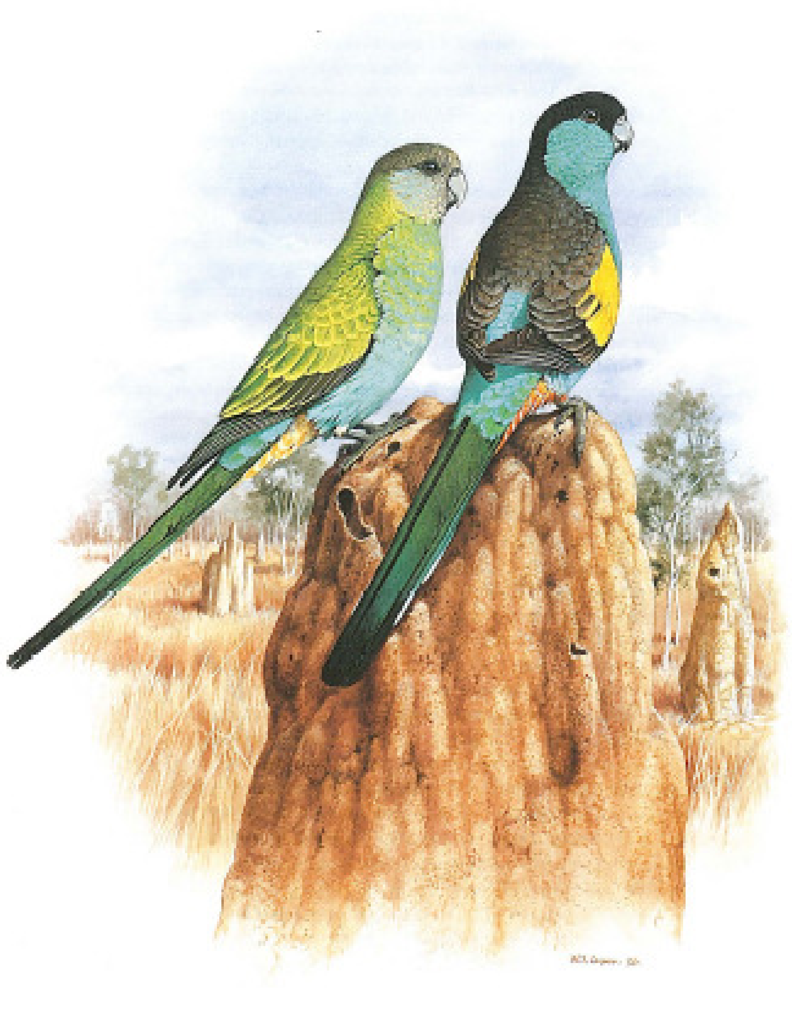
Ecological Associations

of the

Hooded Parrot (*Psephotus dissimilis*)



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A thesis submitted for the Degree of Doctor of Philosophy of

The Australian National University

April 2009

DECLARATION

The research in this thesis is entirely my own work except where due reference is given in the text. Chapter 4 is co-authored with Edward D. Edwards, Penny D. Olsen and Stephen T. Garnett. Chapter 5 is co-authored with Penny D. Olsen and Stephen T. Garnett. However, I am the principal contributor to all aspects of the work, none of which has been submitted for a previous degree.

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Stuart J. N. Cooney

April 2009

DEDICATION

This thesis is dedicated to my family. To Eliza who is as old as the PhD, to Georgiana who started her school life in Canberra and to my wife Sam. My champion: always encouraging, always loyal and always convinced in my ability to get here, especially when I wasn’t. It seems that there really is no end to her willingness to make me happy. This final act of my PhD is dedicated to those three people who shared the journey most intimately and without whose support it could not have been done.

ACKNOWLEDGEMENTS

A PhD, for better or worse, is a collaborative process. In this case, the amount of support from the University, family and friends has been amazing, and it has been upon the shoulders of this support that I have produced this dissertation. I could not have done it without them. So, I will take a few paragraphs to single out and thank some people who have made significant contributions to this achievement.

Firstly, to Dr Penny Olsen, for her warm reception to the enquiries of a naive sales rep., the conception and genesis of this great project (it ticked my project requirement boxes of a cool bird in a cool location!), her open door policy for all my little concerns and her constant attention to detail. I hope that she is as happy with the results as I am. Prof. Andrew Cockburn similarly welcomed me to ANU, despite my humble academic beginnings and was always there right when I needed him with wisdom and insight (not before or after, but right when I needed him!). Prof. Stephen Garnett has similarly been there to help when I called for it. His calm and enthusiastic assistance early in the first field season was a defining moment in this project. My final supervisor, Dr Rob Heinsohn, has not spent hours of his time on me or my project, and may even feel a bit guilty about that, however his words of encouragement, just when I needed them (pre-field season pep-talks), were immensely important to me and I am delighted to have had him on my supervisory panel. Dr Ted Edwards has also been a keen, if unofficial, member of the project. His enthusiasm for moths, in particular the identity of Stuart's Moth *Trisyntopa neossophila*, has been a great boon to the project. Dr Terry Neeman helped me, in many meetings, with the analysis of chapter VII, which was complicated and beyond my statistical ability.

