogcamsport.com).

4.3.2 Analysis of video data

Video recordings were viewed using VLC Media Player allowing viewing at up to 16 times real speed. All male visits were transcribed and defined as one of three classes. A ‘feed’ was when an item was passed to the female. When possible the item being delivered was identified. Southern Yellow-billed Hornbills only ever bring one item at a time simplifying identification. Examples of delivery of a food item and a piece of nest material are on the supplementary CD (Videos 4.1 & 4.2).

4.3.3 Audio analysis

Audio recordings were analysed in Raven (Cornell Bioacoustics Research Program. (2011). Raven Pro: Interactive Sound Analysis Software (Version 1.4) [Computer software]. Ithaca, NY: The Cornell Lab of Ornithology. Available from http://www.birds.cornell.edu/raven.). Calls were sampled for 7 seconds after each provisioning. Most calling bouts had ended within 7 seconds. Calling bouts longer in duration could not be distinguished from bouts caused by subsequent male visits or male post feed calling. Calls were characterised by their duration (seconds), peak frequency (Hz) and the number of calls per bout. All call parameters used are robust measures of signal and depend little on human measurement error (Charif, Strickman, & Waack. 2010).

4.3.4 Availability of nest lining

Fifteen nests were observed within a week of female incarceration during the 2009-2010 breeding season. Observations were carried out with binoculars, sitting at a distance of approximately 30-50m from the nest. The 15 nests were observed for 2 hours each, starting at sunrise. All male visits to nests were recorded along with all male activity within sight of the observer. Generally the observer could see males while they remained within 100m of the nest. For all male provisioning bouts, the supplied item was recorded along with where the male had come from. In order to examine the relative costs of obtaining bark and food, items were divided into those obtained within 10m of the nest and those obtained further afield. The percentages of food and bark obtained within 10m of the nest were compared.

4.3.5 Natural variation of nest lining provision

Nests were recorded for two hours after sunrise at key points during the breeding cycle. Most nest provisioning occurs during the first few hours after dawn before summer temperatures get high. In order to assess how the delivery of bark and food changes through time, nests (n = 23 individual breeding attempts) were recorded throughout the nesting period from the first 5 days, before any eggs had been laid (n=21), during egg laying (n=21) and throughout incubation (n=18). Repeated observations were taken from the same breeding attempts and the attempt is included as a random factor in analysis to control for nesting attempts that failed. The vast majority of nest material consisted of the bark of the Camelthorn tree (*Acacia erioloba*). Bark from Grey Cametlthorn (*Acacia haematoxylon*) and Shepherds tree (*Boscia albitrunca*) were delivered very rarely as were Camelthorn seed pods. All Hornbill nests were in Camelthorn trees and loose bark was plentiful throughout the study. Millipede shells were provisioned and sometimes dropped by the female into the lining or used to seal the nest. Some millipede shells were also eaten, possibly as a source of calcium (Borrell 2004). The delivery of millipedes and millipede exoskeleton was therefore excluded for the purpose of this analysis.

4.3.6 Experimental manipulation of nest depth

Paired experiments were conducted to investigate whether the amount of lining in a nest influenced both male provisioning and female solicitation behaviour. Experiments were conducted just after the mid lay period (around day 17 ± 6 days after female entry) when bark was still being brought but females are less likely to abandon the nest than earlier.

Thirteen nests were each given two treatments, in random order within three days of each other. In both treatments, the nest was approached after sunset on the evening before observations. The female and any eggs were carefully removed and stored in a bag or on thick soft matting respectively. Most of the nest lining was removed, leaving approximately 5cm of bark on which the female and eggs could sit. This lowered the floor of the nest by an average of 134.2mm (± 3.91), with nests changing from 120mm (±10.21) deep during controls to 253mm (±2.38) during ‘Removal’ treatments. In the ‘Removal’ treatment, the nest lining was stored in a plastic bag and the female and eggs were returned to the nest. The ‘Control’ treatment controlled for the disturbance to the nest by simply returning the bark to the nest straight away. Six nests experienced the control treatment first and seven experienced the removal first. Nest material was largely homogenous throughout the nest with no distinct layers. Though the floor of the nest was covered in fine material such as sand and tiny pieces of bark, this is likely to be due to settling of such fine particles and in any case this layer was undisturbed during either treatment.

Nests were fitted with internal recording equipment the following morning before sunrise approximately 20minutes before males began foraging. Recordings were conducted for three hours from sunrise. After the recording period the equipment was removed and nest lining material returned.

Any differences in behaviour between treatments can be attributed to the amount of nest lining material present. Conducting the experiment early in the morning standardises female hunger, while the paired design of the experiment controls for individual differences in female begging. The amplitude of begging calls was not analysed in this experiment as removing bark changes both the size of the resonating chamber and the distance from the female hornbill to the microphone. Acoustic analysis was conducted on the second male visit of the morning as often females were still asleep during the first male visit, so may not have had a chance to assess nest depth.

4.3.7 Natural variation in female hunger

Testing the influence of adult female hunger on begging was not as simple as that of nest depth. Adult female hornbills will not accept food from humans in the same way that chicks will in the many previous studies of begging (e.g. Kilner et al 1999). This means that while females can be experimentally deprived of food, no suitable control could be conducted. In an attempt to relate hunger and begging, natural variation in periods of deprivation were used. Male hornbills at the study site typically provisioned nests most around dawn and dusk. While males evening visits were typically very close to dusk (in 19/20 trial focals on different nests, males visited less than 10 minutes before sunset), there was considerable variation in how soon after dawn males visited the nest. Calls were recorded from 16 incubating females in the 2009-2010 and 2010-2011 breeding seasons. Begging calls emitted during the first feeding visit of the morning were compared to the time of the visit. To control for seasonal variation in the time between dawn and dusk, time was expressed as minutes since dusk the previous evening. Time since dusk seems to be a reasonable proxy for hunger as while females' hunger will increase over periods of deprivation the depth of the nest will remain unchanged. The timing of dusk was calculated using calculations from the crepuscule function of the "maptools" package in R, based on Algorithms from National Oceanic & Atmospheric Administration (NOAA). Dusk is classified as 'Civil Dusk', when the sun is 12° below the horizon, which corresponds well with the activity periods of foraging hornbills (Personal observation). Call features and deprivation were compared using a linear mixed effect model.

4.3.8 Statistical analysis

Analysis was conducted using R (R version 2.13.1, The R Foundation for Statistical Computing). Data were analysed using linear mixed-effect models (lme function) with individual as a random factor or paired sample Wilcoxon tests in order to control for repeated sampling from the same nests. Rate data were transformed by adding one to the rate and taking the natural log. Other non-normal data were transformed using square root transformations. All data are reported correct to two decimal places. For analysis of acoustic data a sequential Bonferroni correction (Holm 1979) was applied to assess significance with all call parameters included in analysis.

4.3.9 Failed experiments

Two sets of experiments were attempted but failed due to unpredictable responses by females to treatments. Artificial feeding of females was attempted in an effort to experimentally manipulate hunger. Unfortunately, while some females would eagerly accept food offered with a hornbill beak (taken from road killed individuals) at the nest entrance, others would react defensively, while most individuals varied in their response unpredictably.

In an attempt to manipulate male provisioning playbacks of female begging were trialled. Unfortunately female hornbills also react unpredictably to playbacks of their own calls. While they do sometimes ignore them, frequently playback causes the female to ignore the arrival of the male or even to act defensively. Changes in female behaviour would have influenced male provisioning and confounded any effects of playback on male behaviour. Potential alternatives to these experiments are explored in the discussion.

4.4 RESULTS

4.3.1 Availability of Nest Lining

Bark was much more abundant close to nests than food was. Eighty three pieces of bark along with 80 food items were delivered in the 15 focals. On average 67 (±9.71) percent of the bark delivered came from within 10 meters of the nest. This was significantly larger than the 4.30 (± 2.54) percent of food delivered from within 10m (Figure 4.1)

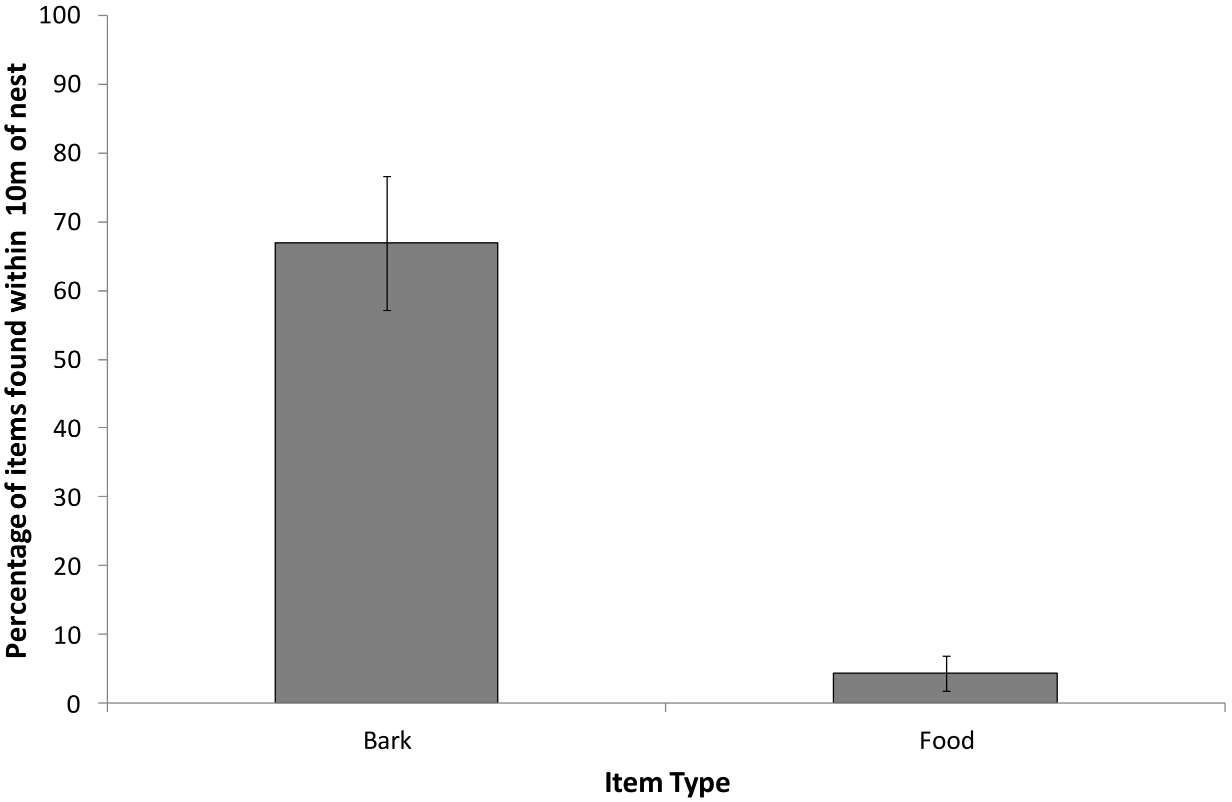

Figure 4.1: A greater proportion of bark was found within 10m of the nest than food (Wilcoxon signed ranks test V = 91, p = 0.002)

4.3.2 Natural variation in nest lining delivery

Overall, more food was delivered than nest materials (LME, $F_{1,121} = 78.02$, $p < 0.0001$). While pairs added lining to nests before females entered the nest (Chapter 3), most pairs quickly bred following rains (Chapter 3) and males continued providing nest lining during female confinement. Once the female was sealed, bark delivery by the males was high early in nesting and tailed off to practically nothing by the time chicks hatched (Figure 4.2). This demonstrated that male hornbills reduced the amount of bark as nesting progresses but does not suggest what cues male hornbills use to adjust the items they bring to the nest.

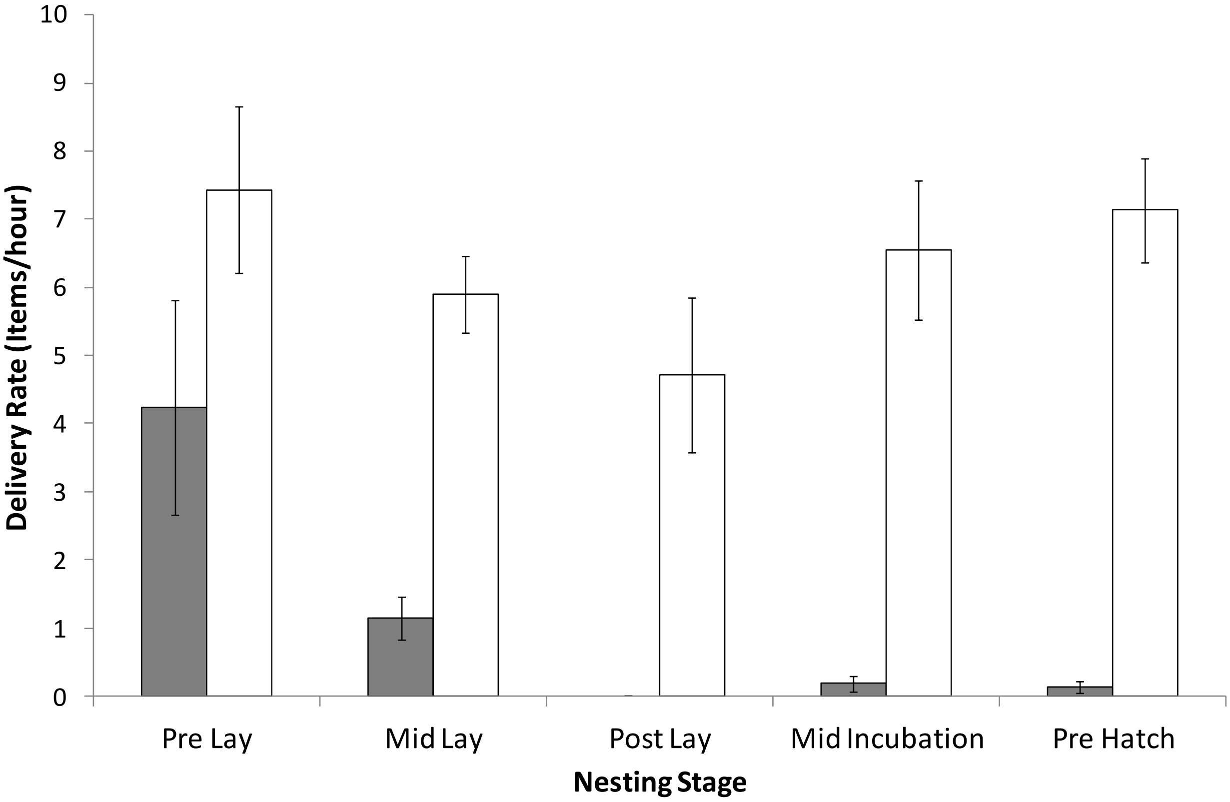

Figure 4.2: Delivery of bark (shaded bars) to nests declined during confinement. (LME: ln(Bark delivered per hour +1), $F_{1,121} = 8.96$, $p = 0.0033$) however the rate of food delivery (white bars) did not (LME: ln(Food delivered per hour +1), $F_{1,121} = -0.45$, $p = 0.66$). For presentation purposes, data is divided into biologically relevant stages: Pre lay, before any eggs have been laid (average = 3.95 days of confinement ± 0.16, n=21), Mid lay, while eggs are being laid (average = 9.81 days of confinement ± 0.5, n=21), Post lay, within 5 days of clutch completion (average = 19.00 days of confinement ± 0.51, n=7), Mid incubation, middle 5 days of incubation (average = 24.91 days of confinement ± 0.38, n=11) and Pre hatch, the 5 days before the first chicks hatched (average = 28.13 days of confinement ± 0.35, n=15)

4.3.3 Experimental manipulation of nest depth: Male behaviour

Removal of nest material influenced male provisioning. During control treatments (n=13), only one male delivered any bark but when bark was removed 7 of the 13 nests brought bark. Food delivery did not change between treatments (Figure 4.3).

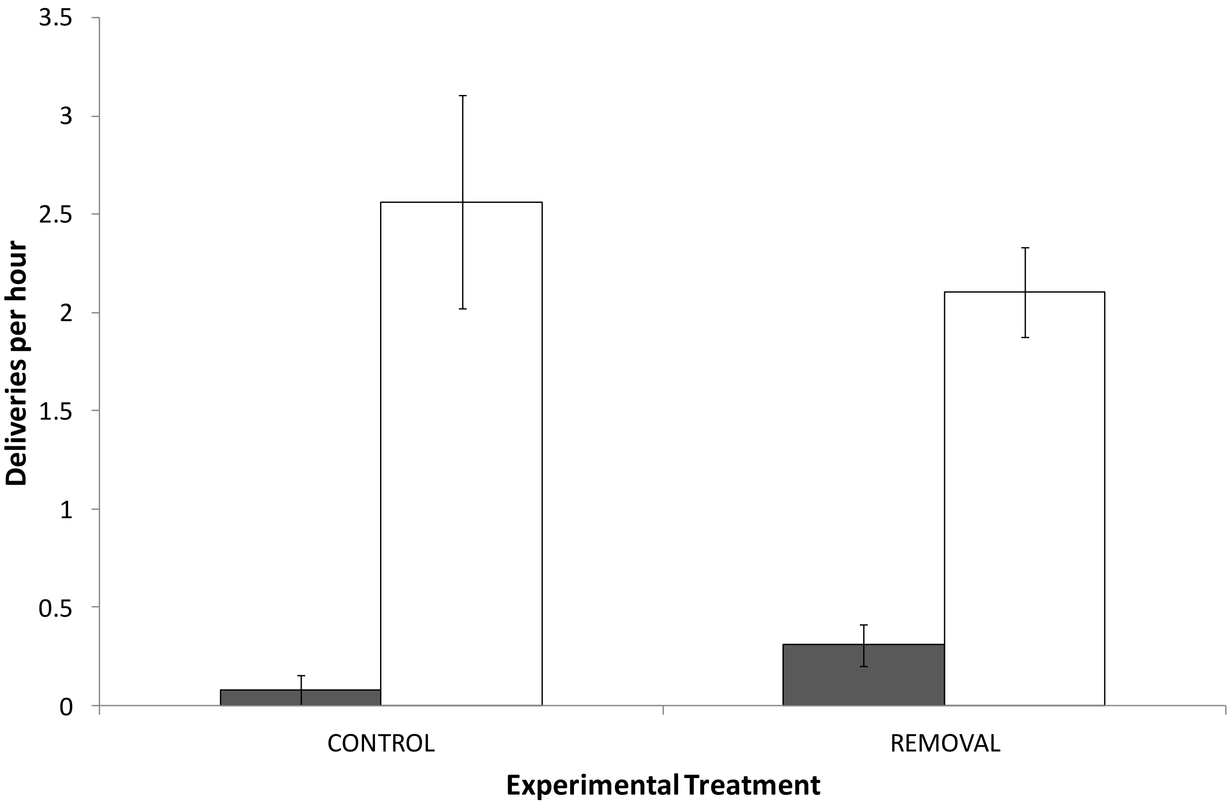

Figure 4.3: Nest material removal resulted in increased delivery of bark (shaded bars, Wilcoxon signed rank test V = 0, p-value = 0.016), but no change in food delivery (white bars, Wilcoxon signed rank test V = 34.5, p-value = 0.5071). All nests (n=13) received both treatments. Bars represent mean ± S.E.

This demonstrated that the items males delivered were related to nest depth, not just to the time the female had been in the nest. While it is unlikely that males could see into the nest, the following section investigates if females gave any vocal cues related to the amount of lining in the nest.

4.3.4 Experimental manipulation of nest depth: Changes in female begging

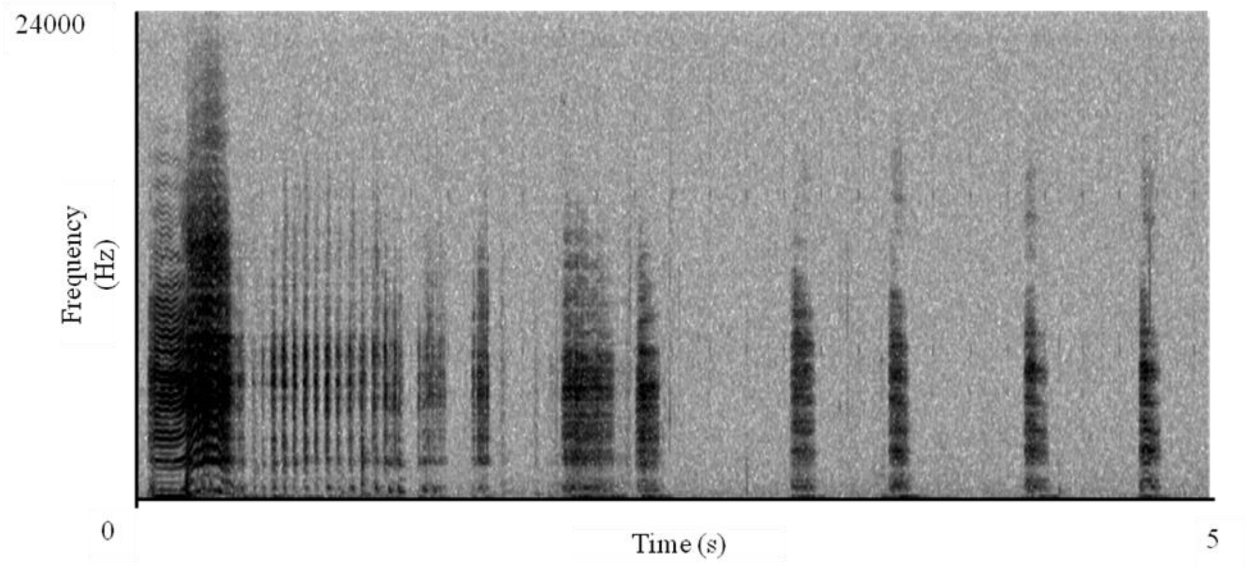

Figure 4.4: Spectrogram of typical hornbill begging bout. All calls are female begging calls. Note broadband, highly non linear calls and high variability in begging call length.

Removal of nest material indeed influenced female begging behaviour. Females (n=13) gave more begging calls during the begging bout when lining had been removed from their nest than during the control treatment (Figure 4.5).

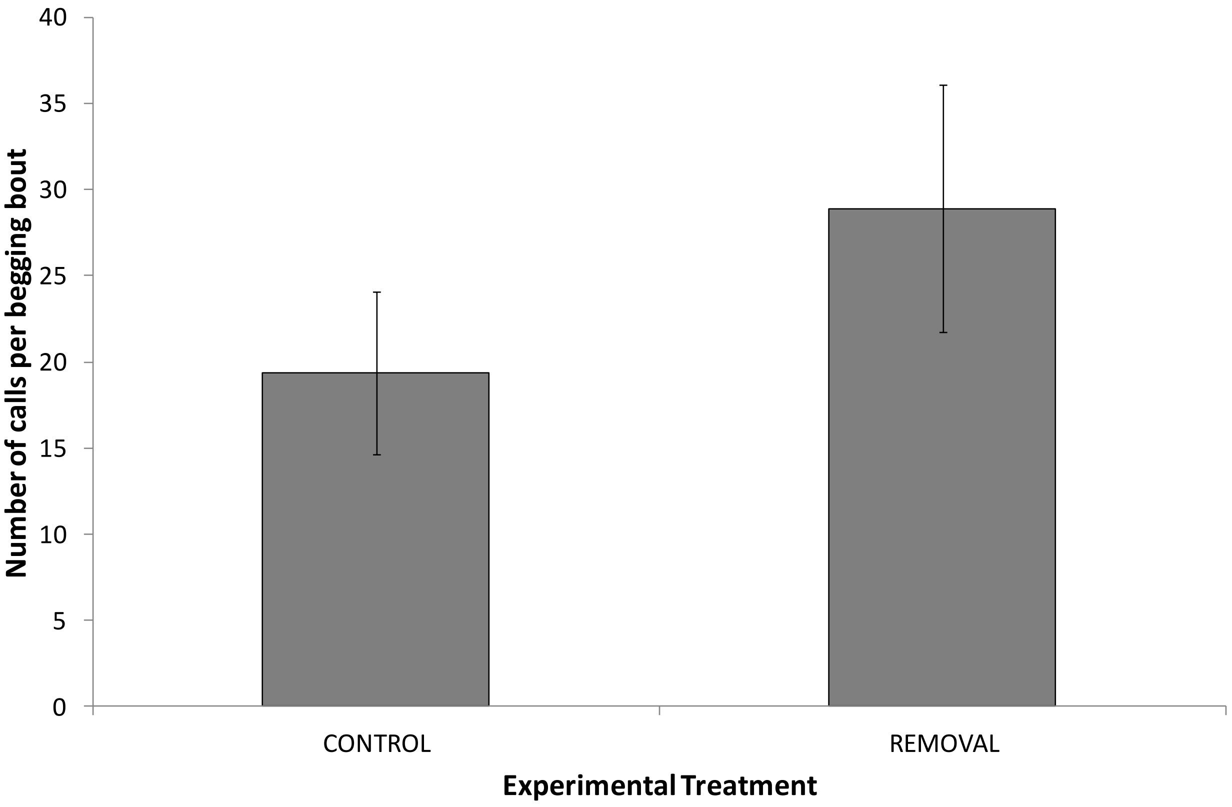

Figure 4.5: Females gave more begging calls when deprived of nest lining than when nest lining was at natural levels. (Wilcoxon signed rank test V = 14.5, p-value = 0.016)

Looking at individual calls, females (n = 13) gave longer calls when deprived of bark (Figure 4.6). The pitch (peak frequency) of begging calls though did not change in response to nest depth (LME using square root transformed data $F_{1,517} = 0.018$, $p = 0.89$).

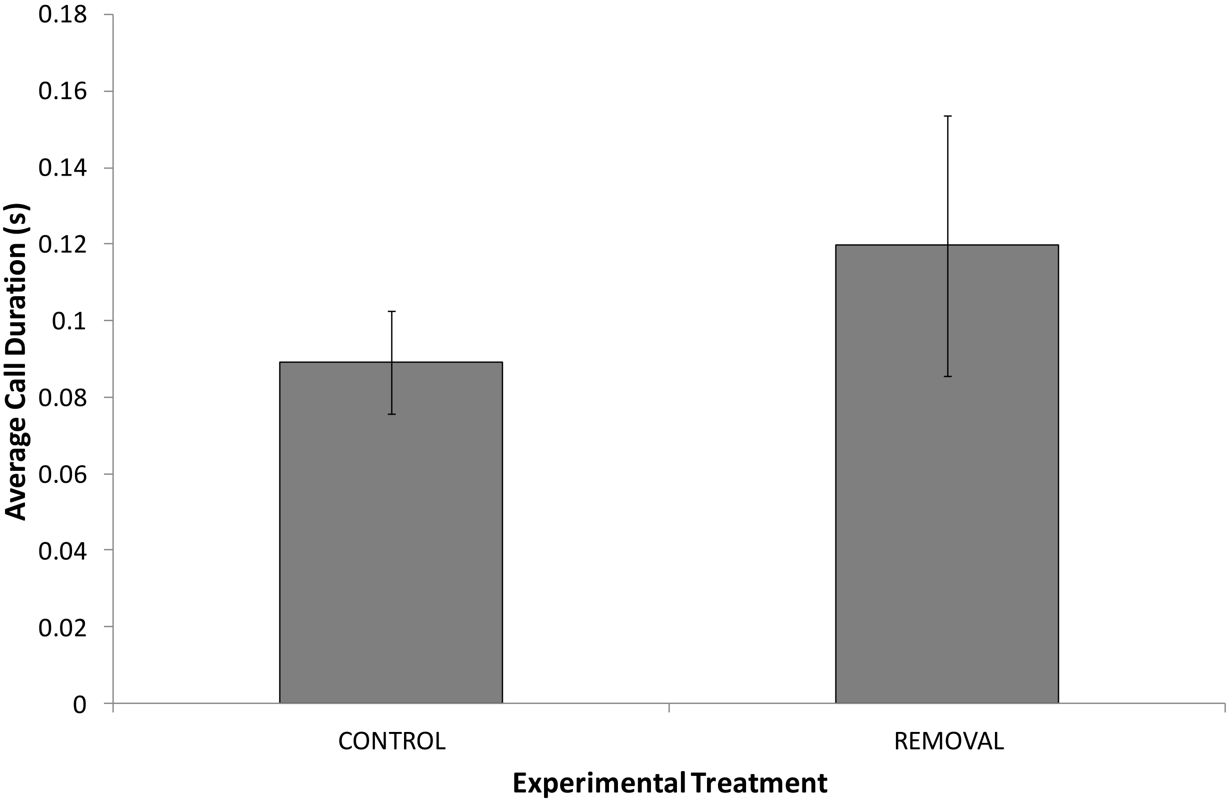

Figure 4.6: Females gave longer begging calls when bark was removed from the nest (LME using square root transformed data $F_{1,517} = 11.23$, $p < 0.001$).

In summary, removing lining from nests caused females to give more and longer begging calls but did not influence their pitch. Males in turn brought more bark when nest lining had been removed.

4.4.5 Natural variation in female hunger

Without being able to experimentally manipulate hunger, natural variation in time without food had to be used instead. The begging given by 15 females during the first male feeding visit (n = 21 visits) of the morning were recorded. The timing of these visits varied from 581 minutes after dusk the night before to 711 minutes (mean = 622.63 ± 7.88). Features of female calls varied significantly with the period between dusk and the first male feeding visit. Call length increased with time (Figure 4.7), though the number of calls did not (Figure 4.8). The pitch of calls was related to the time since dusk. The longer a female waited until feeding, the higher pitched her begging calls became (Figure 4.9)

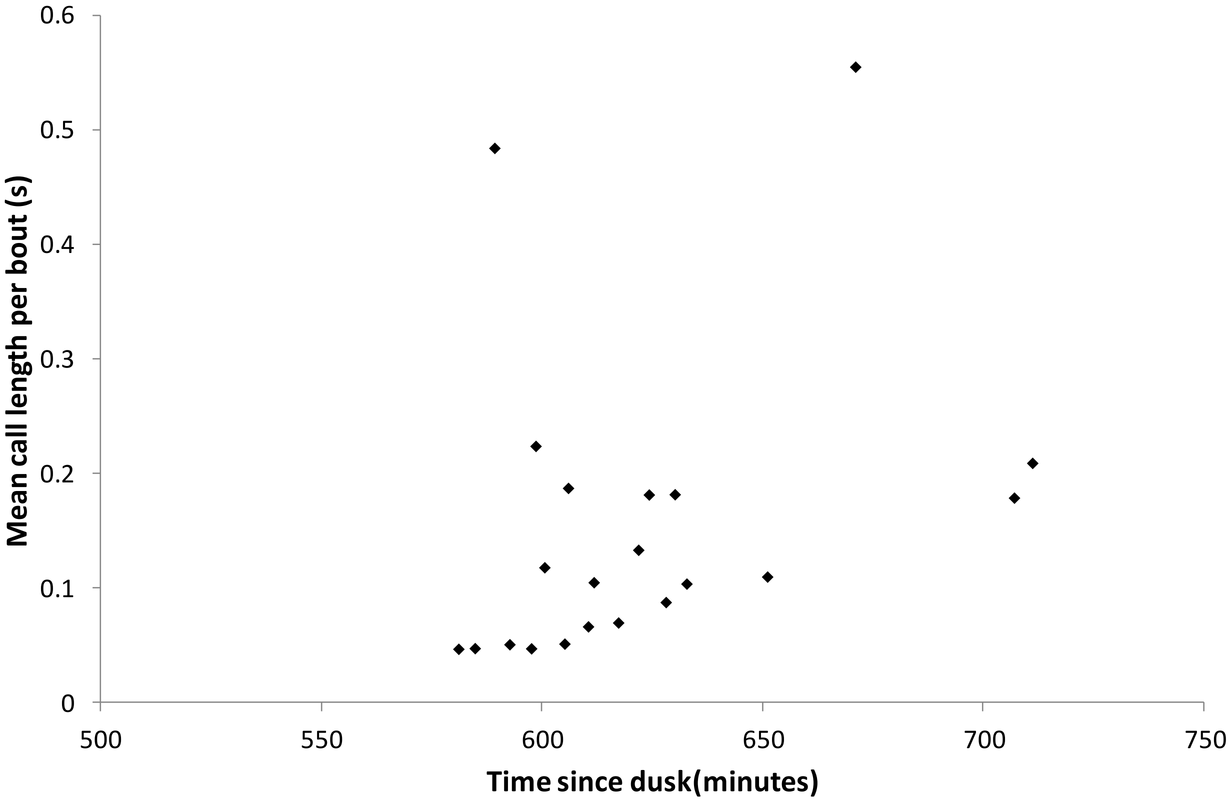

Figure 4.7: Begging calls increase in length as the time between dusk and the first feed of the morning increases. LME: $F_{1,412} = 3.56$, p = 0.0004

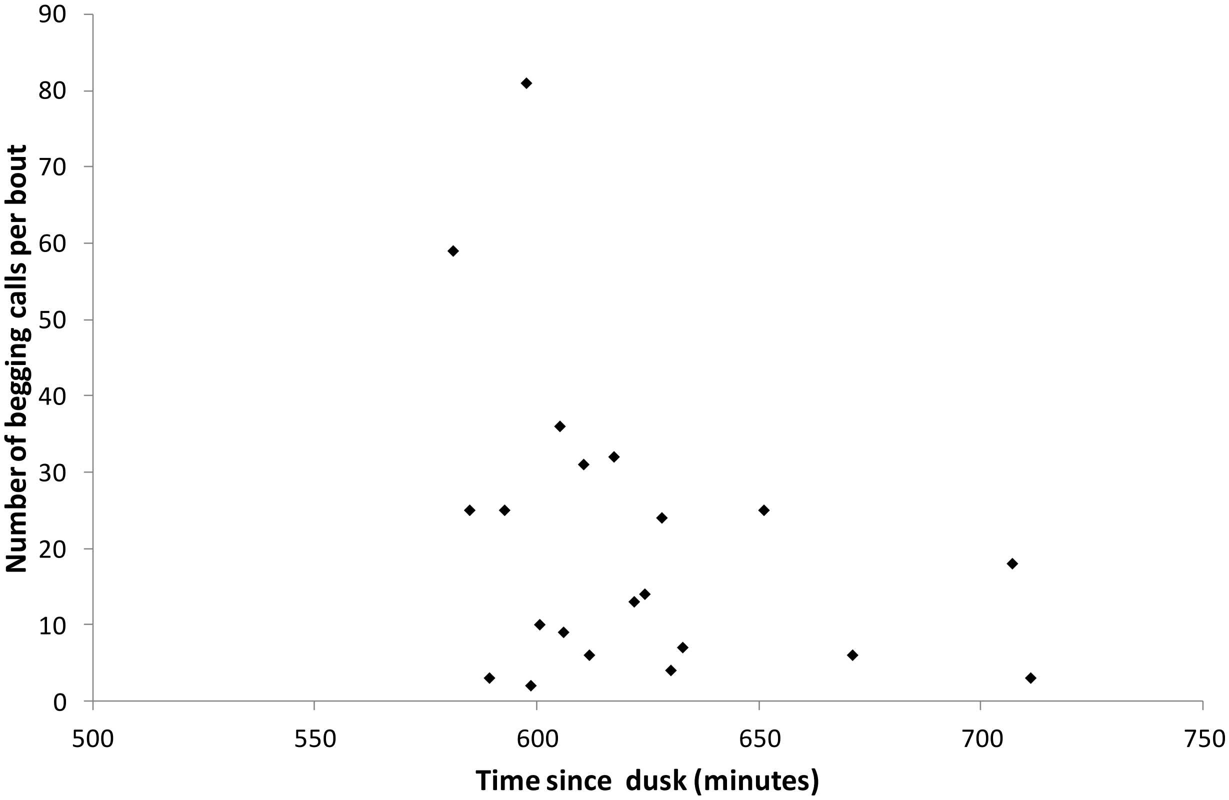

Figure 4.8: The number of begging calls per bout was unrelated to time since dusk LME: $F_{1,412}$= -1.57, p = 0.19

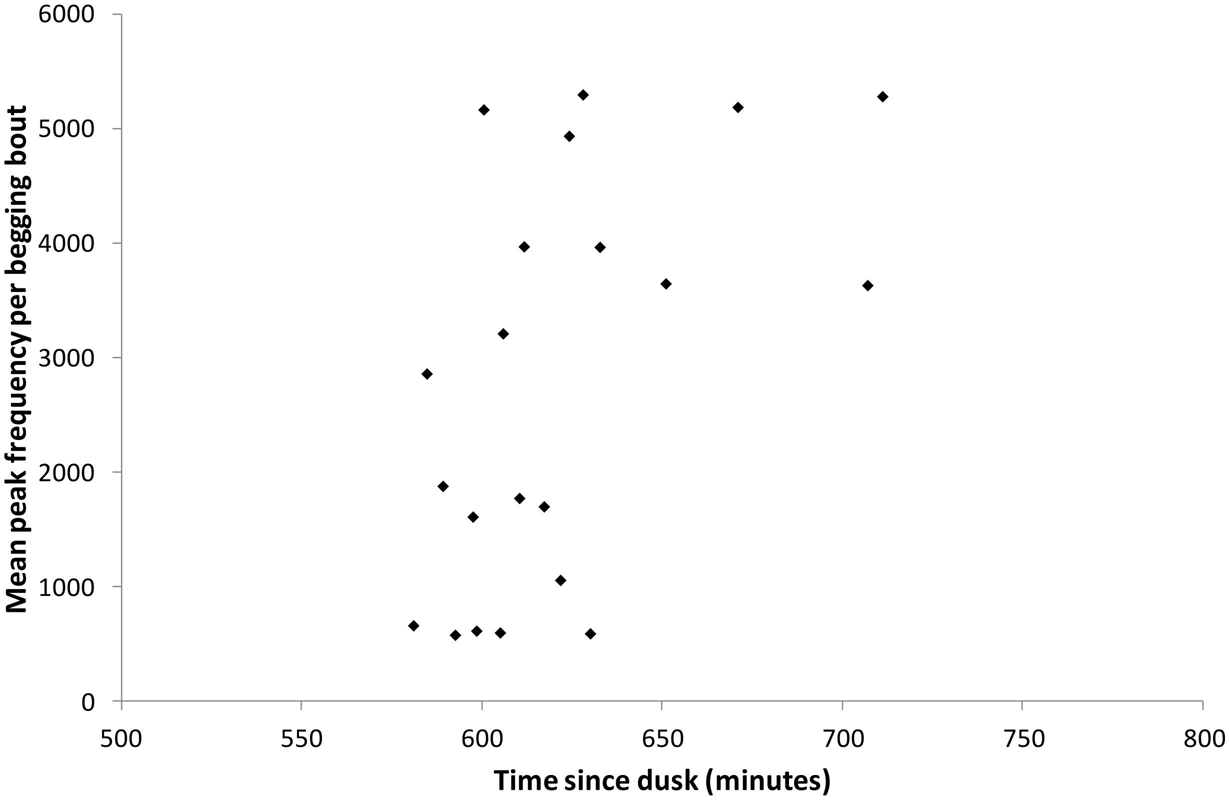

Figure 4.9: Begging calls increase peak frequency (pitch) as the time between dusk and the first feed of the morning increases. LME: $F_{1,412}$ = 11.68, p = 0.0007

4.5 DISCUSSION

Male hornbills cannot easily see into the nest. The sealing by the female leaves only a narrow slit approximately one centimetre wide and at most five centimetres high. Hornbills' visual fields are also limited by objects held in the bill (Martin & Coetzee, 2004). Indeed adult hornbills cannot provision chicks in the nest unless the chicks physically take food items from the parent's bill (personal observation).

Despite a lack of visual cues, male hornbills did change the rate at which they delivered bark throughout nesting. Bark was delivered at a high rate when the female was first in the nest and declined rapidly once laying was complete. Bark was plentiful in the environment, with the majority coming from within 10m of the nest and was constantly available (Figure 4.10)

Figure 4.10: Male hornbill foraging with nest tree in background. The floor is covered with bark shed by the nest tree.

Males provided more bark to the nest when bark was experimentally removed but the amount of food delivered remained constant. Since males could not see into the nest, the greater amount of bark delivered to bark deprived nests was therefore likely to be due to communication from the female. The unchanged rates of food delivery suggest some aspect of specificity in begging cues.

Females did indeed beg more and emit longer begging calls when bark has been removed. Female begging also appeared to be influenced by hunger. Females that had been deprived for longer, gave longer, higher pitched calls. This fits closely with the widely shown effect of hunger in chicks of many species (Leonard & Horn, 1995; Mondloch, 1995; Villaseñor & Drummond, 2007).

Since females did not change their begging in identical ways when deprived of nest materials or food, it is possible that begging contained information about what the female needed. Call length increased when need for both food and nest lining increased. This could convey a general, non specific signal of need. The number of calls only increased when material was needed so this may be related to nest depth. Call pitch on the other hand only changed with food deprivation so may be the key signal for hunger. The coding of hornbill begging is likely to be much more complicated than this, especially as males also deliver fresh millipedes and dung which the female uses to seal the nest and old weathered pieces of millipede shell, possibly as extra calcium during egg laying. Hornbills are certainly capable of processing complex vocal information. Indeed, Rainey et al (2004) showed that Yellow Casqued Hornbills (*Ceratogymna elata*) can distinguish different classes of primate referential alarm calls, responding appropriately to alarm calls given in response to both eagles and leopards.

Ideally, playbacks could have been used to further examine the way hunger and nest depth influences female begging. While female hornbills reacted badly to playback it may still be possible. Male hornbills are not very discerning in where they deliver their provisions, being known to feed nests of other species (Kemp 1995) and even the wrong hole in nest trees (personal observations). This provides an opportunity to manipulate male behaviour without relying on the female. The female could be temporarily removed from the nest and replaced with a remote control dummy beak that can accept food, while begging calls are played. If male hornbills could be convinced by this, it would allow an exciting opportunity to further test the extent of communication in breeding hornbills.

The role of longer term condition was not tested. Female adjustment of metabolism (Klaassen et al 2003) may play a crucial role in her condition and hunger. Female metabolism dropped during confinement in Monteiro’s Hornbills (Klaassen et al 2003). This, if begging signalled short term need, could influence how begging changes throughout the nesting period. Given that hornbills appear to form long term pair bonds, there may be many more factors influencing female demand.

How females and chicks interact in the nest could also prove an interesting system. Females continue to beg and eat once the chicks have hatched. Experimental feeding of chicks could be used to test whether mothers play a part in the chain of communication between chicks and the father.

Many studies of begging have focussed on the conflicts occurring between signaller and receiver and whether begging has to be costly (Godfray 1991, Moreno-Rueda 2007). Brilot & Johnstone (2003) suggested that cost free signalling is much more likely to evolve in begging 'games' when the signaller can have 'zero-need', i.e. when the signaller does not benefit from obtaining the resource. There has been much debate around the concept of 'zero-need' in terms of food supply. Is food ever supplied at such a high rate that the receiver cannot digest it fast enough, so gaining no benefit from additional delivery? Certainly, the digestive systems of animals have a maximum rate of absorption (Karasov & Wright 2002). Whether this limit can ever actually be met by parents feeding altricial young is a source of contention (summarized in Brilot & Johnstone 2003). Begging by nesting female hornbills could provide an interesting model system for research into begging. Theoretically, begging for nest lining materials must involve a point of 'zero-need'. If too much nest lining is provided, the nest would become too shallow, possibly even blocking the entrance. Bark is also a plentiful resource that the male has no use for outside the nest, presumably making it much 'cheaper' than provisioning food. Whether females can ever have 'zero-need' for food is much more uncertain. Nesting in nest boxes however could allow detailed study of female physiology and metabolism. Klaassen et al (2003) have already demonstrated that hornbill nest boxes can be turned into effective respirometers, while such easy access to individuals would enable the use of doubly labelled water techniques (Butler et al 2004). Begging by female hornbills will almost certainly not be determined purely by short term need. Females are reliant on males to feed the chicks and many pairs stay together across multiple seasons (Chapter 3), meaning that females may have interests in male condition both in the long and short terms. Females certainly seem to have the opportunity to energetically exploit their mates, some continuing to beg after cannibalising entire clutches (Chapter 3). The safety of hornbill nests (Chapter 3, Kemp 1995) means that one of the major potential costs of begging, that of attracting eaves-dropping predators (Haff & Magrath 2011) is essentially removed. Since females are confined to nest boxes, hornbills could be an excellent model for studying the other proposed cost of begging; physiological energy expenditure (Butler et al 2004).

Communication between female hornbills and their mates involve complex interactions, involving physiology, sexual conflict and environmental uncertainty. What this chapter demonstrates however is simply that female hornbills express the need for two different resources via the same channel, expressing specificity by modulating different aspects of the signal. This provides the signal receiver with more accurate information, in much the same way as referential alarm calls (Seyfarth et al 1980).

Chapter 5

What Proximate Factors Influence The Duration Of Female Confinement?

5.1 ABSTRACT

Female Yellow-Billed Hornbills seal themselves into their nests approximately 10 days before laying their clutch. After laying their asynchronous clutch they moult their flight feathers. Once their feathers have re-grown females leave the nest. The chicks, approximately 20 days old, then reseal the nest entrance. Here I examine the relationships between the timing of female emergence from the nest with factors concerning her own condition and moult status, food availability and factors relating to the brood.

Natural observations from 36 breeding attempts of Southern Yellow-Billed hornbills demonstrated that brood size and asynchrony influenced when females left the nest. Females with one chick left the nest at the same time and stage of feather re-growth as females who had abandoned their brood. Females with 2 chicks left the nest later with much more complete feathers. If females with two chicks departed at the same stage of moult as females with 1 chick then they would have left on average 5 days earlier than they actually did. Among females with multiple chicks, females with more asynchronous broods stayed in the nest longer so that their younger chicks reached the same age as junior chicks from the more synchronous nests. Female condition at the start of breeding and her relative condition by departure had no influence on when females left the nest or how complete their feathers were. Provisioning by the male also had no influence on timing or moult completion.

This suggests that regulation of intrabrood conflict may be important in determining the timing of female departure. Mothers may play an important role in ensuring that younger offspring have a chance to compete with their older siblings after their mother departs. Data are supplemented by similar results from interspecific comparisons.

5.2 INTRODUCTION

Conflict between parents and offspring over the duration of parental care is one of the central ‘battlegrounds’ in the study of parent offspring conflict (POC). Indeed Trivers introduced the concept of POC with the example of a nursing caribou and her calf (Trivers 1974). The calf will benefit energetically from a long period of nursing, while the mother would do best to terminate milk production earlier, to save herself energy and allow her to breed again. Conflict over the duration of care centres around the trade off between investing in current or future reproduction, otherwise known as interbrood conflict (Mock & Parker 1997). Offspring, genetically favouring their own survival, will demand care from their parents that would reduce the parents’ future reproductive success. The duration of parental care can impact future reproduction by delaying subsequent attempts, or by lowering parental condition and survival (summarized in Davies et al 2012). There is plenty of evidence, both that extended care increases offspring success (Sunde 2008) and that it is associated with reduced success of subsequent breeding attempts. Survival of Galapagos fur seal pups is greatly reduced if the mother is still nursing young from previous years (Trillmich & Wolf 2008). Despite such evidence of costs and benefits, it is hard to find empirical evidence for actual conflict between parents and offspring. Even the ‘weaning tantrums’ seen in mammals may be nothing more than squabbles where parental and offspring interests still overlap (Mock & Forbes 1992, Bateson 1994). The first step in discovering if conflict exists is to try to find what tradeoffs parents face over the termination of care.