After a shaky start in the first field season, for the second field season, I recruited some helpers. Kathryn Smith, Ona Alminas, Isobel Booksmythe, Murray Hunt (the self-appointed entertainment coordinator—who excelled by providing distraction and entertainment while I fussed over the all-consuming project and its dramas) and Richard Milner. I had no idea how I would go living with four young people (sorry Murray), up to 15 years my junior, but it was great. Their hard work, attention to detail and zeal for the project made the second season the success it needed to be. Sure, Katy lost pens in the field and cut herself all the time. OK, so Ona got lost, either accidentally or on purpose (what was nest CAT037BUNT all about?). Yes, occasionally some of Iso's food was a touch gritty and she was incredibly rude to me. Murray may have come and gone and come and gone (he did have a job to maintain after all!). And, Richie… well, if I had a brother, hopefully he would be like him. If I had to choose another set of vollies for a project, I would be doing extraordinarily well to get another group as good as them!

Support has also come from other quarters… such as Happy House! Now long dismantled, Rachel, Leeann and Michelle, and their male sidekick Golo, welcomed me to ANU when it was all new and shiny and even let me share their coffee! Rachel and I shared a supervisor, which was a great help to me, and our discussions and her encouragement were invaluable. Similar talks with Leeann and Michelle also helped me formulate and work through ideas, focus on the important things and convinced me that I wasn't too bad a scientist. Fellow birder Golo was a constant source of encouragement, good ideas, preposterously harsh editing and valuable downtime (I will always happily recall that we ticked his 500th Australian bird together!!). I speak of these people in the past tense because they all moved on to bigger and better things and it was only then, in the final stages of my project, that I realised how truly important they have been to me. I miss them already, but know that I have made life-long friends with the members of the Happy House coffee consortium.

A range of other people provided smaller contributions to the project that were no less important in their own way. My thanks go to: Gay Crowley, Sarah Pryke and Louise Warburton for helping with the reccy way back in 2005 and being the first people to put their hands in parrot tunnels and losing skin in the process of enlarging them for me to put my hands in!; Judith Scarl and Dan Gowland for letting me handle their parrots; Jade Irwin and Jak Andrews, the managers of Manbulloo Station, where I worked (paradise on earth!) and Brian, Stephanie, Bronwyn, Bob and Zach, for their hospitality at Manbulloo Homestead, my home for 4 months a year; Mike Reed, the previous hooded parrot guru, for sharing his advice and experiences; fellow entomologists; Michael Braby for moth discussions, Dave Spratt for analysis of the blood

smears and David Yeates and Thomas Pape for maggot discussions and identification; Chris Hayes, Nadeena Beck and Rachel Sims for helping a non-chemist follow the PCR recipe and showing me my first DNA!; Christine Donnelly and Ann Cowling from the ANU Statistical Consulting Unit who taught me (almost) everything I know about stats; the people at NARU (Lyle, Andrew and, in particular, Helen Sainsbury) for always being accommodating, helpful and friendly, even when I was completely disorganised; everyone at the school of Botany and Zoology from the guys in the workshop for the burrow-scopes and computer expertise; to Madeleine Haag, Audra Johnstone, Karen Scholte, Leigh Prado and Garry Mayo for patience when I had inane questions to ask (for a second time!) and couldn't just do things for myself; and, to all the staff and students of BoZo that made me feel so welcome (and especially the purple shins boys and girls); Bill Cooper for giving me permission to use his beautiful painting of some beautiful birds; and finally, the staff at the ANU, Chifley and CSIRO, Gungahlin libraries for prompt and courteous assistance.

Money is an important issue in any project (my project expenditure exceeded $30,000!). Therefore, I want to acknowledge the generous support of the philanthropic organisations that support this kind of science and whose small contributions make a huge difference to struggling students. I was lucky enough to receive contributions from: the Trust of the Late Violet Winifred Scott ($12 100); the Norman Wettenhall Foundation Grant ($4 400); the Cayley Memorial Scholarship ($2 000); the Birds Australia, Stuart Leslie Bird Research Award ($1 000); the Joyce Vickery Scientific Research Fund ($900); and the Ethel Mary Reid Award ($750). Throughout the project, my wage was provided by an Australian Postgraduate Award sponsored by the Commonwealth Government.

This work was conducted under permits from the Australian National University Animal Experimentation Ethics Committee (Proposal F.BTZ.87.05), the Northern Territory Parks and Wildlife Commission (Permit no. 22857) and the Australian Bird and Bat Banding Scheme (Authority no. 721).

My final thanks go to four special people that must be held accountable for me taking this course. To Dr David M. Watson, who started my research career and then told me that I could do anything that I wanted to in pursuing my PhD ambitions. His infectious enthusiasm for doing science played a huge part in my decision to continue in higher education. To my parents; Nolene and Norm Cooney. It has taken a while, but it seems that all those happy weeks camping in the National Parks of Victoria have finally infected me, and infected me in a big way! Who'd have thunk it? And finally, to Sam. Who always believes in me, always supports me, always puts up with me, and will always be there for me.

ECOLOGY

Comprising the relation of the animal to its organic as well as its inorganic environment, particularly its friendly or hostile relations to those animals or plants with which it comes in contact.

Haeckel, E. (1870). Uber entwicklungsgang und aufgabe der zoologie. *Jenaische Zeitschrift Für Medizin Und Naturwissenschaft*. **5**, 353–370.

THESIS ABSTRACT

Interactions between nesting birds and invertebrates are a common, yet poorly understood ecological phenomenon. Many of these types of interactions are close and prolonged, and therefore potentially critical to one or both of the species involved in the interaction. However it is unusual for the nature of the interaction to be evaluated in a manner that reveals the impact of the relationship on both parties to the interaction. This study examines two relationships between nesting birds and invertebrates, both of which involve the hooded parrot (*Psephotus dissimilis*), a small grass parrot that inhabits the tropical savannas of northern Australia.

The field-work for this project was conducted over two parrot breeding seasons in 2006 and 2007 near Katherine, Northern Territory, in the Australian dry tropics. In chapter II, I present data on the breeding biology of the hooded parrot as background for the study that follows. Nest building commenced in January, with peak activity in February and the last chicks fledged in April. Fifty three active nests were located. The mean number of eggs laid per nest was 4.5 (s.d. ± 0.9), of which 3.0 (± 1.79) hatched and 2.0 (± 2.0) fledged. Clutches were laid asynchronously over a period of a week and chicks remained in eggs for 18.6 (± 1.95 days). Chicks were 29.2 (± 2.9) days old when they fledged from the nest. These data are typical for Australian parrots.

In chapter III, the unusual nature of the parrot's nest site is examined. Many species of bird nest in natural cavities or those they excavate. Whilst cavity nesters as a whole experience increased nesting success, the greatest success is experienced by species that can excavate their own nests. Certain arboreal cavity nesters, such as woodpeckers, require extensive morphological adaptation for this behaviour, but this has not occurred in Australia, despite competition among birds and a suite of arboreal mammals for naturally occurring cavities. Some species, however, have adapted their behaviour to make use of substrates that are not as hard as wood. Hooded parrots excavate nests in terrestrial termitaria, releasing them from competition for limited arboreal cavities. However, I show that only termitaria with a high level of termite activity, and which are more than two metres tall, are suitable, and that the parrots exhibit a strong preference for the cathedral mounds of *Nasutitermes triodiae*. Nests placed in highly active mounds had a significantly higher success rate than those in mounds where activity was somewhat lower, suggesting that the behaviour is adaptive.

The thesis then shifts focus from the parrot to its nest symbiont, first describing the species involved in the interaction in chapter IV, and then its behaviour in the nests of hooded parrots in chapter V. *Trisyntopa neossophila* sp. n. (Lepidoptera: Oecophoridae) was reared from the nest of the hooded parrot and described using morphological characters. Aspects of its biology are reported and similarities to the biology of *Trisyntopa scatophaga* found in the nests of the golden-shouldered parrot (*Psephotus chrysopterygius*) are discussed. The possibility that a moth was associated with the extinct paradise parrot (*Psephotus pulcherrimus*) is considered in the light of the phylogenetic relationships between the parrots.

Trisyntopa neossophila is an unusual moth whose breeding cycle is shown to be closely synchronised with the hooded parrot. *T. neossophila* is one of three coprophagous, nest dwelling moths in the genus *Trisyntopa*. True coprophagy is rare in the Lepidoptera, although some species occasionally consume faeces to gain rare nutrients. *T. neossophila* lays its eggs in the nest of hooded parrots so that larvae hatch in synchrony with the hatching of the parrot's eggs. The larvae spend their larval period in the nest and exclusively consume the excrement of the nestling parrots. When the parrot chicks fledge, the larvae move to the walls of the nest cavity to pupate, emerging the following wet season to repeat the process during the next parrot breeding season.