Mills et al (2005) proposed that hornbills (Bucerotiformes) may be a useful taxonomic group to study the tradeoffs between current and future reproduction. The unusual breeding behaviour of hornbills puts the costs of parental care into stark relief. When laying a clutch, female hornbills seal themselves into their cavity nest and then simultaneously moult all of their flight feathers, their wing feathers or remiges (both primaries and secondaries) and their tail feathers or retrices (Figure 5.1). Feathers are shed within a few days effectively trapping the female in the nest. Incarcerated females are dependent on feeding by their mate until their wings have re-grown enough to allow them to fledge. All female hornbills shed their feathers at breeding apart from the two species of ground hornbill (genus *Bucorvus*). Such a moulting strategy is unusual. Most passerines moult their flight feathers sequentially, typically taking several weeks to months, maintaining the ability to fly, though there are a few exceptions in extreme climates (Haukioja 1971). Even in sequentially moulting species flight can be impaired by rapid moult (Swaddle et al 1996). Several other groups of aquatic birds such as the Anatidae (Skead & Dean 1977), Alcidae (Mosbech et al 2012) and Procellariiformes (Watson 1968) exhibit simultaneous moult, becoming flightless during feather replacement.

Such species however avoid overlapping breeding and moult (Hedenström 2006). A similar situation does exist in many raptors though. While not confined to the nest by lack of feathers, breeding females will often stay at the nest from the onset of incubation until the nestlings are very large (Newton 1979). Females will commonly not forage for themselves and will rely on provisioning by their mate.

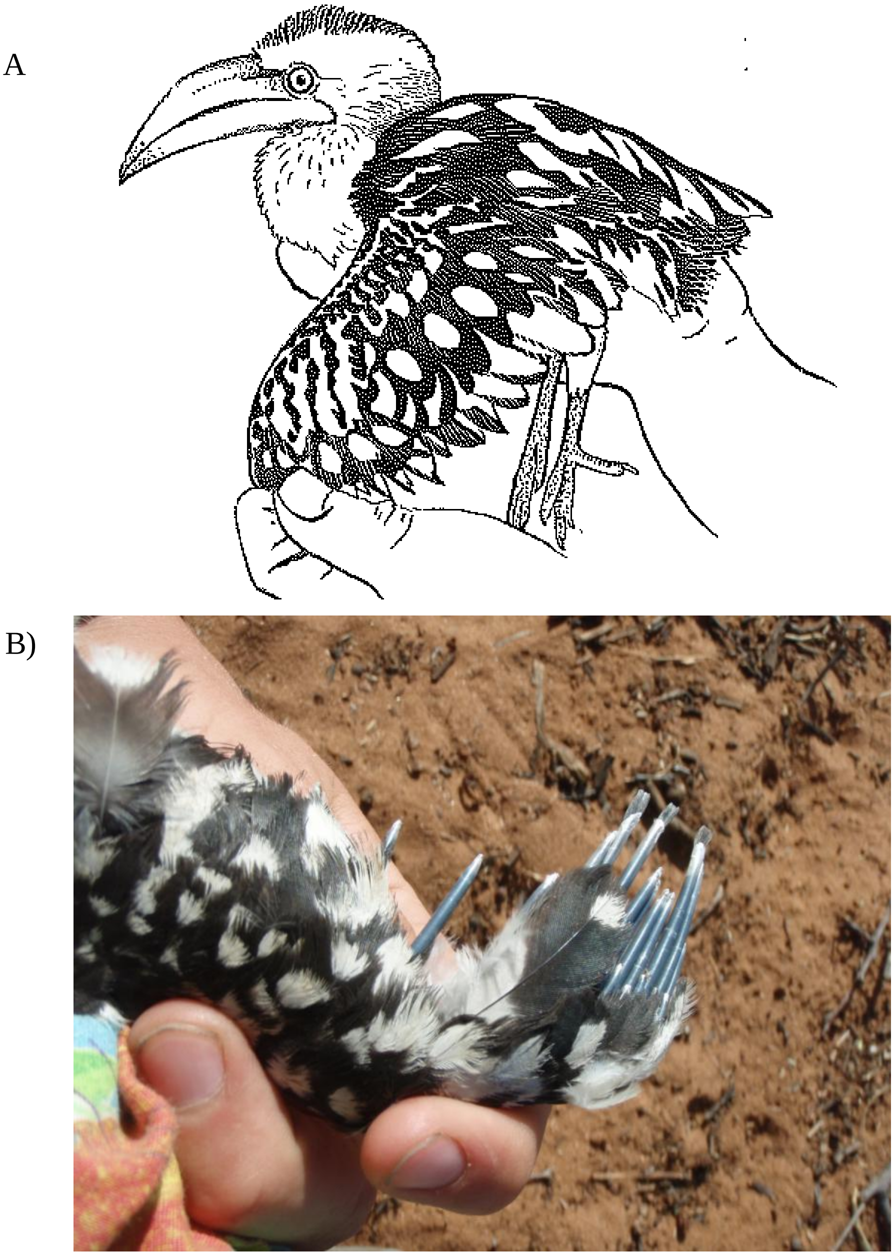

Figure 5.1 A: Female Southern Yellow-billed hornbill just after shedding flight feathers. Taken From Kemp (1995). B: Wing of flightless female approximately 10 days after shedding of feathers

Breeding in hornbills takes at least 2 months from the beginning of nesting to the fledging of chicks even in the smallest species (Kemp 1995). Most species also appear to have post fledging care (Kemp 1995). For species of the *Tockus* genus, that inhabit the African savannah, breeding is limited to one attempt per year in the wet season, with success highly dependent on rainfall. Hornbills are also long lived, so Mills et al (2005) suggested that females should favour their own condition and future success over any one breeding attempt. Mills et al (2005) investigated what factors influenced the timing of departure from the nest of breeding Monteiro's hornbill females. They concluded that females were not influenced by factors concerning their current brood (such as clutch size and chick condition) and merely fledged in response to the re-growth of their own flight feathers. Mills et al (2005) based their conclusion on the concept of stabilising selection. The variation in female moult completion was lowest at the time of departure than at any preceding stage. This logic is slightly flawed. As feathers grow logistically, variation between individuals will decline as time progresses and they all approach the asymptote of growth. Variation would continue to decline, the longer females stayed in the nest. That feather length is the primary determinant of when a bird chooses to fly from its nest should though come as no surprise. Obviously the mother's ability to fly efficiently is important not just for her own future reproduction but also for the success of the current attempt. If we want to look at the importance of any factors on the timing of female departure we should really examine it from the point of view of how ready the mother is to leave in terms of her readiness to fly i.e. the re-growth of her wings. If we accept the idea that a female's feathers must reach a certain state of re-growth for her to leave the nest we can use variation in moult completion at fledging between females as a measure of how early or late females leave. Some females abandon their broods and fledge with no chicks. These females' departure dates are obviously not influenced by their brood as they don't have any chicks. Females with chicks can then be compared and the importance of brood factors can be assessed.

One aspect that Mills et al (2005) did not investigate, was the asynchrony within the brood. Hornbills have highly asynchronous clutches, commencing incubation as they lay. In Southern Yellow-Billed Hornbills eggs are usually laid two days apart and clutches can be of up to 6 eggs (Kemp 1995). Female Southern Yellow-Billed Hornbills do not lose their flight feathers until after they have completed laying (Chapter 3). This automatically puts a constraint on the timing of female depature. Females with more asynchronous clutches start feather regrowth later than females with more synchronous clutches. Once the chicks have hatched, mothers control access to the nest entrance, passing food to the chicks. This could give mothers control over sibling rivalry for food. When the mother leaves the nest, chicks reseal the entrance. The longer the mother stays in the nest, the longer she retains control over food distribution. One might expect females with asynchronous broods to spend longer in the nest, raising the younger chicks to a level where they can compete with their older siblings. Rather than being a measure of interbrood conflict, the length of maternal confinement may well be closely linked to parental control of intrabrood conflict. Many other factors could influence both brood size and asynchrony and the time females spend in the nest. Such factors include female condition and how that changes throughout breeding as well as the amount of food males can deliver.

This chapter aims to take a closer look at the factors governing when hornbill mothers leave the nest. The central objective is to explicitly test the hypothesis proposed by Mills et al (2005) that female departure is dependent solely on moult completion. Can other factors, either relating to the brood or the females own condition, influence how complete females' feather growth is when they depart? Firstly I shall examine the extent of variation in both confinement duration and the completion of feather re-growth. I will then investigate how factors relating to a female's own condition, her offspring and food availability, all relate to how long she spends in the nest.

5.3 METHODS

The study was conducted on a colour ringed population of Southern Yellow-billed hornbills in ranch land in the southern Kalahari Desert, South Africa (26°58’S, 21°50’E). Data were collected in two consecutive breeding seasons, between October 2009 and March 2011. Birds bred in nest boxes, allowing all nest occupants to be weighed and measured regularly. Typically breeding females and chicks were measured every two to three days. Females and chicks were weighed with an electronic balance to 0.1g. Chick tarsus was measured with electronic callipers to 0.01mm, while adult wing length was measured with a steel rule to the nearest 0.5mm. Measurements were taken as described in de Beer et al (2001). Nests were visited daily during hatching and around the time of female departure to increase accuracy. Female condition was calculated by dividing their mass (in grams) by the tarsus (in mm) cubed. Only breeding attempts in which the female stayed in the nest long enough to shed her flight feathers were used for this analysis. Thirty six such breeding attempts were followed across the two seasons. Twelve females bred in both seasons and female identity was controlled for in statistical analysis. In order to control for variation in male quality, the provisioning rate of males was recorded using internal video cameras. Provisioning rate was recorded in the last 10 days before mothers departed.

To assess the importance of brood size, the number of chicks present in the nest on the day the female departed was used. Nests in which the brood size changed within 2 days prior to female departure were excluded. Brood reduction was common due to drought conditions in both seasons so brood sizes were 0, 1 or 2 chicks. One nest had 3 chicks alive the day the mother departed and was grouped in with the broods of 2 chicks for analysis.

5.3.1 Statistical Analysis

Sample size varies for analysis of different factors as every variable could not be collected for every nest. Analysis was conducted using R (R version 2.13.1, The R Foundation for Statistical Computing). Data were analysed using linear mixed-effect models in the lme function from the nlme package. Female ID and season were included as random factors. Models were simplified by stepwise removal of non-significant terms. This can account for multicollinearity in independent variables. Separate models were analysed for timing and feather growth. Female condition, both at the start of breeding and the relative condition at fledging and male provisioning rate were included as independent variables in the maximal models. Sample size varies for different brood sizes.

5.3.2 Female departure and brood characteristics

The feather growth of each female was adequately explained by a simple logistic curve:

$$l = a(1 - e^{-cx})$$

Where:

l = Feather length (mm)

a = Asymptote of feather length (mm)

c = Growth rate constant

x = Days since first feather shed

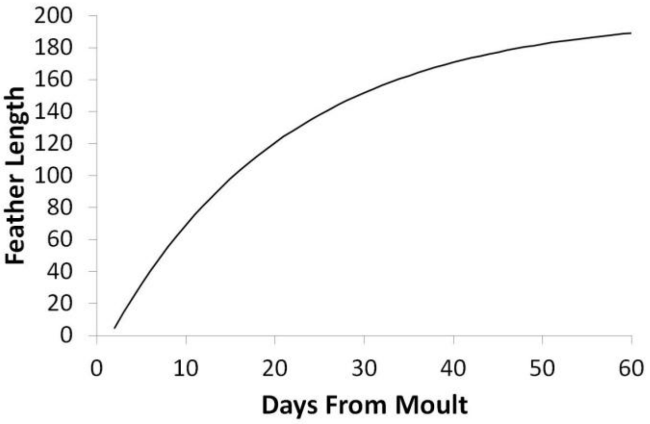

Figure 5. 2: Growth curve based on a logistic model

Using this equation allowed the estimation of feather growth completion at the time of female departure. This was calculated as a percentage of the asymptote of growth for each female. This gives a measure of how ‘ready’ females’ feathers are when they fledge. Feather completion was compared against brood size for both relative feather length and relative growth rate. For females that had only a single chick, chick tarsus growth was compared against moult completion. Comparison was again conducted using the linear mixed effects models with season as a random factor. Chick growth was best described by a Richard’s model (Figure 5.3) of logistic growth:

$$t = \frac{a}{(1+e^{b-cx})^{1/d}}$$

Where:

t = Tarsus Length in mm
a = Asymptote (mm)
b = Growth constant
c = Growth constant
d = Growth constant
x = Age of chick in days

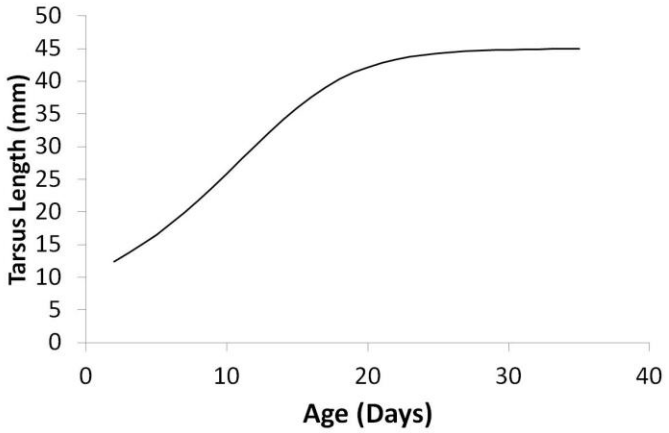

Figure 5.3: Growth curve based on a Richard's model

5.3.3 Hatching asynchrony Vs timing of female departure.

If maternal departure was not related to asynchrony within the brood then the overlap in the nest between the mother and her youngest chick would decrease as asynchrony between first and last chick increased (Figure 5.4a dashed line). If however females extend their stay in the nest, overlap will not fall with asynchrony. If females judge their stay by the needs of the youngest chick then overlap will remain constant irrespective of asynchrony, as females extend their stay by the magnitude of the asynchrony between chicks (Figure 5.4a solid line). In order to quantify this, the difference between the overlap predicted by the null model (based on the average age of older chicks) can be subtracted from the observed overlap. If females are extending their stay as asynchrony increases then the deviation between observed and null prediction will increase with asynchrony between chicks (Figure 5.4b). Correlation was assessed using linear mixed effect models with season as a random factor.

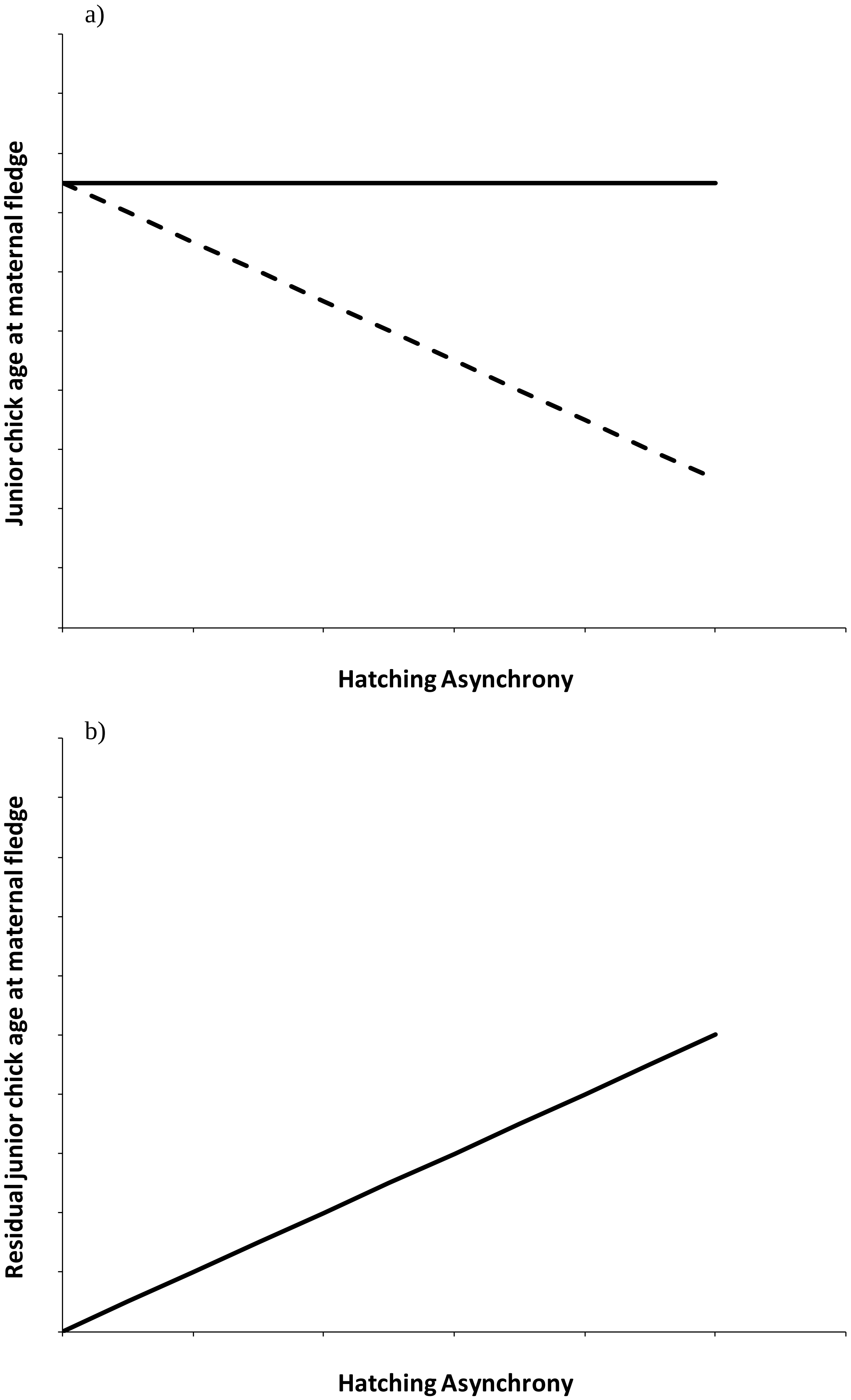

Figure 5.4: Theoretical relationship between hatching asynchrony and the age of the youngest chick in the nest when the mother leaves. a) Predicted chick age if female stay in nest is unrelated to asynchrony (dashed line) or if females stay is determined by age of younger chick (solid line). b) Difference between the two models. As asynchrony increases the discrepancy between predictions based on the age of the youngest chick and the prediction based on stay being unrelated to asynchrony increases (solid minus dashed).

5.3.4 Interspecies variation in asynchrony

The importance of hatching asynchrony on female departure was examined using data taken from Kemp (1995). Analysis was limited to 7 species from the *Tockus* genus. All species used had documented incubation times, brood size; inter-egg hatching asynchrony and length of female incarceration. Total hatching asynchrony was calculated as a function of the asynchrony between eggs and the clutch size. Averages were taken for species where data were available for different populations of the same species. The age of the last chick to hatch was calculated for each species and this was regressed against hatching asynchrony. In order to control for differences in size and developmental period, age of the last chick was divided by incubation time. Phylogenetically independent contrasts were not conducted as insufficient data were available with which to estimate branch lengths (Ord & Martins 2010). The tree also features unresolved polytomy as well as lacking data for several species. All these species live in similar habitats and are phylogenetically similarly separated (Kemp 1995). A phylogenetic tree is included alongside the results to provide an idea of the relationships between species included in the analysis. The strength of correlation was examined using a Pearson’s rank correlation.

5.4 RESULTS

5.4.1 Variation in the timing of female departure

There was considerable variation in both the total time females spent in the nest (Figure 5.5) and the time from the shedding of feathers to departure (Figure 5.6). Females spent an average of 53.27 (±0.76) days in the nest, ranging from 41 to 61 days (n=36). The time between the shedding of remiges to departure averaged 33.25 (±0.73) days with a similar range from a minimum of 23 to a maximum of 41 days (n=36).

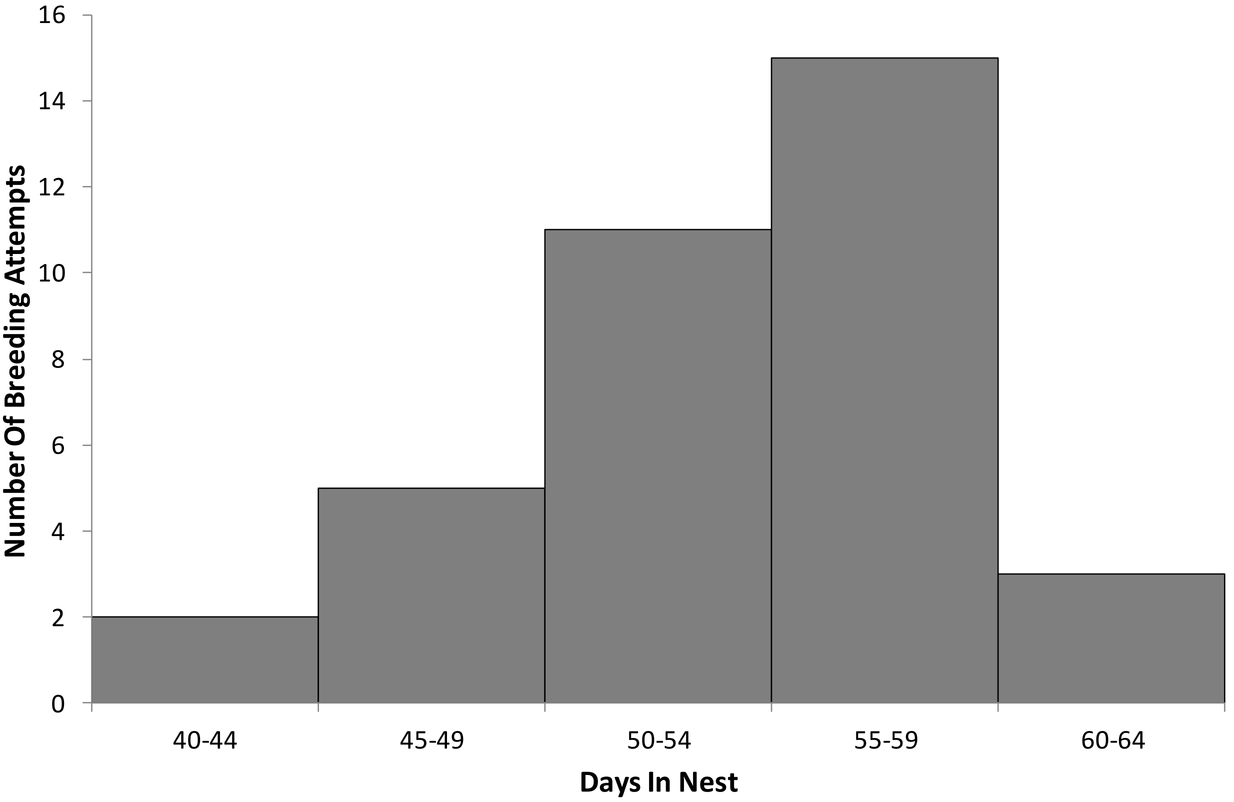

Figure 5.5: Distribution of time females spent in the nest. Data from 36 breeding attempts, 17 in 2009-2010 and 19 in 2010-2011

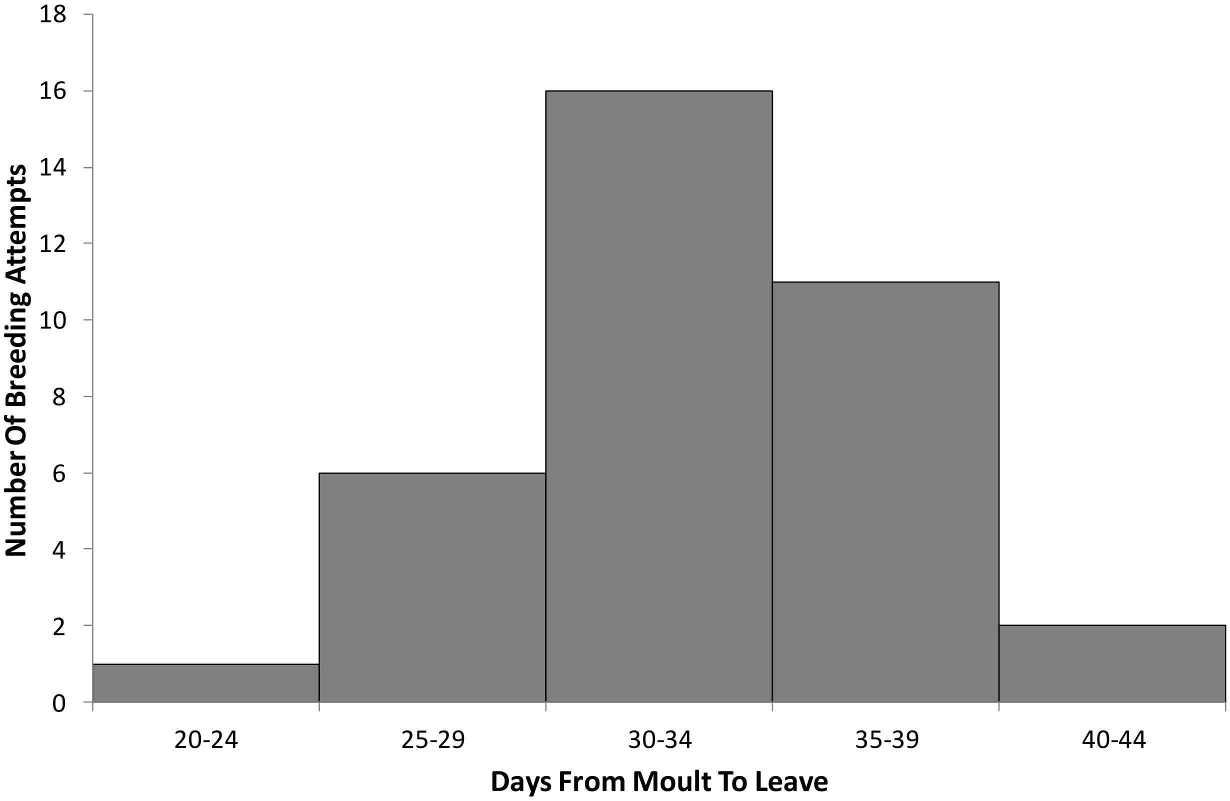

Figure 5.6: Distribution of time females spent in the nest after shedding of their flight feathers (n=36)

5.4.2 Variation in female feather growth at departure

There was also marked variation in the extent of feather growth by the time females left the nest (Figure 5.7). On average females feathers were 84.49% (±1.13) complete (n=36). The least complete feathers were 67.73% grown, while the most complete feathers were at 95.71% of their full extent. Female feather growth closely followed a logistic growth curve with no lag phase (Figure 5.8). Feathers grew to an average 169.60 mm (±2.32) in length

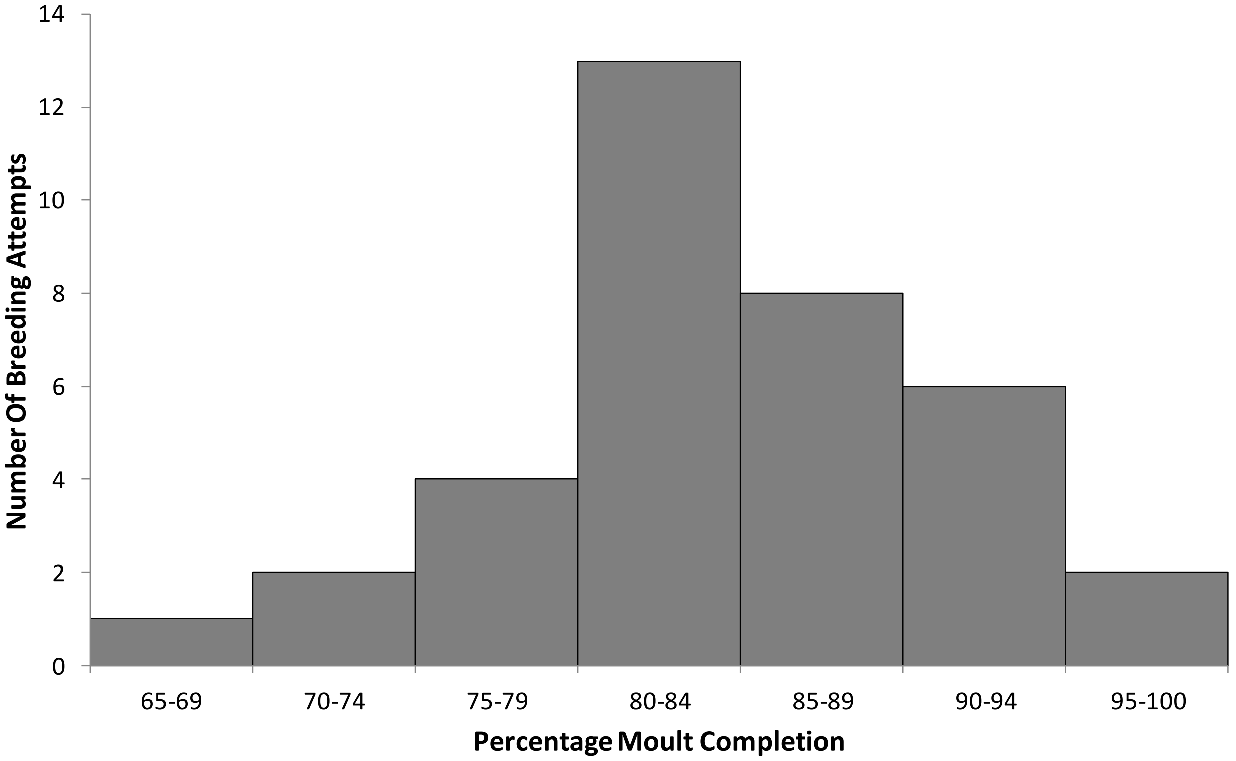

Figure 5.7: Distribution of feather completion at departure from nest, expressed as a percentage of maximum length (n=36).

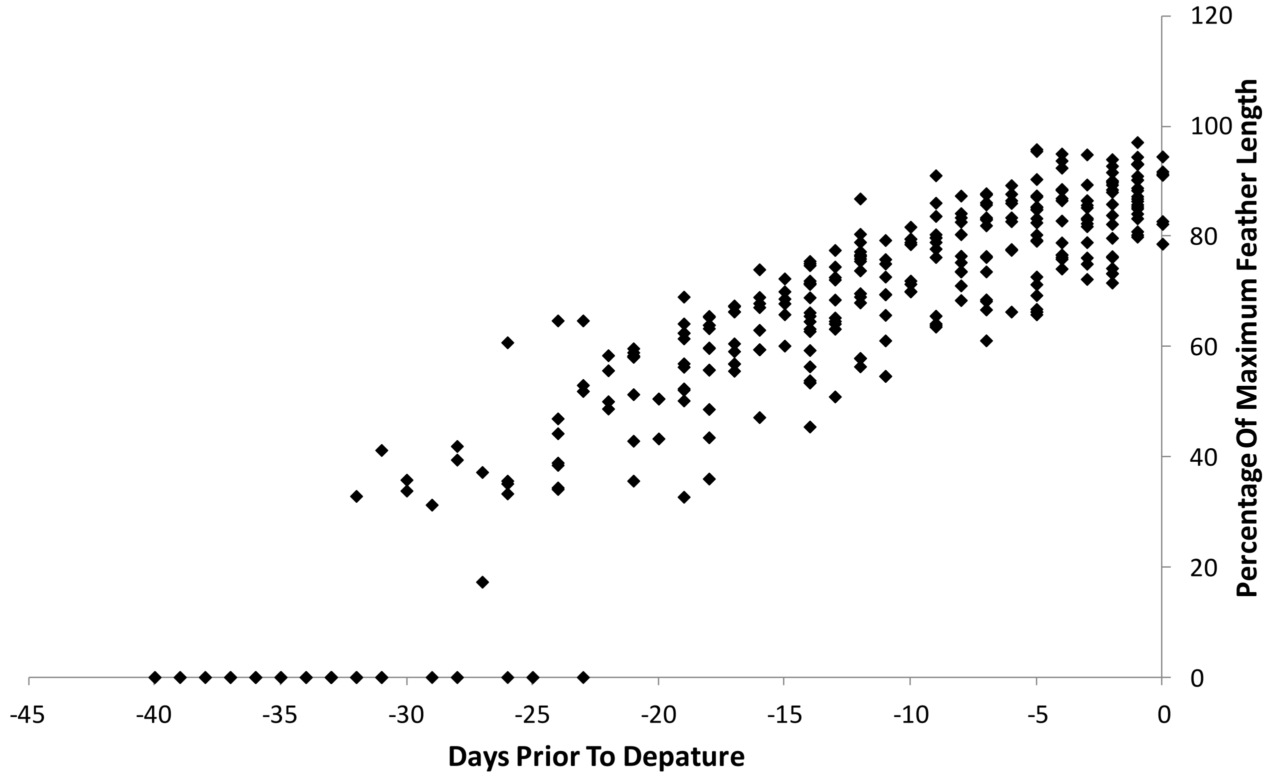

Figure 5.8: Feather growth relative to date of departure. Data collected from 36 breeding attempts. Each data point represents an individual measurement from one female.

5.4.3 Variation in departure timing in relation to female condition, food availability and brood factors

Female condition at the start of breeding (Figure 5.9) and relative condition by fledging (Figure 5.10) had no significant effect on the total or post moult time in the nest or moult completion by departure. Male provisioning (recorded for 25 breeding attempts) to either the whole nest (Figure 5.11) or just the female (Figure 5.12) also had no influence on either departure timing or moult completion.

Brood size at the time of female departure did however have a significant effect on both the timing of departure and moult completion (Figure 5.13). Females that abandoned their brood (n = 7) left between 25 and 34 days (mean = 29.29 ± 1.60) after shedding their wings with moult completion ranging from 71.59% to 86.03% (mean = 80.16 ± 1.92). Females with one chick (n=16) did not stay significantly longer, leaving between 23 and 39 days (mean = 33.25±1.11) after shedding their wings. They also left with similarly complete wings, between 67% and 93% complete (mean = 82.76 ± 1.81). However females with broods of two chicks (n = 13) stayed in the nest longer, departing between 32 and 41 days (mean = 35.38 ± 0.79) fledging with more complete feathers ranging from 82.25% to 95.71% (mean = 88.96 ± 1.18). Brood sizes were similar in both seasons of the study; in 2009-2010 there were 5 breeding attempts with a brood size of 0, 5 attempts with 1 chick and 7 attempts with 2 chicks. In the 2010-2011 season there were 2 attempts with 0 chicks, 11 with 1 chick and 6 with 2 chicks. Brood size when females left the nest was mainly due to brood reduction (chapter 3) females with different sized broods started off with similarly sized clutches. Females who abandoned (n=7) had brood sizes of 3.86 eggs (±0.26), females with 1 chick (n=16) had 3.56 eggs (± 0.18) while females with 2 chicks (n=13) laid on average 4.15 eggs (± 0.15). All three classes had a modal clutch size of 4 eggs.

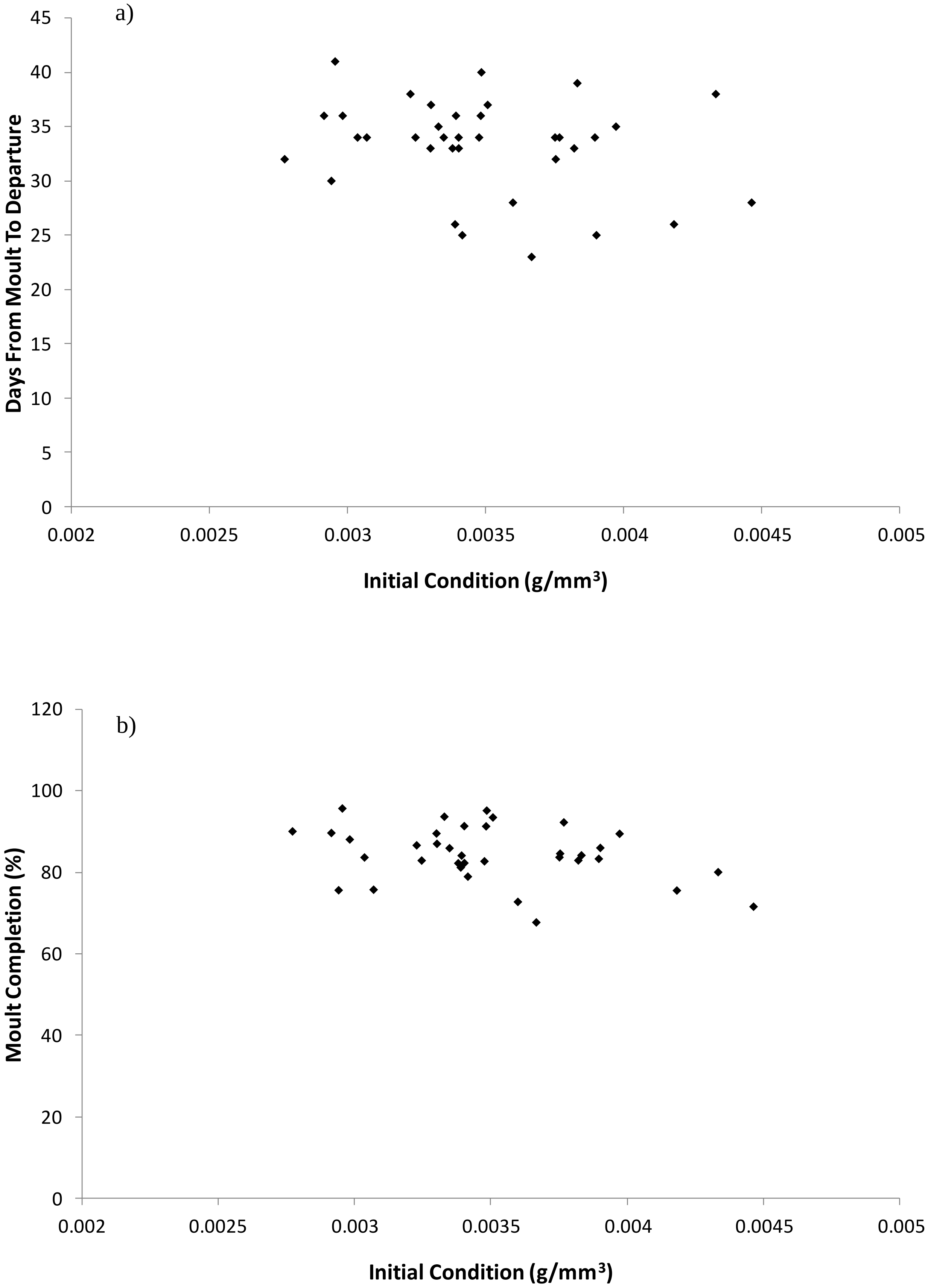

Figure 5.9: Female condition at the start of breeding has no influence on either a) the timing of departure (LME: Initial condition, $F_{4,36}$ =0.23, p = 0.84) or b) how complete feathers are by departure (LME: Initial condition, $F_{2,36}$ =0.70, p = 0.56)

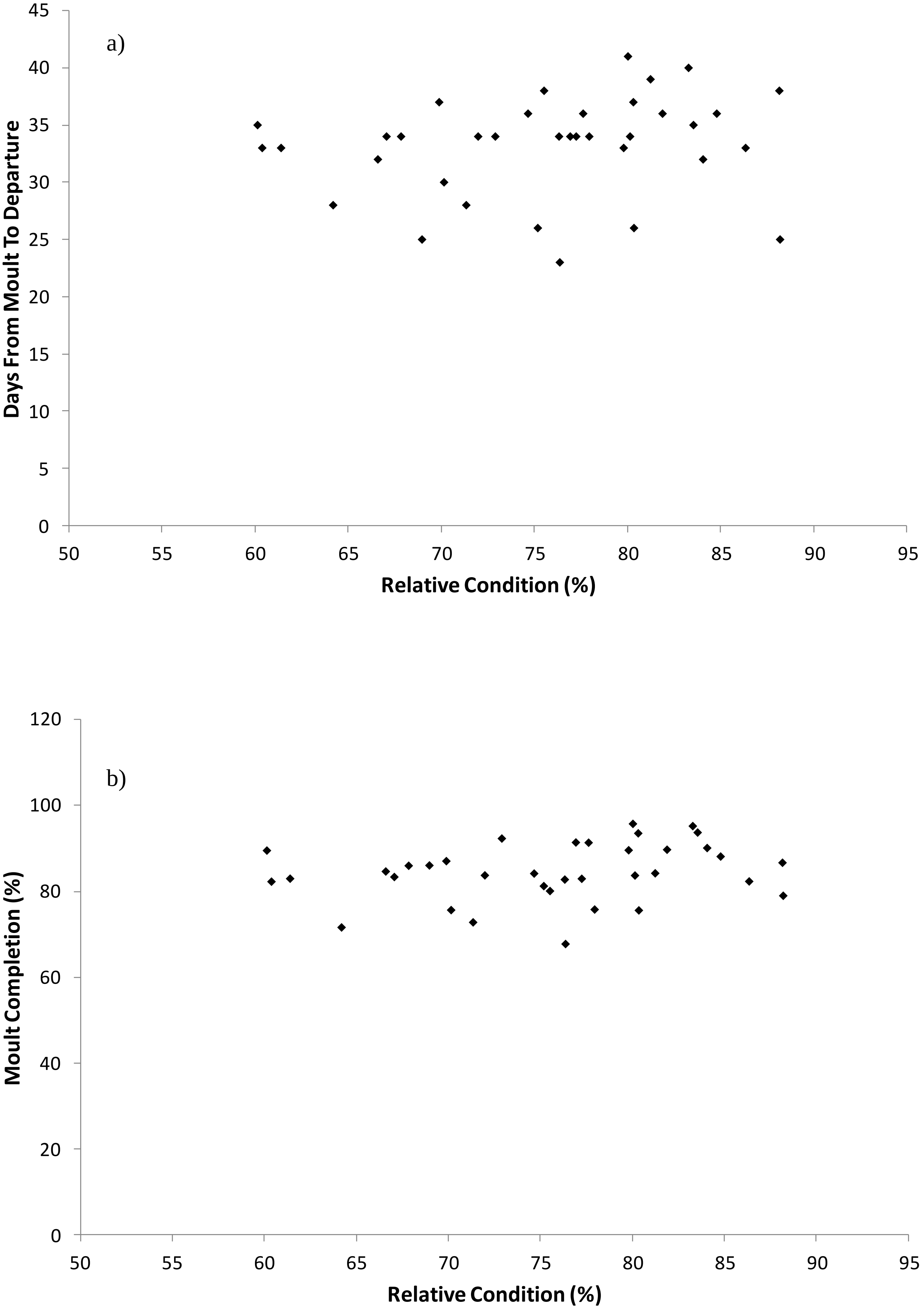

Figure 5.10: Female condition at fledging relative to female condition at the start of breeding has no influence on either a) the timing of departure (LME: Relative condition, $F_{4,36}$ =0.93, p = 0.40) or b) how complete feathers are by departure (LME: Relative condition, $F_{4,36}$ =1.86, p = 0.14). (n=36)

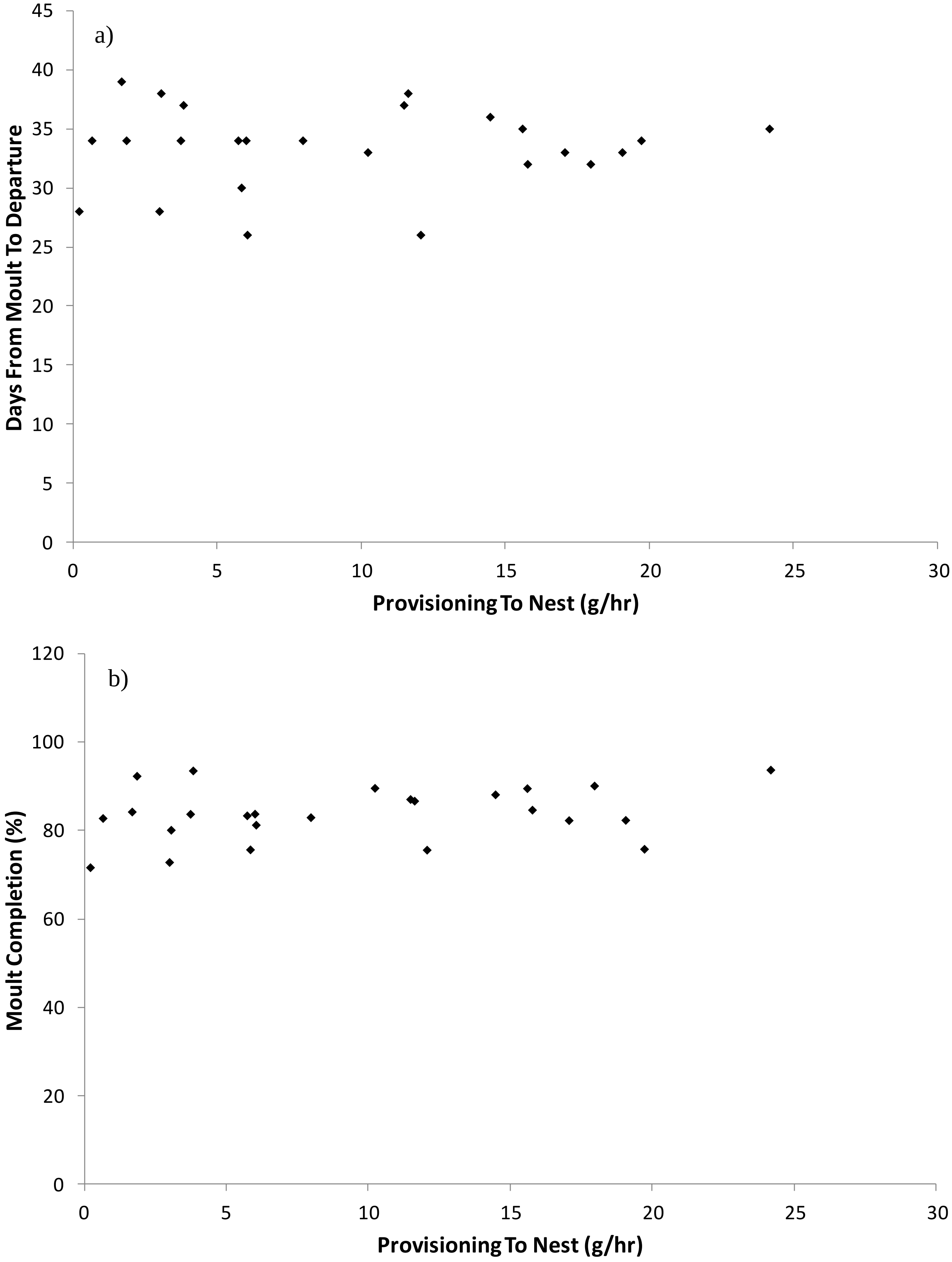

Figure 5.11: Male provisioning to nest had no influence on either a) the timing of departure (LME: Provisioning to nest, $F_{2,25}$ =0.78, p = 0.52) or b) how complete feathers are by departure (LME: Provisioning to nest, $F_{1,25} < 0.01$, p = 0.99). (n=36)