With a description of the ecology of both species involved in the nesting symbiosis, chapter VI reviews the literature surrounding other interactions between nesting birds and invertebrates. A large number of birds are shown to nest in, or in close proximity to, structures made by invertebrates and avian nesting material provides a reliable shelter for many invertebrate species. However, the nature of such relationships has rarely been experimentally demonstrated. I propose that in order to understand the nature of these relationships they need to be explored within the theoretical framework of community ecology. Putative commensal and parasitic relationships have all been documented in the bird/invertebrate nesting literature, yet researchers, with few exceptions, repeatedly overlook the impact that these relationships are having on the invertebrate, at best assuming the nature of its impact, but more often ignoring its impact entirely. Here I present a framework for formulating hypotheses to ensure that the nature of the relationship can be identified. Only by explicitly stating the level of organisation at which the experiment is to occur (individual or population), identifying the net cost or benefit of the interaction, the range of conditions under which such costs or benefits would apply and the spatial and temporal context in which they apply, can an investigator expect to recognise and describe the often complex nature of these relationships.

While parasitic and commensal relationships between nesting birds and invertebrates are commonly reported, mutualisms between birds and invertebrates have not been reported. Despite this, candidates for this type of relationship exist. Chapter VII uses the framework outlined in the literature review (chapter VI) to experimentally examine the relationship between the hooded parrot and *Trisyntopa neossophila*. By manipulating the populations of moth larvae in a sample of hooded parrot nests, we sought to establish the impact of the relationship on each species. The moth depends on the parrot for provision of shelter and a reliable food source. The parrot however, was neither benefited nor harmed by the interaction in terms of short term reproductive output or chick growth, although differences between the experimental and control nests were noted. The relationship between the hooded parrot and *T. neossophila*, at least during the study period, is therefore concluded to be commensal.

Collectively, the chapters of this thesis explore the complicated interactions between species. The dependence of the moth on the parrot and the parrot on the termite, demonstrate the importance of understanding interactions between species in a manner that reveals the impacts of the interactions, the range of conditions under which they would apply and the level of organisation at which they apply, as outlined in chapter VI. The dependence of the animals in this study on each other makes them more vulnerable to extinction than previously thought. Whilst this may not be immediately significant for the hooded parrot/*T. neossophila* system, which is thought to be secure, the ecologically similar system on the Cape York Peninsula, involving the golden-shouldered parrot and its nest attendant moth *Trysintopa scatophaga*, is vulnerable to extinction and subject to intensive management to ensure its persistence. This study brings new information to the management of the golden-shouldered parrots and urgently recommends increased protection for *Trysintopa scatophaga*.

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CHAPTER I

Ferdinand Bauer's hooded parrot painting: courtesy Natural History Museum

General Introduction

The overall aim of this thesis was to explore the ecological associations of the hooded parrot (*Psephotus dissimilis*). In particular, the focus of this research was to determine the nature of the nesting symbiosis between the termite mound nesting hooded parrot and a moth, reported to inhabit the nesting cavity of the parrot. Interactions between nesting birds and invertebrates are common and have been studied for more than 150 years (Gosse 1847), however such interactions are generally poorly understood, with little experimental evidence to support conjecture about their nature.

Further, the specialised nesting associations of this parrot, including the nesting symbiosis, coupled with its restricted range, make it vulnerable to extinction, as reflected in the fate of its nearest relatives. Therefore this project also examined the parrot's nesting requirements and breeding biology. To provide context, this introductory chapter summarises what is known of the taxonomic relationships and general ecology of the parrot.

Grouped with the broad-tailed parrots Platycercinae, in the family Psittacidae, the hooded parrot is one of five species of grass parrot in the genus *Psephotus* (Christidis *et al.* 1991; Collar 1997). The Platycercinae, consisting of the rosellas *Platycercus*, the ringnecks *Barnardius*, bluebonnet *Northelia*, red-capped parrot *Purpureicephalus*, swift parrot *Lathamus* and the grass parrots, is a group of parrots with its origins and highest levels of diversification in Australia (Christidis *et al.* 1991). The genus *Psephotus*, comprises the hooded parrot, golden-shouldered parrot (*P. chrysopterygius*), paradise parrot (*P. pulcherrimus*), red-rumped parrot (*P. haematonotus*) and mulga parrot (*P. varius;* Schodde and Mason 1997). The hooded, golden-shouldered and paradise parrots occur in northern Australia; they nest in terrestrial termite mounds and are consequently referred to as "Antbed" parrots. The red-rumped parrot and mulga parrot typically nest in natural tree cavities in southern Australia (Higgins 1999).