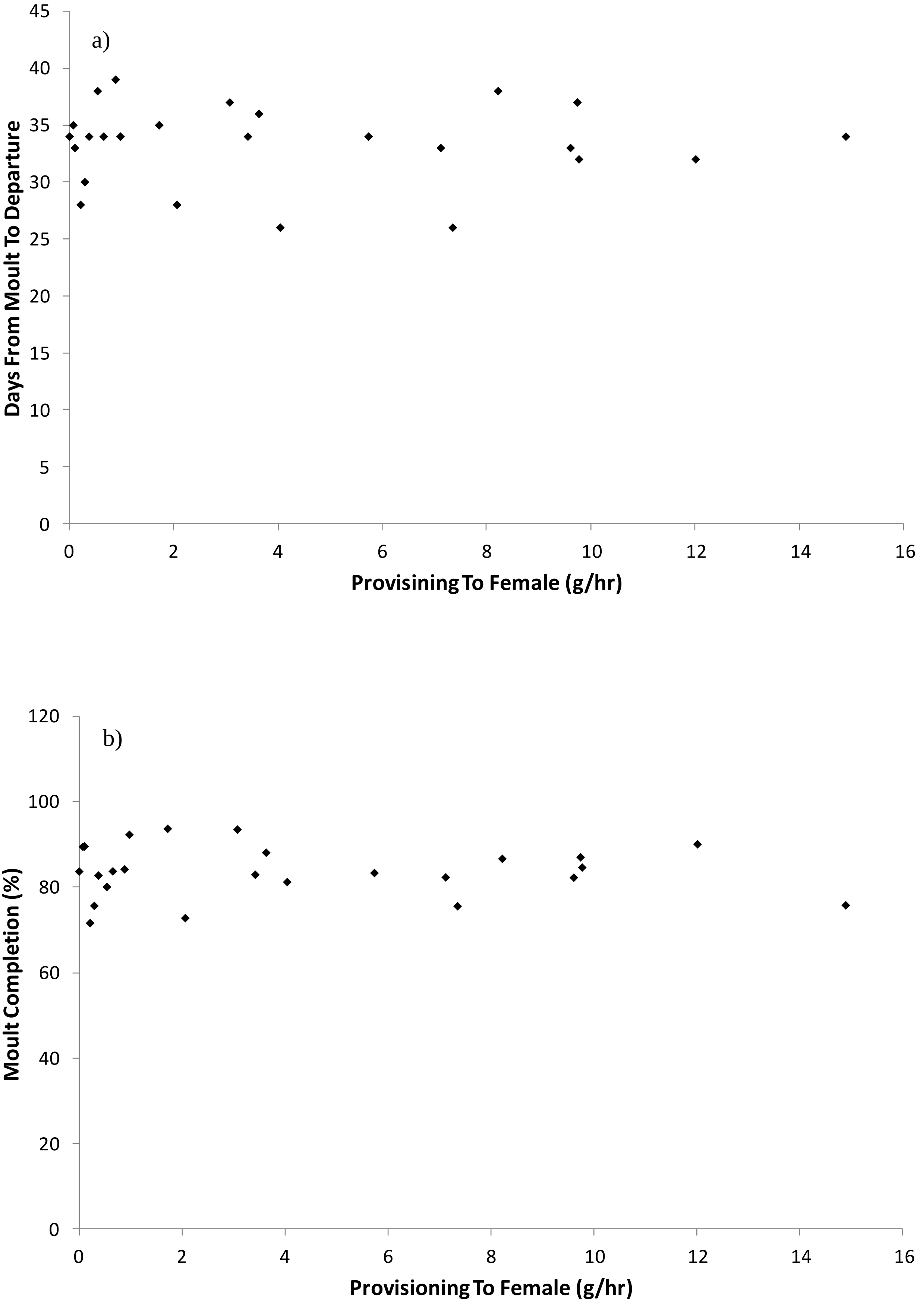

Figure 5.12: Male provisioning to female had no influence on either a) the timing of departure (LME: Provisioning to female, $F_{4,36}$ =0.93, p = 0.40) or b) how complete feathers are by departure (LME: Provisioning to female, $F_{2,25}$ =-0.35, p = 0.76). (n=25)

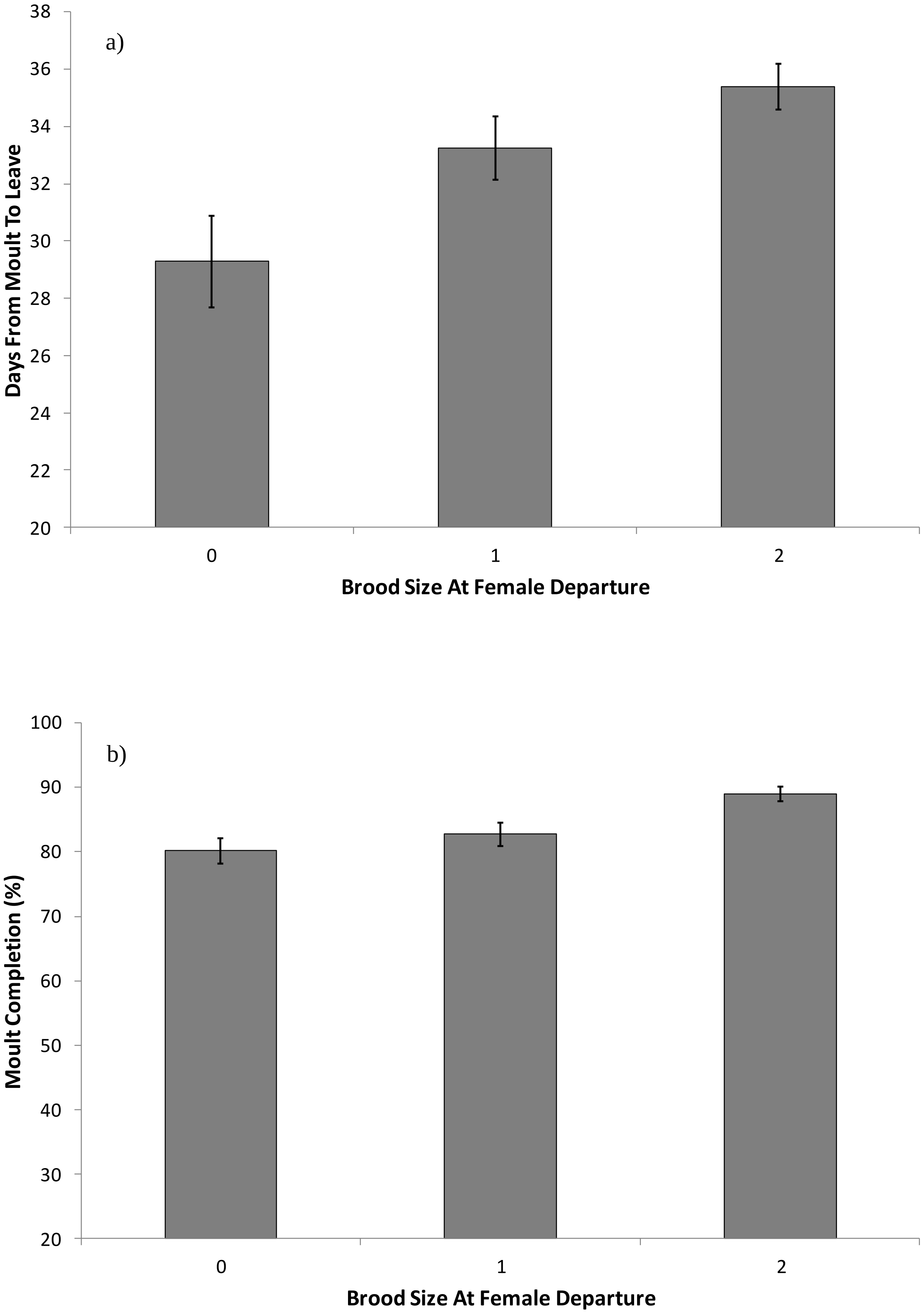

Figure 5.13: a) Females with broods of two chicks (n = 13) stay in the nest longer than females without chicks (n = 7) (LME: Brood Size, $F_{28,36}$ =3.34, p = 0.02), but females with 1 chick (n = 16) do not (LME: Brood Size, $F_{5,36}$ = 2.25, p = 0.07). b) Females with broods of two chicks leave with more complete feathers (LME: Brood Size, $F_{28,36}$ = 3.19, p <0.01), though females with single chicks do not (LME: Brood Size, $F_{28,36}$ = 1.08, p = 0.32).

The fledging by females with broods of 2 chicks with more complete feathers appears to be due to their longer confinement rather than faster feather growth (Figure 5.14). Females with different brood sizes did not differ with respect to either the asymptote of their feather length (LME: Feather asymptote, $F_{4,36} = 0.72$, $p = 0.54$) or their logistic growth rate constant (LME: Feather growth constant, $F_{4,36} = 3.24$, $p = 0.15$).

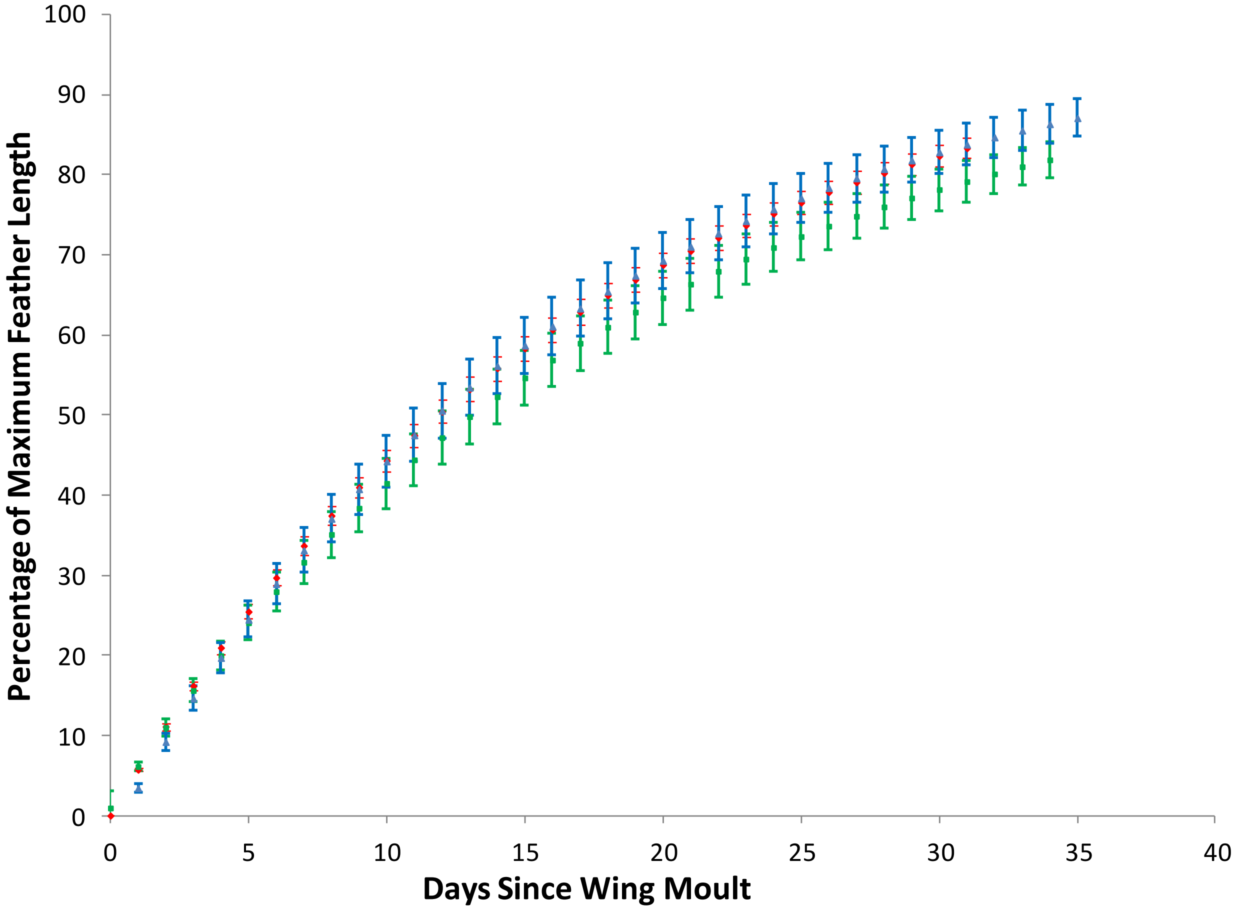

Figure 5.14: Fitted feather growth curves for females of different brood sizes did not differ. Females with no chicks (red points, n = 7), females with one chick (green points, n = 16) and females with 2 chicks (blue points, n = 13). See text for statistics.

To assess the role of chick growth on departure only broods of one chick were examined. Females with no chicks are obviously not influenced by chick growth while taking an average of the two chicks in larger broods might not accurately reflect growth. Chick tarsus completion at 10 days old had no influence on female departure timing or moult condition (Figure 5.15).

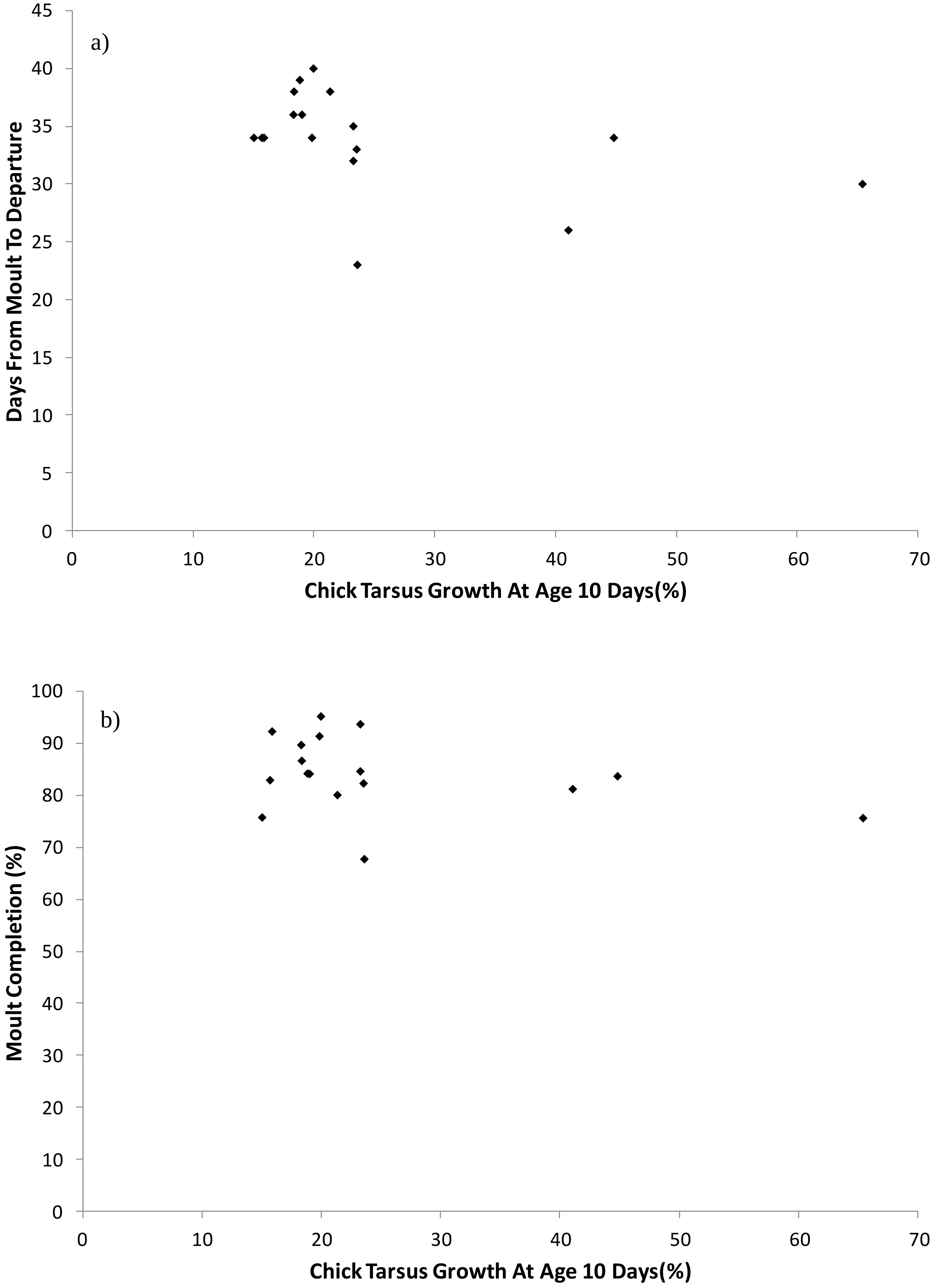

Figure 5.15: Chick tarsus completion at 10 days old had no influence on either a) the timing of maternal departure (LME: Provisioning to nest, $F_{12,55} = 1.71$, $p = 0.42$) or b) how complete female feathers are by departure (LME: Provisioning to nest, $F_{12,15} = 1.25$, $p = 0.46$). n = 16

5.4.4 Hatching asynchrony and timing of departure

Looking at just females with two chicks, females with more asynchronous broods spent longer in the nest with their youngest chick than would be expected if they left a fixed time after hatching commenced (Figure 5.17). Females departed when chicks were between 18 and 22 days old (mean = 20.27 ± 0.33). This suggests that the development of the youngest chick may be important in determining departure.

Figure 5.16: Nestling alone in an unsealed nest after maternal departure. Iris of eye is dark unlike adult birds who have a yellow iris (Figure 3.2).

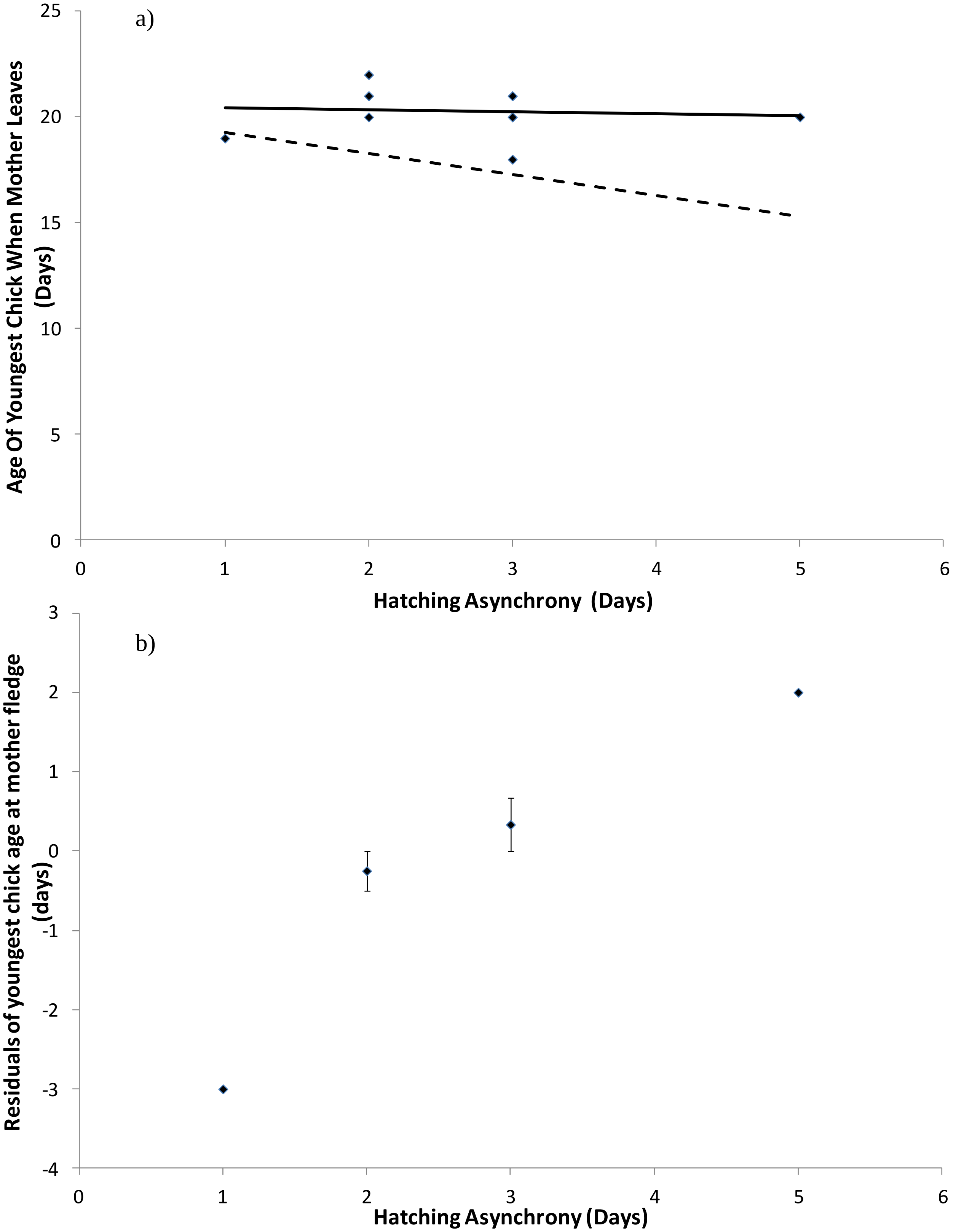

Figure 5.17: a) Age of youngest chick at the time of maternal departure does not decrease as asynchrony increases. data = solid line, predicted value based on hatching of first chick = dashed line b) This is achieved by females extending their stay in the nest as asynchrony increases. (LME: Hatching Asynchrony, $F_{1,7} = 19.13$, $p = 0.003$). See methods for calculation of residuals. (n = 13)

5.4.5 Interspecific variation in hatching asynchrony and departure timing

Looking across species, the relationship between hatching asynchrony and overlap with last chick was even more pronounced than within *T. leucomelas*. Females with highly asynchronous broods actually spend longer with their subordinate chicks than females with more synchronous broods (Figure 5.18). Phylogeny shown in Figure 5.19.