The hooded parrot is a small dichromatic parrot, approximately 28 centimetres long and weighing 40–55 grams (Higgins 1999). Male hooded parrots are chiefly turquoise in colour, with a black hood that extends to the bottom of the eye and back to a slate grey to grey-brown mantle. This colour is continued across the scapulars and down to the tail. The wing coverts are bright yellow on an otherwise almost black wing. The female is less brightly coloured, with a pale green mantle, wing coverts and head. The breast is pale turquoise, as is a cheek patch and female birds also have grey frons. In both sexes the vent is salmon in colour, with feathers edged in white, they have a pale grey bill, black eye and dark grey legs and claws. Immature birds look similar to female birds, although both sexes have a yellow bill.

The first formal description of the hooded parrot was published in 1898 by Professor Robert Collett, who described one male and three females shot by Dr Knut Dahl near Mary River in the Northern Territory (12° 16' S 131° 45' E) in 1895. Two earlier references to the hooded parrot, one by the botanist Robert Brown in 1802 and another by explorer Ludwig Leichhardt in 1845, were overlooked, so that despite the parrot being observed, collected and figured, the formal description was written nearly one hundred years after the birds were first discovered by Europeans (McAllan 1992). Barnard (1914 p. 46) too, claims that he was the first to collect this bird in 1896, however he "missed the honour of being the first to describe the bird" because he assumed that the birds were golden-shouldered parrots.

Uncertainty about the specific status of hooded parrots continued for many years, in part because Collett (1898) described the hooded parrot as having a chestnut rather than black crown and because of confusion with the golden-shouldered parrot. This led North (1909) to provisionally propose the name *Psephotus cucullatus* for some caged parrots he saw with black hoods collected from the same location as Collett's parrots. North further confused the issue by citing (Matthews 1917) and then repeating his assertion of the presence of both hooded parrots and golden-shouldered parrots in Arnhem Land (North 1909). The two species are now recognised as distinct species by most authors (Christidis and Boles 1994; Schodde and Mason 1997; Higgins 1999) with recent molecular analysis supporting this distinction (Garnett and Crowley 1995c). They are allopatric, with the hooded parrot found in the Northern Territory and the golden-shouldered parrot in northern Queensland.

Hooded parrots are endemic to the northern part of the Northern Territory (Higgins 1999; Garnett and Crowley 2000). The range extends north from the Larrimah district (15° 35 S 136° 35 E) to Arnhem Land (13° 00' S 134° 52' E) and east from the western shores of the Gulf of Carpentaria (12° 25' S 136° 35'

E) to the upper reaches of the Daly (13° 46 S 130° 42 E) and Mary Rivers (14° 28 S 132° 16 E, Robinson *et al.* 1992; Higgins 1999; Garnett and Crowley 2000; Forshaw and Cooper 2002). The parrot is most frequently reported from the Pine Creek and Katherine regions (Barnard 1914; Sedgewick 1947; Crawford 1972; Higgins 1999; Barrett *et al.* 2003)—where the field study for this thesis was conducted—however this may be an artefact of survey effort in these more easily accessible and well known areas.

The preferred habitat of hooded parrots is characterised as open woodlands and grasslands where termite mounds are present (Forshaw and Cooper 2002). Characteristic canopy trees of hooded parrot habitat include *Eucalyptus, Erythrophlrum* and *Buchanania* with an understorey of annual and perennial grasses and herbs, including spinifex (Reed and Tidemann 1994; Higgins 1999; Forshaw and Cooper 2002).

Hooded parrots are granivorous; their diet consists primarily of seeds from a changing range of perennial grasses, supplemented in the wet season by seeds from annual grasses and herbaceous species (Garnett and Crowley 1995a). The parrots feed on fallen seed on the ground, reach for seeds that are still attached to the grass and also climb grass stems to pick seed from spikelets (Garnett and Crowley 1995a). During times when the availability of fresh seed is reduced, parrots must utilise fallen seed that accumulates in the crevices created by rocky and pebbly terrains (Woinarski and Tidemann 1991). They usually drink early in the morning (Forshaw and Cooper 2002) or approaching dusk (SJNC pers. obs.), but may drink throughout the day (Heuman 1926).

Like other granivorous birds, hooded parrots feed in association with a range of birds, particularly in the wet season, however none more frequently than the black-faced woodswallow (*Artamus cinereus*; Garnett and Crowley 1995a). In 97% of feeding observations ($n = 29$), the parrots were feeding in the presence of woodswallows, which the parrots may use as sentinels to alert them to the presence of a predator (Garnett and Crowley 1995a). The woodswallows may therefore allow the parrots to concentrate on locating difficult to find food and to forage more efficiently, or they may allow the parrots to look for food in more dangerous situations (Garnett and Crowley 1995a).