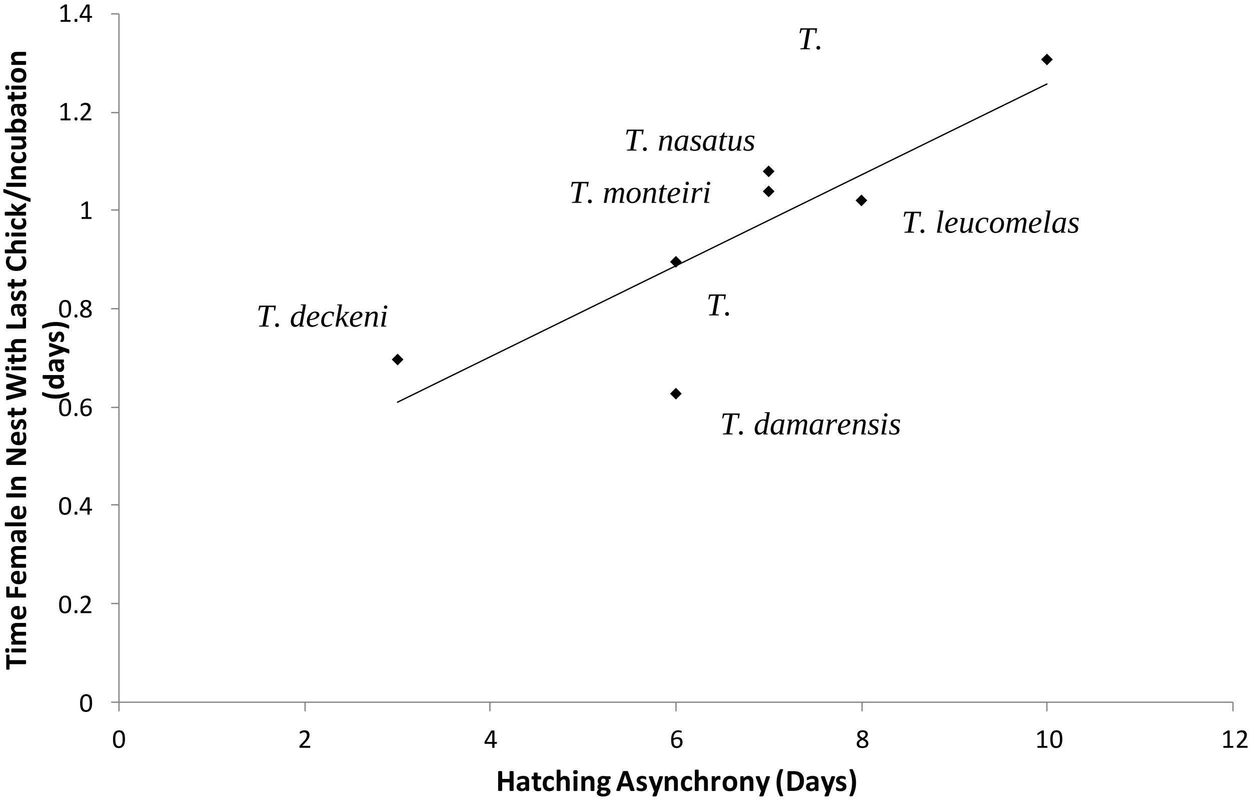

Figure 5.18: Species with greater hatching asynchrony between first and last chicks spend longer in the nest (relative to incubation) than species with lower levels of asynchrony Pearson correlation r = 0.845, N = 7, P = 0.017). Source: Kemp 1995

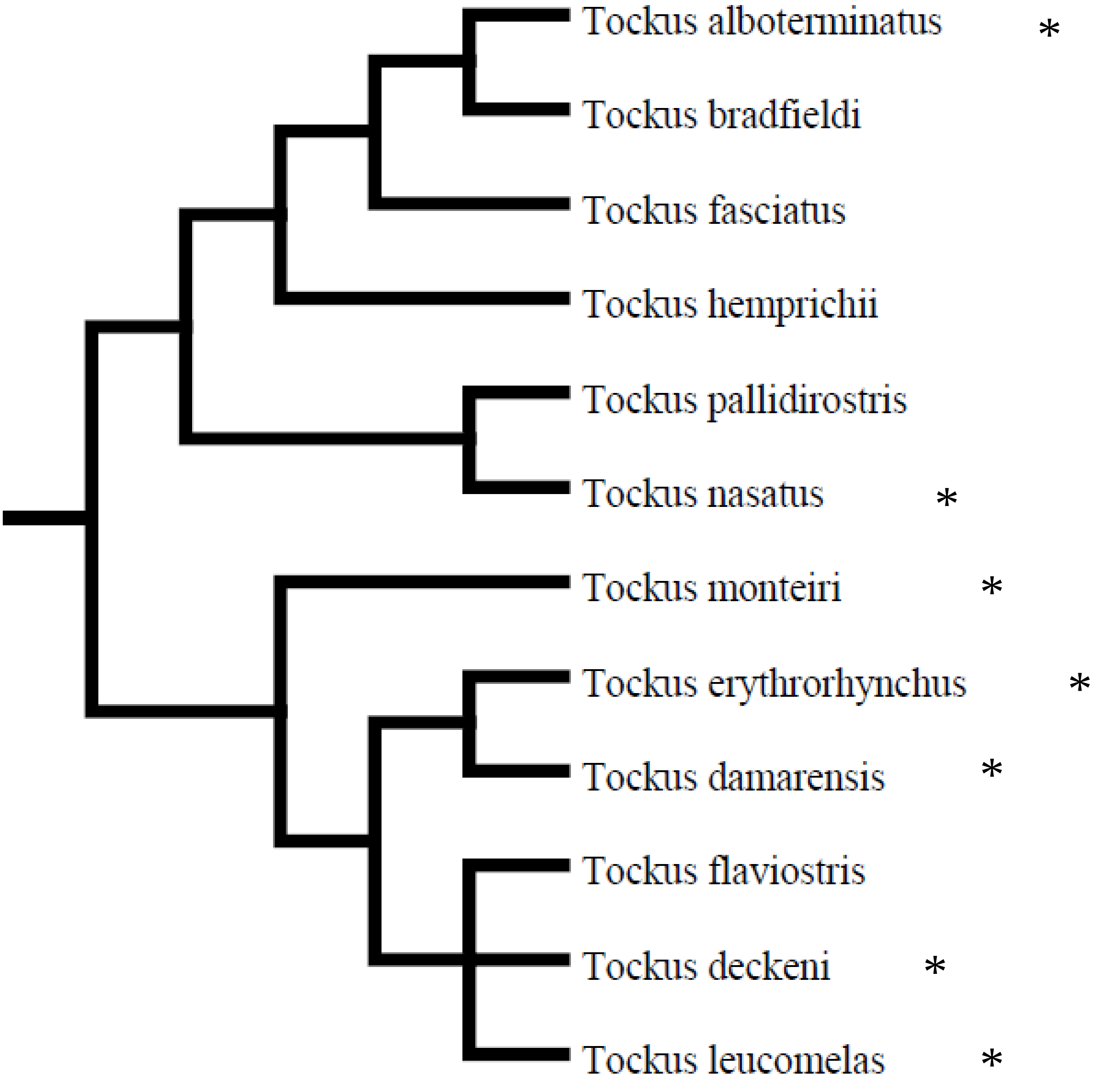

Figure 5.19: Relationships between 12 species within two branches of the *Tockus* genus. Species included in analysis denoted by *.Tree based on relationships from Kemp (1995).

5.5 DISCUSSION

The data collected suggest that the timing of departure of a female hornbill from the nest may not simply be a response to her moult completion. Females left the nest in varying stages of moult, some with nearly complete feathers, others with much more to go. Females could fledge earlier, though anecdotal evidence suggests a limit to feather length. During the study one nest box was knocked off its tree by cattle. The resident female had only dropped her wing feathers 16 days previously. This female could only fly short distances of under 50m at a time. Luckily the territory was heavily wooded allowing the female safe roosting spots while being fed by her mate. While the female survived and retained her mate and territory, even attempting breeding again the following season, she would have been of little use feeding a brood of chicks with such poor flight performance. This female was not included in analysis as her departure from the nest was forced.

Feather growth and timing of departure was not limited by female condition or the food received. Females in better condition neither grew feathers faster nor stayed longer. This corresponds with other studies of moult. Rohwer et al (2009) demonstrated that feather growth scales with mass across a range of species but that species with simultaneous moult, replacing all feathers at once did not have a lower growth rate. They suggested that feather growth rate is therefore not limited by energetic constraints, as replacing all 9 primaries at once would take more energy than one, but by the mechanics of forming feathers from an initially flat surface. While feathers grow logistically, moult is commonly only measured in time from shedding or feathers to completion (Rohwer et al 2009, Hedenström 2006). If we use the data from this study in the same way and calculate the growth rate per day we can see that hornbills grow feathers at a similar rate to other similarly-sized birds. The hornbill feathers grew at an average of 3.77mm/day (±0.10), with the average female weighing 227g (±4.71). This matches the allometric scaling of growth rates and mass form Rohwer et al (2009) and Hedenström (2006). For example, magpies (*Pica pica*) weigh 177g and have a growth rate of 2.6mm/day, Jackdaws (*Corvus monedula*) weigh 199g and have a growth rate of 3.6mm/day, Common Kestrel (*Falco tinnunculus*) weigh 189g and have a growth rate of 4.2mm/day, Rooks (*Corvus frugilegus*) weigh 426g and have a growth rate of 3.8mm/day (Rohwer et al 2009).

Brood size does appear to influence the timing of female departure. Females with no chicks demonstrate what females would do without the conflicting interests of offspring. Females with only one chick left at a similar stage of moult as those with no chicks, while chick growth had no influence on timing. This suggests that females' departure may be influenced more by competition between chicks than any absolute aspect of chick growth. Evidence from both variation between species and within the study population of Southern Yellow-Billed Hornbills suggests that females with more asynchronous brood spend extra time in the nest with their youngest chicks. This does not appear to be due to females taking longer to complete their feathers. Females with broods of 2 chicks in fact left their nests with more complete feathers than females with smaller broods.

Of course females can to some extent control chick growth. Without experimentation these results do nothing more than hint at the trade-offs that could be occurring. Experimental manipulation of brood size, similar to Magrath's (1989) work on Blackbirds was planned as part of this study (Table 5.1). Unfortunately the two years of the study experienced drought conditions. This reduced both the number of breeding pairs and more importantly increased brood reduction, reducing average brood size. Females with multiple chicks were too rare to make manipulation worthwhile. Broods of varying synchrony would have been created by swapping chicks between nests. Nests would have been assigned to one of four groups. Two groups of nests would contain synchronous broods of similar aged chicks. Synchronous large nests would have had 4 similarly sized chicks all of a similar age to the oldest chick hatched in that nest. Synchronous small nests would have had 4 chicks all of a similar age to the youngest chick hatched in that nest. Two groups of nests would have had asynchronous broods. 'Naturally' asynchronous broods would contain cross fostered chicks with a similar level of asynchrony to unmanipulated nests, with chicks 2 days apart. Exaggerated asynchronous broods would contain broods showing a greater level of asynchrony between chicks. The timing of female departure could then be directly tested against both chick growth and brood asynchrony. If competition is important in determining female departure then females with highly asynchronous broods will leave when their youngest chick is older than the youngest chicks in either the nests with natural levels of asynchrony or the nests with synchronous broods of young chicks. Food supplementation was difficult as it could have influenced the behaviour of other study species at the field site, especially pied babblers. A hornbill specific feeder was developed, involving a chicken wire cage through which only the long beaks of hornbills could reach food. Uptake of supplemental food was however unreliable. Under the prevalent drought conditions, manipulation of synchrony would have had little value with younger chicks either starving or being eaten by their foster mother. Since brood reduction in Southern Yellow-Billed hornbills mainly occurred while chicks were young, cross fostering of older chicks (youngest chick over 5 days old) may increase the chances of survival.

Treatment Name	Manipulation	Prediction if intrabrood competition is important
Synchronous Large	Chicks all same age and equal in age to largest chick naturally in nest	Earliest Departure
Synchronous Small	Chicks all same age and equal in age to youngest chick in ‘Exaggerated Asynchrony’ Treatment.	Later than ‘Synchronous Large’ but earlier than ‘Natural Asynchrony’.
Natural Asynchrony	Chicks moved between nests but natural hatching asynchrony maintained (2 days between chicks)	Mother stays in nest for a similar period to unmanipulated nests.
Exaggerated Asynchrony	Hatching asynchrony increased to double natural levels (4 days between chicks)	Latest Departure

Table 5.1: Experimental treatments that would allow us to explicitly test the role of brood asynchrony on female departure.

While this study demonstrates that the timing of female departure may be related to conditions within the brood, female overlap with chicks in the nest only represents a small portion of parental care. Females continue providing care after leaving the nest. Chicks are only evicted from parental territories at the start of the following breeding season (personal observation). The time spent in the nest is therefore a relatively small chunk of the total period of care. Indeed the female's stay in the nest may be just as influenced by intrabrood conflict as interbrood. Earlier maternal departure could be disastrous for younger chicks in a brood who are not yet ready to compete with their older siblings. The timing of female departure is also likely to reflect sexual conflict between parents. When the female leaves the nest, not only does the male have one fewer mouth to feed but also potentially has some help in feeding the chicks (Kemp 1995). A prolonged stay in the nest could well cost the male more than the female. This is dramatically illustrated by the females that abandon their breeding attempt, cannibalising all eggs before then moulting their wings. In these nests, males fed sufficiently that females maintained condition. Their feeding rate was often more than many successful males but they gained no reproductive output from their efforts. Here we see clear potential for conflict as the male has no way of knowing that their mates are not brooding eggs unless informed vocally by the females. In theory, the combination of males dependence on females for any information about the reproductive attempt, combined with putting males in sole charge of providing food would put females in control. Given the extent of female control, males would need a high degree of paternity assurance to make such an investment worthwhile. Indeed, Stanback et al (2002) have demonstrated that the closely related Monteiro's Hornbill has low rates of extra pair paternity.

The duration of female incarceration in hornbills is indeed an interesting model for the study of POC. However the issues involved are a lot more complex than a simple case of interbrood conflict. This study demonstrates that factors relating to their broods may influence the duration of their mother's stay in the nest. Further experiments are needed. The potential for interbrood conflict and sexual conflict remain interesting but untested. The role of the mother in intrabrood conflict is however tested in the next chapter.

While this work has been conducted on the *Tockus* hornbills of the African savannah, other species might provide even greater insights. Females of some species, such as Silvery-Cheeked Hornbill (*Bycanistes cristatus*) stay in the nest until the chicks fledge (Moreau & Moreau 1941). Even more intriguingly some species have very variable lengths of incarceration (Kemp 1995), with some individuals staying as long as the chicks, while others depart much earlier. One such species is the Oriental Pied Hornbill (*Anthracoceros* *albirostris*) which, already being the subject of detailed observation (Banwell & Lim 2009) could prove a fantastic model for investigating the conflicts involved in female confinement.

We cannot yet say if conflict is occurring between parents and offspring over the duration of maternal incarceration. However we can now say that a female’s stay in the nest is not just limited by her moult. This demonstrates that there are complex tradeoffs involved in determining when females leave the nest and poses exciting questions concerning not just interbrood conflict but conflict between parents and between chicks in the same brood. This conflict is explored in Chapter 6

Chapter 6

'Home Alone': Maternal Influence On Sibling Rivalry in Southern Yellow-Billed Hornbills

6.1 ABSTRACT

Conflict is a widely accepted, fundamental aspect of family life. However empirical tests of such conflicts are difficult to stage. Recording lifetime reproductive success is challenging, while parental control of resource allocation means that genuine conflict can rarely be distinguished from behavioural squabbles. The unusual breeding behaviour of hornbills (Bucerotiformes) presents a rare opportunity to test both parent-offspring conflict and parental influence on sibling conflict. Female hornbills seal themselves into the nest at the onset of laying and do not leave until their chicks are midway through development. Prior to leaving, the female distributes food provided by her mate between the offspring and herself. After the female leaves, chicks reseal the nest and parents lose all control over the destination of provided food.

I studied the natural distribution of food within broods both with the breeding female present and after she had left. While females remained in the nest, food distribution between chicks was even. After females had departed food distribution skewed towards older chicks. In order to explicitly test the role of the female in sibling competition, experimental removals of females were conducted. In the absence of the female, older, larger chicks gained a greater share of food and proportionally put on more mass. Chick behaviour also changed from food solicitation to aggressive scramble competition. These results suggest that conflict is occurring between parents and older offspring, with parental action controlling competition between broodmates. This is discussed with regard to both maternal and offspring life history decisions.

6.2 INTRODUCTION

Squabbles and apparent disharmony are fundamental features of family life. Trivers (1974) proposed that intrafamilial conflict was driven by genetic differences within the family. In non – clonal organisms parents and their offspring are not genetically identical. These genetic differences generate theoretical conflicts of interest within the family. Both parents and offspring will act to maximise their personal fitness. If parents could only produce one offspring during their life then the optimal strategy for the parents and offspring would overlap. Conflict arises however when parents can produce multiple offspring. Parents would maximise their fitness by dividing their investment between their offspring. Individual offspring however value their own fitness more than that of their siblings. This predicts that each offspring should demand more investment than the parental optimal, at the expense of their siblings.

Parent offspring conflict (POC) is intuitive and widely accepted theoretically, generating many theoretical models of how it may operate (Royle et al 2004). There has however been little empirical evidence based on real organisms capable of critically testing it. The reason for such a paucity of suitable tests is due to the fundamental nature of the conflict (Mock & Forbes 1992). In order to demonstrate conflict one must show that when one party wins the conflict, it is at the expense of the other. Systems where one party always wins are therefore of limited use for testing the extent of conflict. In the case of POC, it is difficult to find any systems where parents are not in control. If offspring could procure enough resources for their own development, there would be no need for parental care. Even in systems with no post natal parental care, maternal investment in eggs plays a massive part in offspring success (Mock & Parker 1997).

Even in cases such as siblicide (Dorward 1962) which ostensibly show conflict, parental investment (or lack of) still creates the asymmetries between offspring that allow such squabbles to occur. This makes it difficult to test the extent of conflict as it is impossible to discover what offspring would do if they were in charge. Indeed Mock & Forbes (1992) stated that “Only field results showing that offspring win (or at least gain handsome concessions) can constitute an unambiguous demonstration of phenotypic POC.”

The measurement of lifetime reproductive success has allowed some tests of POC (Clutton-Brock 1991). However difficulties of following organisms throughout their lives and of quantifying the costs of behaviours in terms of reproductive success and inclusive fitness have made interpretation of such results debatable (Royle et al 2004). After the revolution in using POC to try to explain the squabbles seen in all forms of family life following the work of Trivers (1974), the pace of empirical research into POC has slumped. Apart from the sex ratio conflicts in social hymenoptera (Ratnieks et al 2006) little concrete evidence has been found for POC. As Kilner & Hinde (1998) suggest, a lack of evidence does not mean that POC is unimportant, it has just proved particularly difficult to test.

Ideally, to test POC, one needs a system in which the outcome of the evolutionary conflict can be experimentally manipulated. Essentially we need to be able to independently ask parents and their offspring what the preferred level of parental investment is. Indeed, parent offspring conflict (and for that matter all forms of intrafamilial conflict) may well be so intuitively appealing because throughout our own lives we are told explicitly and with varying degrees of tact just how our relatives' ideals conflict with our own.

Hornbills (*Bucerotiformes*) have an unusual breeding strategy that may allow us to investigate a situation where offspring can win the battle over parental investment. Hornbills nest in cavities in trees or cliffs and the female will seal herself in to the nest before laying her eggs. Typically, most species begin incubation before their clutch is complete, leading to asynchronous hatching and producing large size asymmetries in the brood. In some species the female remains in the nest until the chicks are ready to fledge. In other species however the female emerges mid way through the nestling period. When their mother departs, the chicks will re-seal the nest entrance (Kemp 1995). Species in which the mother emerges before the chicks present us with effectively two separate provisioning 'games'. When the female is in the nest, she is provisioned by her mate and then distributes the food. This is analogous to the classical avian parental system where the parents choose how much to invest in each offspring. In this situation, while the chicks can attempt to influence their mother's choice of who to provision, the mother is essentially in complete control (i.e. the parents win).

After the mother leaves the nest, power shifts and the game changes. Now, while the parents still control the rate of food delivery, they have no control over its allocation. All parents can do is pass the food through the "letterbox" at the front of the nest to the squabbling chicks within. As soon as parents put food close to the nest entrance nestling beaks dart forward and snatch it back into the nest. Chicks now have a chance of winning the conflict over food allocation. Without their mother in the nest to distribute food, larger more competitive chicks can take charge of access to the nest entrance and therefore to food allocation (i.e. the offspring win). If food distribution while the mother is in the nest is different to that after she had left, it would demonstrate apparent parent offspring conflict. However, just like many intrafamilal squabbles parents may still retain the ultimate power. Mothers control the brood size, any offspring size asynchrony and importantly, the day she fledges (Mills et al 2005). The mother may well leave the nest when she has manufactured a level of synchrony (or asynchrony) between chicks that match her preferred level of competition between them. In order to definitively demonstrate POC one would need to completely remove power from the mother and allow the offspring to win the conflict for a change. One way of skewing the conflict in favour of the chicks would be to remove the mother earlier than she would naturally. This would allow investigation of food distribution, both with the mother in or out of the nest, without the confounding factor of her departure being at her discretion rather than the chicks. One should stress that the date of female departure may or may not be a source of conflict and that it is a separate and exciting question in itself (Chapter 5). Simply, if food distribution is different with the mother in the nest than when she is removed then there is clear evidence of conflict. Indeed, parent offspring conflict is defined as “Disparity in the parental investment optima between parents and offspring” (Mock & Forbes 1992).

To test the possibility of parent offspring conflict in hornbills, I studied food distribution and chick behaviour in nests of Southern Yellow-Billed Hornbills (*Tockus leucomelas*) both before and after female departure. I also conducted temporary experimental removals of breeding females, to demonstrate that any changes were due to phenotypic POC between breeding females and their offspring.

6.3 METHODS

6.3.1 Study site and general recording method

The study was conducted on a colour-banded population of Southern Yellow-Billed Hornbills in ranch land in the southern Kalahari Desert, South Africa (26°58’S, 21°50’E). All pairs studied bred in nest boxes that could be fitted with internal video recording equipment. Video recordings were made using a small CCTV camera fitted with 6 infra red LED’s (http://www.henrys.co.uk/cctv/pro240.htm). Cameras were powered by 8 1.2V rechargeable AA batteries connected in series. Camera output was recorded on to digital video recorders (Mini DVR 1 & 2, www.dogcamsport.co.uk).

Nest boxes were modular with a separate plastic dummy recording box fitted to the lid. When internal recordings were required, the dummy box could be replaced with an identical box containing recording equipment and batteries. From hatching, chicks were marked using non toxic paint markers (Edding 751). Chicks were given unique markings with black or white paint in different locations. Marks were clearly visible on video recordings but wore off after approximately 3 days and did not remain visible on any fledglings.

6.3.2 Natural Variation

Observations were conducted in two breeding seasons from October 2009 to March 2011. For the purpose of this study, only nests containing 2 chicks around the time of maternal departure were used. Nests with more than 2 chicks were rare. Brood reduction was common and many nests had only one chick by the time the breeding female fledged. Questions concerning parent-offspring conflict over brood reduction are however beyond the scope of this study. Seven nests were recorded both while the mother was in the nest (mean eldest chick: 12.44 days old ±1.29, range: 5 - 17) and after she had fledged (eldest chick 28.92 days old ± 3.13, range: 23- 45). Recording occurred for two hours from sunrise, the period of peak food delivery, before heat reduces adult foraging behaviour. Videos were analysed to quantify prey delivery and chick behaviour. Prey size was scored into 6 length classes relative to an adult female’s beak. ‘Very tiny’ for items just held in the very tip <5mm, ‘Tiny’ up to a quarter of a beak (19mm), ‘Small’ up to a half (38mm), ‘Medium’ up to three quarters (56mm), ‘Large’ up to a complete beak (75mm) and ‘Extra large’ for items larger than a beak length, typically up to 120mm. For focals after maternal departure, size classes were estimated compared to the internal width of the nest box (220mm). The biomass of food items were estimated the formula from Rogers et al (1976):

$$B = (0.0305L)^{2.62}$$

Where B is the biomass in grams and L is the length of the prey in mm. This provides a rough estimation only since the equation is designed to deal with adult terrestrial arthropods. Hornbill prey in the study also included vertebrates and larval invertebrates, in particular Lepidoptera (Chapter 3).

All aggressive interactions between chicks were recorded. An aggressive interaction was classed as any rapid peck to the head of another chick or when a chick grasped its nestmate’s beak or head with its beak. Pecking or chewing of other body parts were not classed as aggression as chicks often preened each other while in close proximity. Interactions occurring during periods of intense begging were excluded. Chicks would often try to swallow anything close to their beak during such periods. An example of aggression is given on the accompanying CD (Video 6.1)

6.3.3 Experimental Data

Experimental removal of breeding females was conducted to explicitly test how maternal presence in the nest influences food distribution and aggression within the brood. Experimental manipulation was conducted in the same seasons as the observational data, using the same breeding pairs. Nests containing 2 chicks were used. Six nests were tested in the 2009/2010 season and 3 nests in the 2010/2011 season. Each nest received two treatments. Treatments were conducted in a random order within 3 days of each other. In both treatments the nest was opened approximately 20 minutes before foraging males would leave roost at dawn. The breeding female and chicks were removed and weighed using electronic scales to an accuracy of 0.1g. In the ‘Mother Removed’ treatment, only the chicks were returned to the nest. The nest was then video recorded in the same fashion as the natural observations for 3 hours. During the nest focal, the mother was kept in an extra nest box at a distance of over 300m from the nest, which was kept in the shade and blackened out with thick cloth. An observer stayed with the mother for the duration of the experiment and all removed birds quickly calmed and rested in the darkened boxes. After 3 hours the mother and the chicks were weighed and the mother returned to the nest. The ‘Mother Present’ treatment acted as a control for the disturbance experienced by chicks in the ‘Mother Removed’ treatment. After the first weighing, both the mother and brood were returned to the nest. The nest was again monitored for 3 hours, after which the occupants were weighed. Video recordings were analysed for provisioning rate to chicks and for aggression between nest mates.

Experiments were conducted in the last week before the breeding female was due to fledge (Oldest chick age 19.11 days ± 0.51, range: 15 to 23). Experiments were trialled at earlier stages but failed as chicks were not sufficiently developed to take food from the nest entrance.

6.3.4 Statistical Analysis

All statistics were conducted using R v 2.13.1 (R Development Core Team 2011). In order to analyse the skew in distribution of food between chicks, for every focal, the percentage of the total amount of delivered food taken by the older chick was calculated. Both observational data and experimental data were analysed using linear mixed effects (LME) models. Breeding female identity was entered as a random factor to allow comparison between focals on the same nests. Maternal presence and provisioning rate were included as fixed effects. All models were simplified using a backwards stepwise method until only terms that contributed significantly to the model remained. The validity of assumptions of normality and homoscedascity were checked by visual inspection of residuals and normal probability plots.