As well as being closely related and therefore sharing many biological characteristics, the antbed parrots also share a trait that makes them particularly vulnerable to extinction. Each seems to be vulnerable to modern land management practices, and as a result, all have experienced population declines since European settlement (Fitzherbert and Baker-Gabb 1988; Garnett and Crowley 2000). Most dramatically affected is the paradise parrot. Not definitely seen since 1928 (Olsen 2007), this parrot is now considered extinct and has the dubious honour of being the only bird species of mainland Australia to become extinct in the last 200 years. The fate of the golden-shouldered parrot is only a little better. With a population of approximately 2000 birds and a highly restricted range, this species is the subject of intensive management to ensure its continued survival (Garnett and Crowley 1995b; Crowley *et al.* 2004).

It is thought that the range of the hooded parrot has contracted since European settlement. Historical records from Melville Island (11° 30’ S 131° 00’ E) in the north-east (Goodfellow 1935), Banyan Island (12° 14’ S 135° 07’ E) in the north-west (Barrett 1949) and near Borroloola (16° 04’ S 136° 18’ E) in the east (Barnard 1914), indicate that it was once more widespread. Despite this, Garnett and Crowley (2000) believe that the species is secure, with an estimated population of approximately 20,000 breeding birds throughout their current range. Trapping for aviculture is no longer considered to be a threat and where grazing is minimal and appropriate fire regimes are in place the parrot is relatively common (Garnett and Crowley 2000). Forshaw and Cooper (2002), however, postulate that because populations are increasingly fragmented and that certain fire and grazing regimes may reduce the available food, hooded parrots may not be secure (see also Fitzherbert and Baker-Gabb 1988). More work is required to establish population trends in this species, especially in light of the fate its two most closely related congeners, the golden-shouldered and paradise parrots.

By excavating their own nests in termitaria, the three antbed parrots are primary cavity nesters rather than secondary cavity nesters as are most parrots worldwide (Collar 1997). This is a potentially significant strategy to allow them to nest in areas where there are no tree holes and/or to free them from competition with tree-nesting parrots and other species. In many habitats worldwide, cavities formed through natural processes are a limited resource for breeding birds (Newton 1994; Aitken and Martin 2004) and in some systems, because of this limitation, primary cavity nesters are more successful than secondary nesters (Johnson and Kermott 1994). Furthermore, primary cavity nesters can exploit territory that may be unavailable to secondary nesters, potentially making primary cavity nesters less vulnerable to changes in their habitat (Martin and Eadie 1999). This seems not to be the case with the antbed parrots, which, as stated above, have all declined in range. However, despite being primary cavity nesting birds, a shortage of suitable nests sites may yet restrict the growth of the antbed parrot populations (Crowley *et al.* 2004). If this were so, it may be that suitable termite mounds are not in fact abundant in the habitat of the respective parrots, despite appearances to the contrary. This possibility is addressed in chapter III.

Another peculiarity of the nesting ecology of the antbed parrots is that they nest with a moth. This behaviour was first noted in golden-shouldered parrots in the 1920s (White 1922). The wildlife collector and ornithologist William McClennan described moth larvae living in the nest cavity of golden-shouldered parrots, eating the fallen excreta and cleaning the excreta from the feet and feathers of the parrots, resulting in a clean nest and clean nestlings (Campbell 1924). Since then, this extraordinary behaviour has been regularly noted. A similar relationship between hooded parrots and a moth has also been reported but was thought to be less common. Whilst a description of this behaviour appeared in the literature in the early 1980s (Hutchins and Lovell 1985) and has been cited by various texts concerning parrots (Higgins 1999; Forshaw and Cooper 2002), there have been no studies of the relationship between bird and moth, there were no specimens of the moth lodged at any museum in Australia (T. Edwards pers. comm.) and the species involved remained unknown.

Despite moths being found in nearly all wild nests of both hooded (this study; see chapters IV, V and VII) and golden-shouldered parrots (Garnett and Crowley 1992), the nature of the relationship was unknown. Potentially, the association could be mutual (both species gain something from the relationship), commensal (only one member of the relationship benefits, while the other is unaffected) or even parasitic (one member benefits to the detriment of the other).

Given the high proportion of nests that have moths in them, it is reasonable to expect that over the long-term there are benefits to both the parrot and the moth, however this remains unproven.

While mutualisms are well known in the natural world, indeed critical to the functioning of many natural systems, most consist of an animal–plant, animal–bacteria or a plant–bacteria pair (Begon *et al.* 1996). Far fewer truly two-way relationships are known between two animal species. Bird–insect relationships are generally portrayed as parasitic or predatory (see Hindwood 1951 for a review). Therefore the potential for a mutual relationship warrants close examination and provides an opportunity to detail the attributes of such a relationship. Chapter VII describes the results of an experimental investigation of the relationship over one season.