Provisioning rate was analysed both in terms of rate of prey item delivery and estimated biomass delivery rate. Two nests were excluded from the analysis of natural provisioning rate when at least one of the focal periods produced less than 3 feeds to the chicks. All averages are given by mean ± S.E. Degrees of freedom will vary due to sample size and the sequential removal of terms from models.

6.3.5 Ethical Note

Work was conducted with relevant permits from Northern Cape Conservation and SAFRING. Removed females did not attempt to escape temporary nests and demonstrated no extra weight loss during the removal treatment than during the control (Wilcoxon signed ranks test: $V_{8,9} = 31$, p=0.36).

6.4 RESULTS

6.4.1 Natural observations

The total rate of prey biomass delivery to nests was roughly equal both before (6.63±1.74g/hour) and after (7.27±1.87g/hour) maternal departure, though the actual delivery rate of items was slightly lower before mothers left (4.89±0.96 items/hour) than after (7.44±1.13 items/hour). The share of food that the older chick receives was not influenced by the delivery rate either in terms of feeding rate (LME: Overall item delivery rate, $F_{5,7}$ =1.71, p = 0.25) or biomass delivery rate (LME: Overall biomass delivery rate, $F_{5,7}$ =2.70, p = 0.16). When the mother was present, food distribution, both in terms of the number of items and their estimated biomass, was roughly equal between chicks. Distribution, showed increased skew towards elder chicks after the mother has fledged (Figure 6.1 and Figure 6.2), independently of changes in provisioning rate.

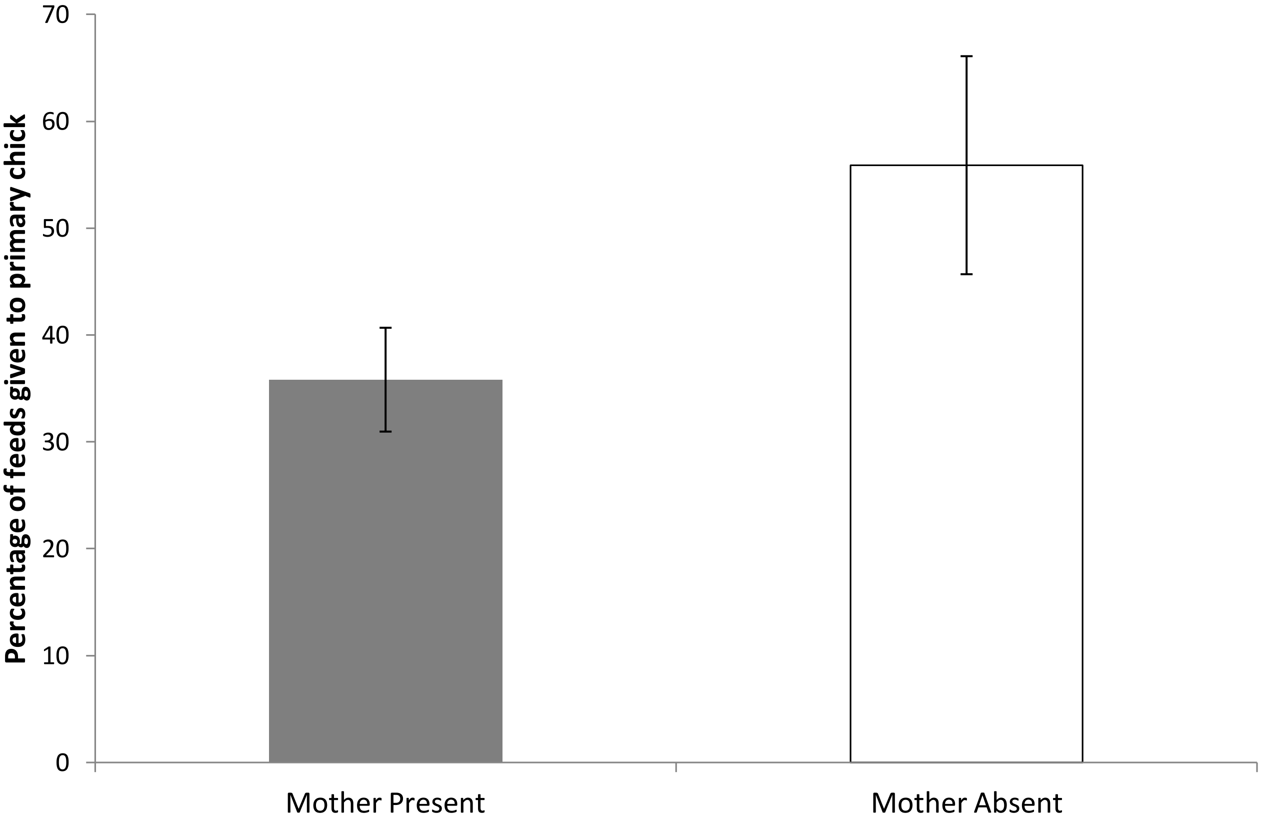

Figure 6.1: Elder chicks may receive a greater share of feeds after mothers have left the nest than when mothers are still present. LME: Maternal presence, $F_{6,7}$ =5.48, p = 0.06

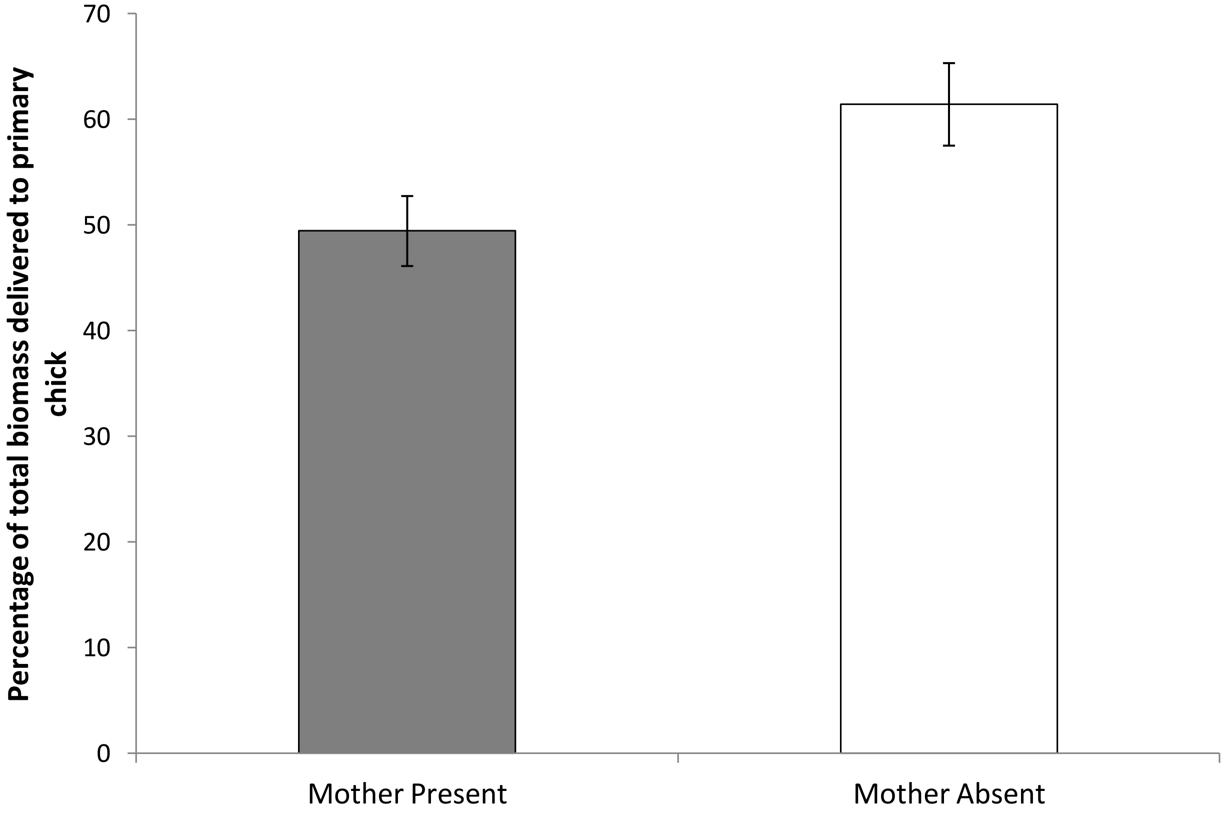

Figure 6.2: Elder chicks receive a greater share of the food biomass delivered to broods after mothers have left the nest than when mothers are still present. LME: Maternal presence, $F_{6,7}$ =7.65, p = 0.03

Chick aggression also dramatically changed when the mother left (Figure 6.3). None of the 7 nests studied experienced aggression while the mother was still in the nest. After maternal departure however, all 7 nests experienced some aggression at an average rate of 10.10 (±3.53) bouts per hour. Provisioning rate had no influence on aggression (LME: Biomass delivery rate, $F_{5,7}$ =0.62, p = 0.27, LME: Item delivery rate, $F_{5,7}$ =3.71, p = 0.11). Older and younger chicks were equally aggressive (Figure 6.4)

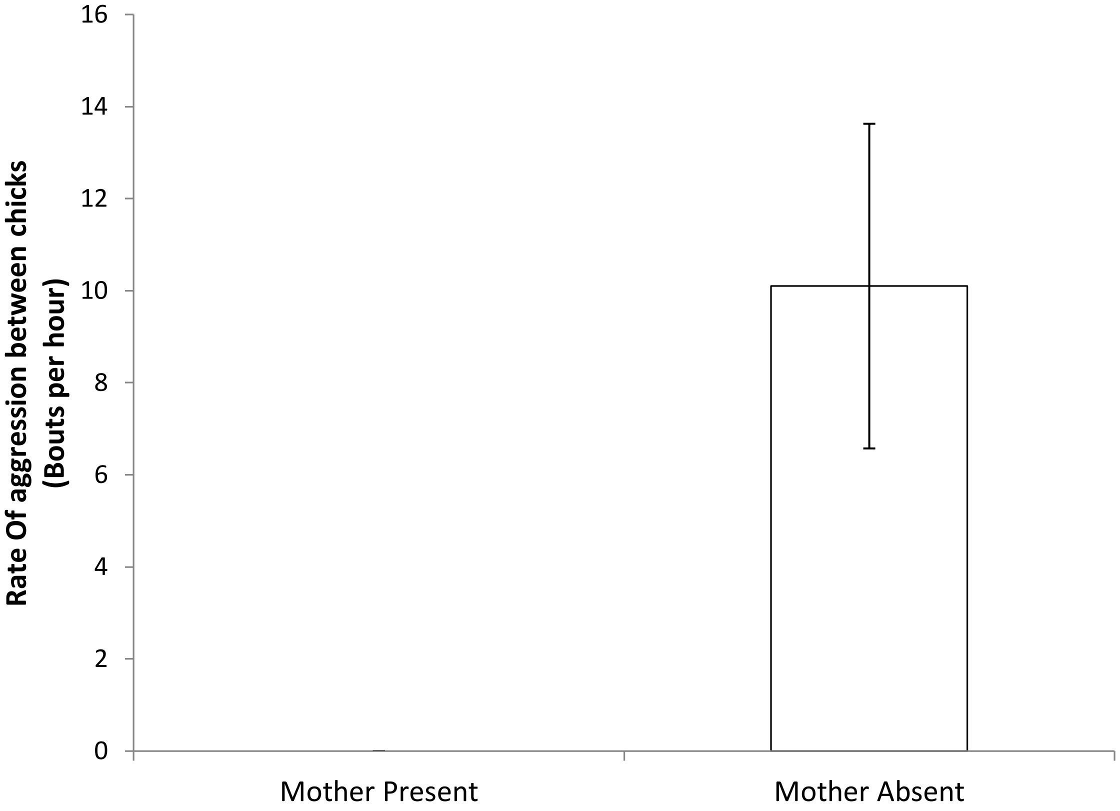

Figure 6.3: Aggression between the two chicks was absent while the mother was in the nest but was present (white bar) after she had fledged (LME: Maternal presence, $F_{8,9}$ =8.21, p = 0.029)

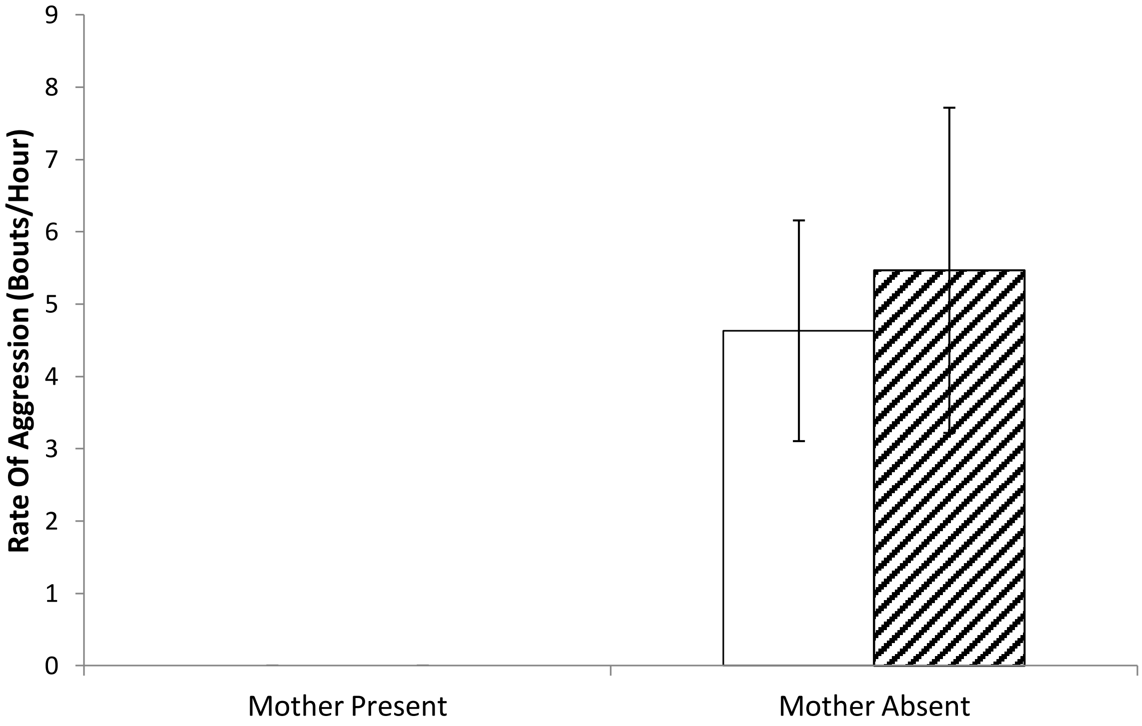

Figure 6.4: While aggression was only present when the mother was absent (white bars), both senior (empty bars) and junior (hatched bars) chicks demonstrated similar rates of aggression (LME: Chick Rank, $F_{1,12}$ =0.31, p = 0.86).

6.4.2 Experimental removal of mothers

Chicks did not receive a different rate of feeding when the mother was removed (4.78 ± 0.96 items per hour) than when she was present (3.67 ± 1.08 items per hour). The estimated biomass was however lower without the mother (2.74 ± 0.49 g per hour) than when she was present (8.73 ± 2.01 g per hour). This was probably due to two factors. Chicks took some time to adapt to having to take food from the nest entrance rather than being fed by the mother. They also competed more strongly for items resulting in more items being dropped and eaten by neither chick. Both of these factors would reduce the rate of intake of large items which are difficult to pull into the nest and have a longer handling time. Overall provisioning rate did not influence the share of feeds taken by the oldest chick, either in terms of item delivery rate (LME: Overall item delivery rate, $F_{7,9}$ =3.51, p = 0.10) or biomass delivery rate (LME: Overall biomass delivery rate, $F_{7,9}$ =0.02, p = 0.91). Older chicks took a greater share of food when the mother was removed than when she was present. This applies both in terms of the number of feeds (Figure 6.5) and biomass received (Figure 6.6).

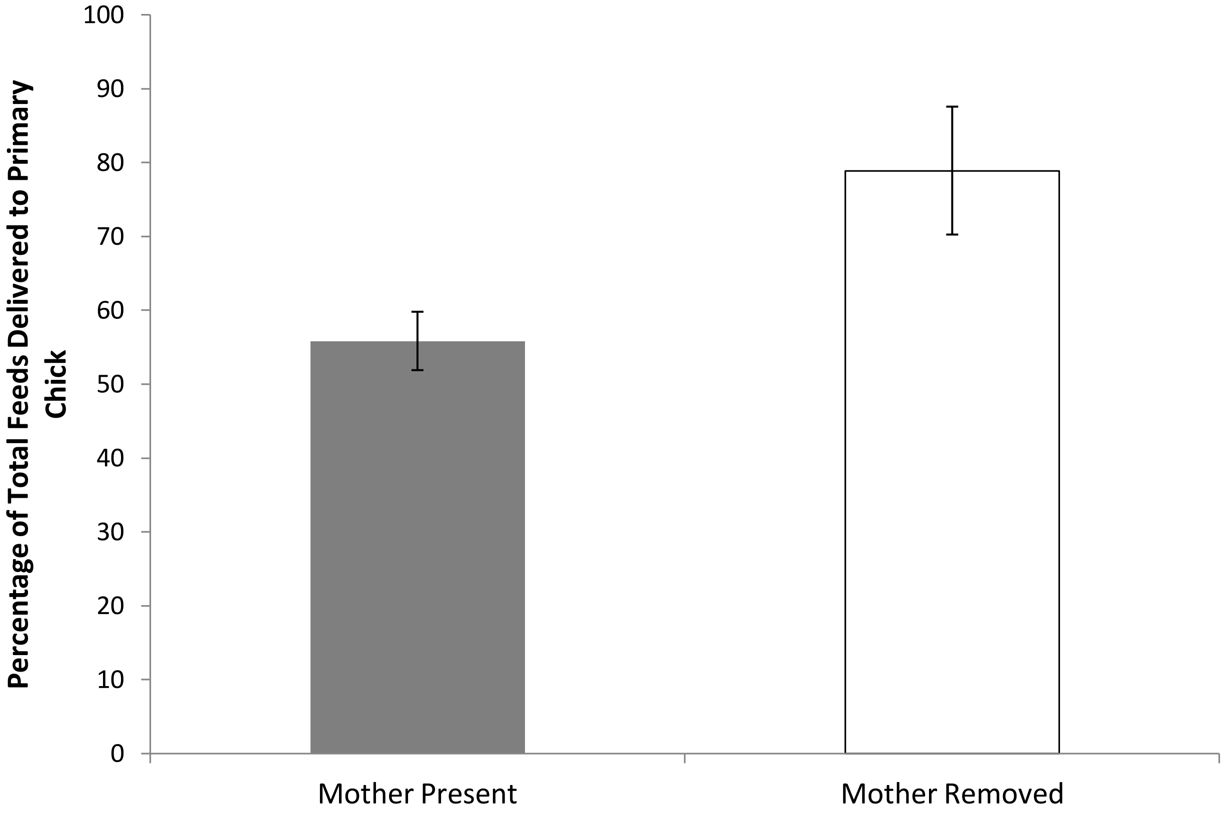

Figure 6.5: Senior chicks took a greater share of food (in terms of number of items) when the mother was present (grey bars) and when she was removed (open bars). LME: Maternal presence, $F_{8,9}$ =7.77, p = 0.024.

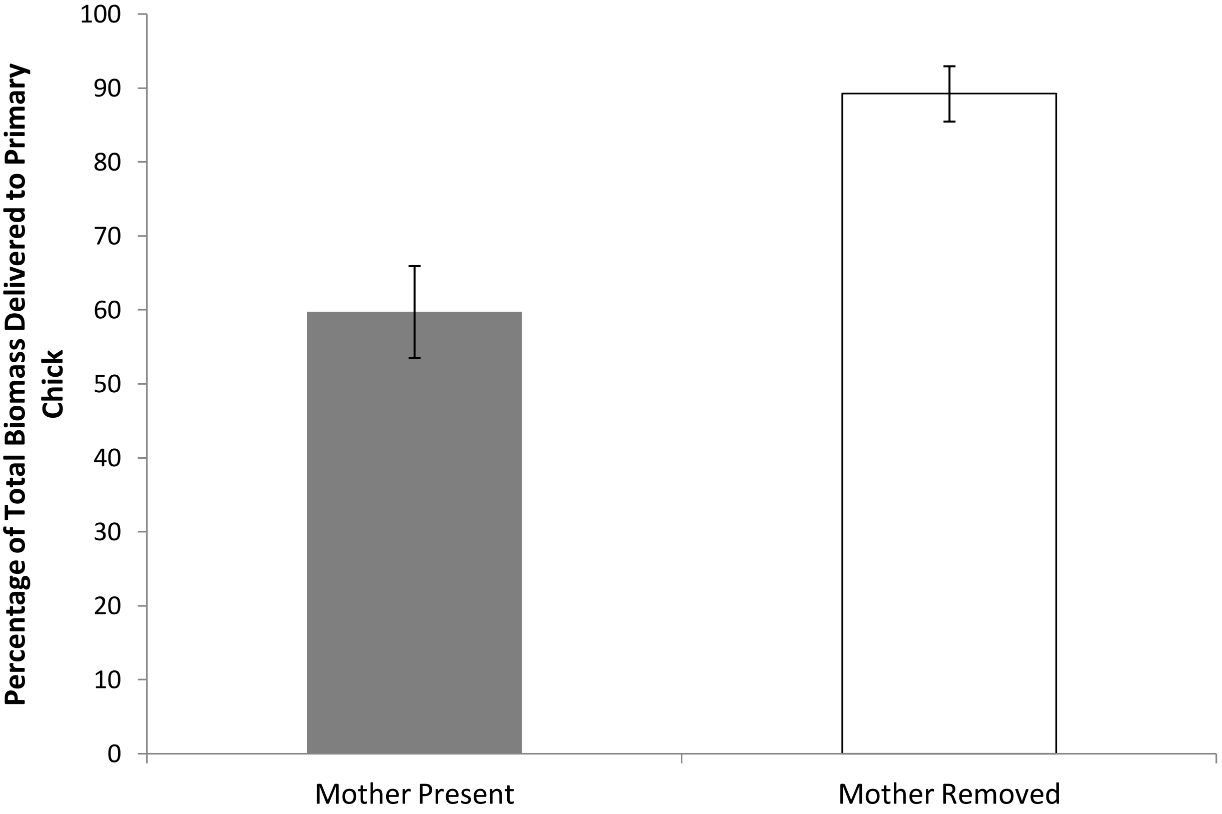

Figure 6.6: Senior chicks took a greater share of food (in terms of biomass) when the mother was present (grey bars) and when she was removed (open bars). LME: Maternal presence, $F_{8,9}$ =32.69, p = 0.0004

This difference in food distribution was reflected in the relative mass changes of older and younger chicks. Older chicks gained relatively more weight compared to their younger siblings when the breeding female was removed than when she was present. Older chicks gained on average 2.05% ± 1.51 more than their younger siblings when the mother was present but 3.79% ± 1.27 more when she was removed. Both siblings gained mass while the mother was present, though when the mother was removed, younger chicks lost mass. The overall provisioning rate had no significant influence on the difference between chicks (LME: Biomass delivery rate, $F_{7,9}$ =5.09, p = 0.06, LME: Item delivery rate, $F_{7,9}$ =5.08, p = 0.06).

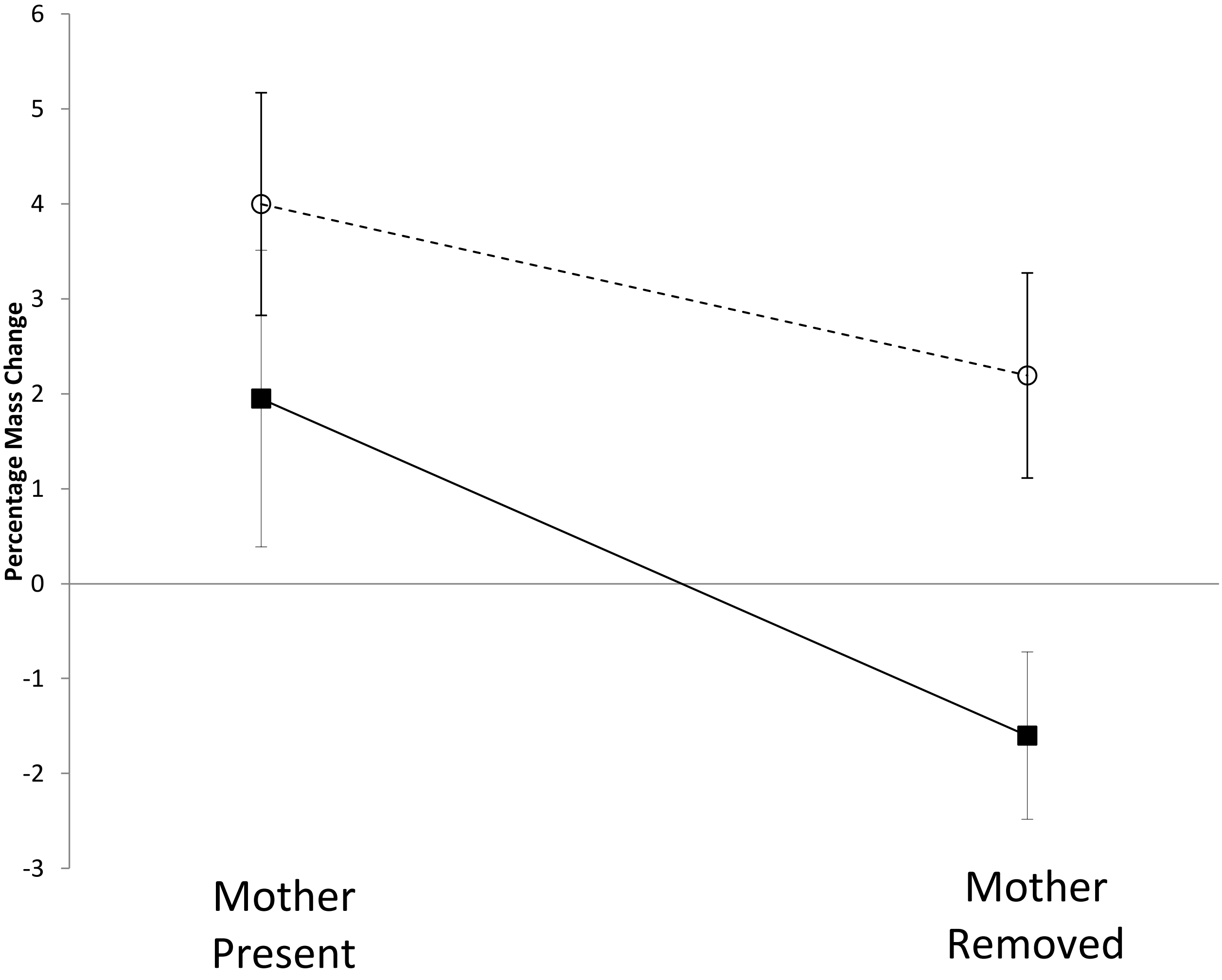

Figure 6.7: Relative mass change of chicks with (left) and without (right) the mother. Older chicks (open circles) fared better than their younger siblings (shaded squares) when the mother was removed (LME: Maternal presence, $F_{8,9}$ =5.50, p = 0.047)

Chick behaviour also changed (Figure 6.8). Aggression was very low when the mother was present, with only 4 out of 9 nests experiencing any aggression at low rates of an average of 0.89 bouts/hour ± 0.42. When the mother was removed, all 9 nests experienced aggression at a rate of 6.69 bouts/hour ± 1.52. Provisioning rate had no influence on aggression (LME: Biomass delivery rate, $F_{7,9}$ =0.01, p = 0.90, LME: Item delivery rate, $F_{7,9}$ =1.02, p = 0.35). Both junior and senior chicks became aggressive, though senior chicks initiated more aggression (Figure 6.8)

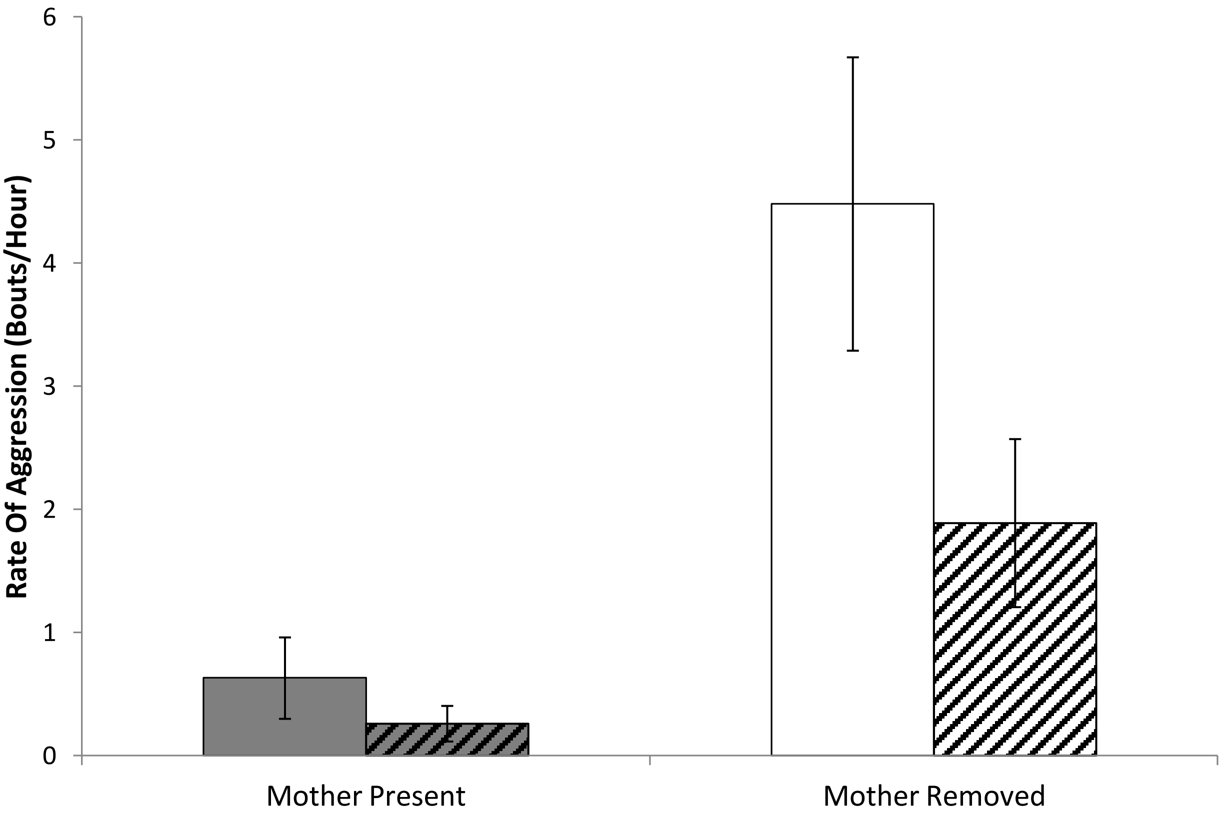

Figure 6.8: Rates of aggression in nest when the mother is present (shaded bars) and when she has been removed (white bars). Aggression increased when the mother was removed (LME: Maternal presence, $F_{8,9}$ =3.51, p = 0.005). Junior (hatched bars) chicks were less aggressive than senior (empty bars) chicks (LME: Chick Rank, $F_{1,16}$ =6.67, $p < 0.001$)

6.5 DISCUSSION

The natural observations of resource partitioning appear to show a difference in parental investment optima between breeding females and their chicks. When the mother was in the nest, she divided food between her brood roughly equally. After her departure, chicks divided the food very differently, with older, larger chicks taking the majority. Levels of aggression were much higher after the mother leaves the nest. This suggests that scramble competition between chicks may become more important when parental control of provisioning is removed. While these observations hint at conflict within the family, on their own they do not explicitly test POC, they merely hint that the game changes when the mother leaves. Several problems, outlined by Mock and Forbes (1992) have persisted in the interpretation of empirical studies of POC. Firstly is the currency in which parental investment is measured. The incremental costs to parents and benefit to chicks of each food item will change as chicks grow. It may be that larger chicks taking a greater share of food is less costly to younger siblings when both are older after the mother has left. At this stage developmental rates may have changed and the mother could supplement paternal feeding if needed. Secondly, parental investment optima are based on a variety of factors that influence an individual offspring’s fitness. Mothers can control the size asymmetry of their brood when they leave the nest so can control the competitive ability of both chicks. The fact that the larger chick could outcompete its younger sibling may not demonstrate conflict at all but simply that the mother established a hierarchy based on the food available and the quality of each chick.

The experimental removal of breeding females attempts to address these ambiguities. Firstly by conducting both the removal and control in a random order in quick succession, differences in the value of parental investments are controlled. We simply look at the share of food taken by the larger chick. When the mother was present she divided food equally among the brood. When the mother was removed, the older chick took a larger share. This demonstrates that the parents distribute resources differently to how the offspring would, irrespective of the actual value of that investment. Importantly the preferred parental resource distribution is demonstrated rather than assuming an equal distribution (Godfray 1995). This addresses the second large difficulty of calculating the value of each chick to its parents. The paired nature of the experiment with treatments in a random order means the value of the primary and secondary chicks do not change between treatments. The same older chick who took the majority of food when its mother was removed, only received an even share when the mother is present.

Older chicks’ mass increase relative to their younger siblings was greater when the mother is absent. This suggests that any conflict occurring over resource allocation could have important consequences for long term condition and future reproductive success (Monrós et al 2002).

Chick behaviour was highly dependent on maternal presence. Just as in the natural observations, aggressive interactions between chicks increased when the mother was removed. This demonstrates that sibling competition is much more important when the chicks are alone in the nest. Whether breeding females actively reduce aggression or chicks simply change their behaviour due to the changed provisioning game is unclear. Aggressive interventions such as those displayed in moorhens (Leonard et al 1988) were not observed. Females did though spend considerable time brooding the chicks which may have reduced their opportunity for aggression.

With a larger sample size it may have been possible to examine whether chick condition influences maternal provisioning decisions. If larger chicks are at an advantage when the mother departs then mothers could even up the contest between offspring by preferentially feeding young that are much smaller than their larger sibling. This could be complex to investigate as chicks would require different feeding rates at different ages (Hussell 1972) and maternal choices over brood reduction depending on environmental conditions could change competitive asymmetries. Krebs & Magrath (2000) demonstrated that Crimson Rosella (*Platycerus elegans*) mothers will favour junior chicks when conditions are good, maximising their reproductive output. However when conditions are poor and the whole brood is underfed, mothers will switch to favouring senior chicks, consistent with the idea of strategic brood reduction.

Since chicks reach an asymptote of growth females can even up the contest without preferential feeding. By staying in the nest longer, mothers can allow smaller chicks to catch up with their older siblings. Indeed Chapter 5 demonstrated that females with more asynchronous broods stay longer in the nest, irrespective of other factors. The experimental removal of females hinted at this role. After females left naturally, elder chicks took around 60% of feeds (Figure 6.1 & Figure 6.2). However when females were removed prematurely, senior chicks took between 80% and 90% of food (Figure 6.6 & Figure 6.5). This is supported by the observation that when mothers left naturally, junior and senior chicks were equally aggressive but when mothers were removed prematurely, senior chicks were more aggressive than their younger siblings. The mother staying a little longer in the nest could make a massive difference to the competitive abilities of junior chicks.

Several other breeding systems feature similar situations, where control passes from the parents to the offspring. For instance, in many raptor species, the female will stay on the nest throughout incubation and the first weeks of the nestling period (Newton 1979). The female is not confined to the nest as in hornbills but nevertheless remains on the nest, relying on the male for food for both her and her brood. While on the nest, females divide up food items and feed the chicks. Similarly to a confined female hornbill or most systems of parental care, the parents are ultimately in control of which chicks are fed. Females will however leave the nest before the chicks are ready to fledge. Often, when chicks have become large, parents feed simply by dropping carcasses into the nest, sometimes without landing. Now competition between chicks is unregulated and if there was a distinct hierarchy, subordinate chicks would suffer. However as with hornbills, most brood reduction occurs while the mother is still present (Newton 1979). This highlights the importance of distinguishing behavioural squabbles from genuine POC. Females can ensure that when they pass direct control of resource distribution to the offspring, the results of the ensuing competition should fit with maternal interests.

Brood hierarchies exist in many systems of parental care. They are well known in birds (Mock & Parker 1997), but also occur in many other taxa providing opportunities to investigate the extent of POC. While mammalian littermates are generally born simultaneously, there is still potential for distinct brood hierarchies. Compared to asynchronously hatching avian broods, mammalian litters appear simultaneous but small time differences do occur and these may be enough to generate hierarchies. In the spotted hyena (*Crocuta crocuta*), twin siblings are generally born about an hour apart and the elder twin will attack its younger sibling within minutes of birth (Smale et al 1995). In the wild, spotted hyena give birth at the mouth of a burrow made by a smaller mammal such as a warthog. These burrows are too small for mothers to fit down, so mothers only interact with the offspring when they emerge from the burrow. Dominant siblings can deny their subordinates access to the mouth of the burrow, monopolising suckling opportunities when the mother arrives. If conditions are good, the pups are moved to a communal den at between 1 and 6 weeks of age, when they will interact with their mother and other group members constantly. By this stage however, distinct dominance hierarchies are already established between siblings. Smaller siblings bear extensive scars and many subordinate siblings are either killed by their twin (Frank et al 1991) or have starved to death, denied access to the burrow mouth and food from the mother. If conditions are bad however, pups can remain at the natal den for several months (Mock & Parker 1997). This system bears many similarities to the hornbills, though the timing is reversed. Early on, mothers have little control over sibling rivalry, being physically separated from the conflict, though as pups emerge or are moved to a larger den, mothers can potentially intervene. Indeed, White (2008) demonstrated that when sibling aggression occurs above ground, the mother will physically intervene, generally favouring the subordinate pup, sometimes even carrying the subordinate away from the dominant so that it can suckle unmolested. Investigating choice of den site and timing of moving the pups to a communal den could provide great insight into POC in spotted hyenas.

This study for once gives offspring a chance to ‘win’ the evolutionary conflict with their parents. As such, the changes in chick behaviour and resource partitioning clearly demonstrate that phenotypic parent offspring conflict is occurring. Such a short term study cannot demonstrate what effects such conflict will have on lifetime fitness of either the chicks or parents. This leaves the goal of testing genetic POC unfulfilled. However demonstrating that parents and offspring actually differ in the distribution of parental care is a big advance in our understanding of intrafamilial dynamics. For once, field results have shown that offspring can gain some “handsome concessions” from their parents.

Chapter 7

General Conclusions

This final discussion briefly reviews the main findings of the thesis. The implications of the findings are discussed along with the great future potential for research on hornbills.

According to Plutarch (Perrin 1914), in ancient Rome vestal virgins that broke their vow of celibacy suffered a cruel punishment, known as immurement. With great ceremony, the unfortunate girl was taken to a stretch of the city wall by the Colline gate. Here a small room with a bed, lamp and a little food was prepared beneath the wall. The girl would enter and the entrance sealed after her, never to be opened again. The sealing of hornbill nests has often been regarded in a similar light. The female, incarcerated in the nest, sealed in and stripped of her wings, forced to survive on the food brought by her mate. The findings in this thesis support the increasing consensus that female hornbills are in fact anything but passive victims. Females sealed the nest themselves, gaining many advantages by doing so. While females started to seal their nests as soon as they enter, they delayed egg laying for around 6 days, and only finally commit to breeding by moulting their wings after 18 days. This gave female hornbills a chance to assess male ability in safety before fully committing to breeding. A sensible poker player does not go ‘all in’ without being confident of winning the hand. Female hornbills similarly gradually increased their commitment to breeding. If males are killed, abandon or simply do not come up to scratch, females could abandon breeding with minimum cost.

By eating eggs and chicks, females could recoup some of their energetic investment. Cannibalism by the female is a very effective strategy for controlling risk when the future is uncertain (Dall & Johnstone 2002). Not only is cannibalism of chicks an efficient extension of brood reduction, removing chicks quickly and preventing infection from rotting chick carcases, cannibalism of either chicks or eggs allows females to get back some energy to improve their own condition. Males however do not have this luxury. They cannot directly control clutch size or brood reduction. Cannibalism of offspring has been recorded in one other hornbill species (Chan et al 2008), though not to the same extent as here. Due to the difficulty of examining and recording hornbill nests, filial cannibalism may be common but unrecorded for many hornbill species. With approximately half of the world’s hornbills declining in the wild (IUCN 2012), examining the causes of filial cannibalism could be useful for conservation. Harvesting of later hatched chicks from threatened populations could provide a sustainable source of individuals for captive breeding (eg Kemp et al 2007).

By sealing herself in the nest the female also forces the male to care. The male is solely responsible for provisioning the female and the brood. If males abandon, are killed or cannot feed enough, females alone simply cannot raise a brood. Chapter 3 describes the failure of the only male in the study that attempted to breed while courting a second female.

Nest sites were limited so a male would generally have to wait for his current female to leave the nest before attempting to breed again, by which stage the breeding season would be coming to an end. Many socially monogamous species suffer lower breeding success if one partner is removed (Clutton-Brock 1991). However, only few species, such as some raptors (Newton 1979) are as constrained to monogamy as the hornbill. Single parent care after female fledging would not cause total failure, as males raised broods alone, either when female help was low or in the one case of a female dying in the nest. Presumably females could also finish raising nestlings alone, once out of the nest. Males would still be constrained from raising a second brood until the current brood fledged by a lack of nest sites. Of course, such reliance on male only care for much of the nesting period makes hornbills particularly susceptible to poor or variable conditions. The hornbills on the study site suffered in two of the seasons because of extended dry periods between in November and December even though rains late in both years meant that neither season was particularly dry. This limits nest sealing to either long lived species or species that breed in high quality environments.

Sealing the nest also protects females from intraspecific brood parasitism, a large risk in a population with limited nest sites (Clawson et al 1979). The high extent of cooperative breeding in hornbills (Kemp 1995) would also raise the potential risk of subordinate female breeding and sealing the nest would allow dominant females to control maternity of all offspring. Very little is known about cooperation in any hornbill species. Given the importance of limited control and reproductive concession in cooperative breeders (Clutton-Brock 1998), hornbills could provide an alternative approach to the study of cooperation.

If either parent is exploited by the sealing of the nest, it is more likely to be the male. The nest seal limits male information about the nest contents. Whenever the male arrives at the nest, the female is up by the nest entrance, ready to receive the provisions he is carrying. Males are forced to rely on vocal signals from the female for any knowledge about the contents of the nest. In two breeding attempts this resulted in the male feeding a nest that contained only the female after she had eaten the entire brood.

Chapter 4 demonstrated that females can communicate need for nest materials and food to their mates. Further experimental tests of begging by both females and chicks could reveal more details about intrafamilial communication. Since females appear to use similar calls to signal for two very different resources, food and nest lining, hornbills could prove interesting subjects for the study of honesty in communication. Females could exploit males by demanding extra food but begging for bark is potentially very different. Provisioning food provides a direct benefit to the female and is costly to the male. Bark on the other hand is plentiful and useless to the male outside of the nest so delivery has little cost. Females gain no direct benefit from bark, since it merely raises the floor of the nest, allowing chicks to reach the nest entrance when their mother fledges. While females could benefit energetically by demanding extra food at a cost to males, both males and females get equal benefit from bark in the nest.

The mother's role in communicating the needs of chicks could also be interesting. Females continued to beg after chicks hatched. This may either be to communicate her hunger or pass on the needs of the chicks to the male. Chick satiation experiments were trialled (n=6) and females appeared to reduce their begging after chicks were satiated. Since there is no competition for food between mothers and chicks as mothers control the nest entrance, this hints that chicks may be begging to the female, who in turn passes the signal to the foraging male. Such a complex system has high potential for cheating and would be a good model for investigations of honesty in communication.

No nests out of 67 breeding attempts were predated in the study, suggesting that hornbill nests are very safe indeed. Since most of the breeding attempts were in nest boxes, the lack of predation could be an artefact of nest box safety. The findings however fit with previous research on natural nests (Kemp 1995), though it would be interesting to investigate the rates of predation of sympatric cavity nesters in the Kalahari such as Red Billed Woodhoopoe and Lilac Breasted Roller. The effectiveness of the seal alone could be tested by the use playbacks and dummy nestboxes. Playbacks of chick begging to attract predators could be transmitted from paired nests, one sealed and one open, containing a food source (such as eggs) and a camera, recording if a predator broke into the nest and how long it took to do so. Similar protocols have been used to test the potential predation cost of vocal begging in other species (Haskell 1994).

Only one nest was inundated during a heavy rain storm. The seal may act to reduce the damage caused by rain, a major cause of nest failure in other cavity nesters (Radford & Du Plessis 2003). The effectiveness of the seal in weatherproofing the nest could be tested using a similar protocol to that used by Radford and Du Plessis (2003). Pairs of empty nests could be placed side by side, one with a seal and one without and the amount of rain in the nest at the end of the shower recorded.

The nests are not completely impregnable. Predation has been recorded in other studies (Kemp1995). When threatened, chicks emitted a piercing scream that seemed to attract parents. The role of the scream was tested using playback, comparing screams with the similar sounding 'acceptance screech' (Kemp 1995) given by chicks and females on receipt of food and a control noise of a loud broadband territorial call of a common sympatric bird the Crimson Breasted Shrike (*Laniarius atrococcineus*). Parents (n = 8 pairs) did indeed have higher nest attendance when alarms were played than when ‘acceptance screeches’ were played. This may however be due to each parent perceiving an increase in feeding from the other when acceptance screeches are played and decreasing their own feeding rate (McNamara et al 1999). The shrike playback was intended to provide a neutral control. Unfortunately, what was believed to be a territorial call was in fact perceived as an alarm call by the hornbills. Further playbacks to both foraging hornbills and Southern Pied Babbler revealed that both species responded to the call like an alarm call.

Nest sealing does not always favour the mother’s interests. Chapter 6 revealed that when chicks resealed the nest, females were deprived of choice over resource allocation. Females therefore timed their departure so that smaller younger chicks had developed sufficiently to compete with their older, larger siblings (Chapter 5). This change in provisioning strategy seemed to cause behavioural changes in the chicks. Intrabrood aggression was absent while mothers were in the nest but common when they left or were removed. Provisioning was no longer decided by begging to the parent but by physical interactions between chicks. Chicks however still continued to beg. Begging from a sealed nest would not just be an individual signal but would provide benefits for all nestmates. Hornbill nests could therefore be a great system for testing theories of competitive versus cooperative begging. While the mother is present, begging can be competitive. However once the mother leaves, begging has no competitive role. Chicks should switch from escalatory begging (Godfray 1995) to compensatory begging (Bell 2007). Experiments to test this were trialled in the 2010-2011 season though sample size was limited (4 nests) due to the lack of nests with multiple chicks.

Hopefully modern technology will continue to help provide insights into previously unknown aspects of ecology and behaviour. This study provides a detailed account of only one of 54 species of hornbill. While the Southern Yellow-Billed Hornbill is ecologically similar to many others in its genus, hornbills range in form and function as much as any other order of birds. It would be fascinating to investigate how the peculiar strategy of nest sealing persists across diverse environments and breeding systems. Nest boxes are cheap and easy to construct and digital recording is becoming ever more compact and affordable. Comparative studies of different species of hornbill could provide data valuable for both conservation and our understanding of the evolution of family life.

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Appendix: Contents of supplementary CD

The attached CD contains examples of video recording collected during the 3 years of study. They are intended to supplement the descriptions provided in the body of this thesis. Files should be viewable using windows media player. If files cannot be viewed, VLC media player can be downloaded for free from http://www.videolan.org/vlc/index.html.

Video 3.1: Female hornbill sealing the nest
Video 3.2: Cannibalism of live chick
Video 3.3: Cannibalism of dead chick
Video 4.1: Female receiving food
Video 4.2: Female receiving bark
Video 6.1: Aggression between nestmates