There are also important conservation implications for determining the nature of the parrot–moth relationship. Plans for the reintroduction of the endangered golden-shouldered parrots to parts its former range, on the Cape York Peninsula, have been proposed to the Australian Government. Before this occurs, it is vital that the nature of the relationship between the moth and the parrot is understood. Should the relationship prove to be mutualistic, it will be important that moths are also involved in any plans for relocations or reintroductions.

This thesis comprises eight chapters focused on the breeding ecology of the hooded parrot and its nest attendant moth. Chapter II reports on the breeding biology of hooded parrots, including the outcome of nesting attempts monitored during this study, and provides a baseline for many of the subsequent chapters. Chapter III examines the relationship between nest site characteristics and nesting success. To shed light on the question of the availability of termitaria suitable for nesting, nest-sites used by the parrots were compared to a representative subset of all termitaria in the study area. The thesis then explores the parrot’s relationship with the moth. The new moth species involved in the interaction is described in Chapter IV, and aspects of its ecology and life cycle in the nests of hooded parrots are detailed in Chapter V. A literature review (Chapter VI) follows that explores the myriad interactions between nesting birds and invertebrates and concludes with a proposed theoretical framework within which such interactions should be described. Chapter VII reports on an experimental attempt to determine the nature of the relationship between the moth and the parrot. Finally, Chapter VIII draws the disparate threads together to examine the implications of this research for our understanding of avian nesting ecology generally and specifically for the conservation of the hooded parrot (and by analogy, its congener the golden-shouldered parrot) and recommends fruitful areas for future research.

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CHAPTER II


Photo: S. J. N. Cooney

Breeding biology of the hooded parrot

(*Psephotus dissimilis*)

Abstract

This study examines the breeding biology of the hooded parrot (*Psephotus dissimilis*), a termite mound nester, near Katherine, Northern Territory, in the Australian dry tropics, over two breeding seasons, 2006 and 2007. Nest building commenced in January, with peak activity in February and the last chicks fledged in April. Fifty three active nests were located. The mean number of eggs laid per nest was 4.5 (s.d. ± 0.9), of which 3.0 (± 1.79) hatched and 2.0 (± 2.0) fledged. Clutches were laid asynchronously over a period of a week and chicks remained in eggs for 18.6 (± 1.95 days). Chicks were 29.2 (± 2.9) days old when they fledged from the nest. These data are typical for Australian parrots. This research contributes to our growing, yet limited understanding of wild parrot populations.

Introduction

Parrots (family Psittacidae) are the third largest non-passerine bird family (Higgins 1999). They are found on all continents, except Antarctica (Collar 1997), with a bias towards tropical latitudes (Higgins 1999). Parrots are largely secondary cavity nesters that rely on pre-existing hollows as nest sites (Higgins 1999), although a number of other niches have been exploited (see for example Burger and Gochfeld 2005).

Ninety-four species of parrot (28%) are threatened with extinction and another 40 are considered to be near threatened (IUCN 2007). At least 19 species have become extinct since the year 1600 (IUCN 2007) and parrots are among the most threatened groups of birds in the world (Bennett and Owens 2002). Despite this, parrots are generally a poorly known group (Collar 1997; Heinsohn and Legge 2003).

The hooded parrot (*Psephotus dissimilis*) is a small (40–55 g; Higgins 1999) grass-parrot of the northern Australian dry tropics. It lives in open eucalypt woodland with an understorey of grasses and herbs (Woinarski and Tidemann 1991; Garnett and Crowley 1995), and feeds on or near the ground, on seeds of annual and perennial grasses and herbs (Garnett and Crowley 1995).

Like its congeners, the endangered golden-shouldered parrot (*P. chrysopterygius*) and the extinct paradise parrot (*P. pulcherrimus*), the hooded parrot breeds in large, terrestrial termitaria into which it excavates its nest. Two other Australian species in the genus *Psephotus* also nest in termitaria. In contrast to its congeners, the hooded parrot is not considered to be threatened, despite evidence of a range contraction since European settlement (Garnett and Crowley 2000).

Little is known of the breeding biology of hooded parrots in the wild. Between 1979–1982, Reed and Tidemann (1994) conducted the only study of the parrots' nesting behaviour in the wild and collected a range of data on nest-site characteristics, however they present only limited data on the breeding biology of this species, based on a small sample size. Therefore much of what is known of the breeding biology of hooded parrots comes from aviculture, where birds nest in boxes rather than termitaria, are protected from predators, have abundant food and usually experience a temperate rather than tropical climate (for examples see Lendon 1951; Boyd 1985; Schmidt 1986).

Here, data on the breeding biology of hooded parrots collected during an intensive study of a wild parrot population west of Katherine, Australia are presented, and compared with that of other termite mound and arboreally nesting Australian parrots.

Methods

Study Site

Manbulloo Station (S 14º 40' 08" E 132º 05' 27"), a private cattle property 30 kilometres east of Katherine, Northern Territory, Australia, was searched for nests of hooded parrots between January and April 2006 and January and May 2007, spanning two full breeding seasons. No active nests were encountered when nest searching began in January, leading to the conclusion that the nest searches captured the first nesting attempts in each year and the timing of the breeding season is corroborated by Reed and Tidemann (1994). The area has a monsoonal climate, characterised by hot, wet summers and cool, dry winters. The landscape at Manbulloo Station includes both rocky ridge country, characterised by shallow gullies that form peripheral rocky ridges, and black soil country, characterised by well drained, sandy flats. The vegetation is an open tropical savannah, with an overstorey of northern salmon gum (*Eucalyptus bigalerita*) and Darwin stringybark (*E. tetrodonta*), and an understorey dominated by grasses from the genus *Sarga*.

Experimental protocol

Once a hooded parrot nest was located, its position was marked with a GPS. When first located, nests were approached only if the attendant birds were not in the process of excavation. This precaution minimised the risk of the parrots deserting the nest. On subsequent visits, nests were approached only in the absence of potential predators such as pied butcherbirds (*Cracticus nigrogularis*). The nest contents were accessed by cutting and removing an approximately 10 cm × 10 cm square plug from the side of the termite mound. Once the visit was complete, the plug was replaced and the portal resealed with mud. The birds always resumed nesting soon after the disturbance and there was no desertion of eggs or young as a result of the procedure. Nests were visited every four days for the entire nesting period.

Eggs were marked with a felt tip pen to designate laying order, measured (length and breadth in mm) using digital vernier callipers (model CD-6”PS; Mitutoyo Corporation) and weighed using a digital scale (model DW-100AX, 100g/0.01g; Digiweigh). At each nest visit, the chicks were removed from the nest and their claws marked with nail polish to allow identification of individuals (after Masello and Quillfeldt 2002). Flattened wing chord, from carpal joint to the end of the primary feathers, was measured using a butt-ended ruler. Head length was measured with callipers from nape to front of relaxed bill. Finally, birds were weighed to the nearest 0.5 g using Pesola scales, before being returned to the nest. At a mean age of 17 days (s.d. ± 3.09, range 12–25, n = 64), approximately 50 µl of blood was taken from the chicks’ brachial vein to identify the sex of the bird using the CHD technique (Griffiths *et al.* 1998). The condition, size and success of the entire brood were recorded.

Analyses

A generalised linear model was used to model the development of feathers in the nestling birds and linear regression modelling used to model changes in fitness (i.e. size and weight) over the course of the breeding season. Sex ratio was calculated as the proportion of males out of the total number of nestlings. Chi-squared tests were used to analyse frequency data. Student *t*-tests were used to analyse clutch size differences between years, sexes and based on whether nests were early or late nests. In 2007, three late nests were so defined because they were established three weeks after the next latest nest was established. Data are presented as (± s.d., range, *n*), and differences are considered significant at $P < 0.05$. All data were analysed using GenStat 10.2 statistical software (Payne *et al.* 2007).

Results

In 2006, 11 and in 2007, 42 active hooded parrot nests were found during the course of the two breeding seasons (Fig. 1). The difference in the number of nests between seasons can be attributed to the amount of effort in each field season. In 2007, with four field assistants, the area searched was larger than that searched unassisted in 2006. Although 11 nests in the 2007 season were used in an experiment, no differences were detected between treatments, and therefore all 42 nests are analysed here (see Chapter VII). Because birds were not individually marked, it is possible that some pairs were observed in both breeding seasons, however the extent of the lack of independence between the two years is unknown.

Twenty-four (45%) nests failed to fledge any chicks and 12 (23%) fledged all the eggs that were laid, the remainder fledged a portion of the eggs laid. Five of the 24 failed nests were abandoned and eggs remained in the nest, one nest was flooded and the only chick that hatched died in the nest and in 18 nests the contents disappeared between visits, which was assumed to be the result of predation. Overall 75% of eggs hatched (mean for Australian parrots 71%; appendix 1) and 61% of those chicks fledged (mean for Australian parrots 54%; appendix 1).

The first eggs were laid on 20 January in 2006 and approximately 20 January in 2007. The last egg was laid on approximately 7 March in 2006 and 2 April in 2007. The first chick of the season was hatched on 9 February in both 2006 and 2007 and the last chick of the season to fledge left the nest on 22 April in 2006 and 14 May in 2007. Nest initiation stopped in both years as heavy

March rains developed. While these rains persisted in 2006, and no further nesting took place, a small number of late nests did occur in 2007 once the rains stopped.

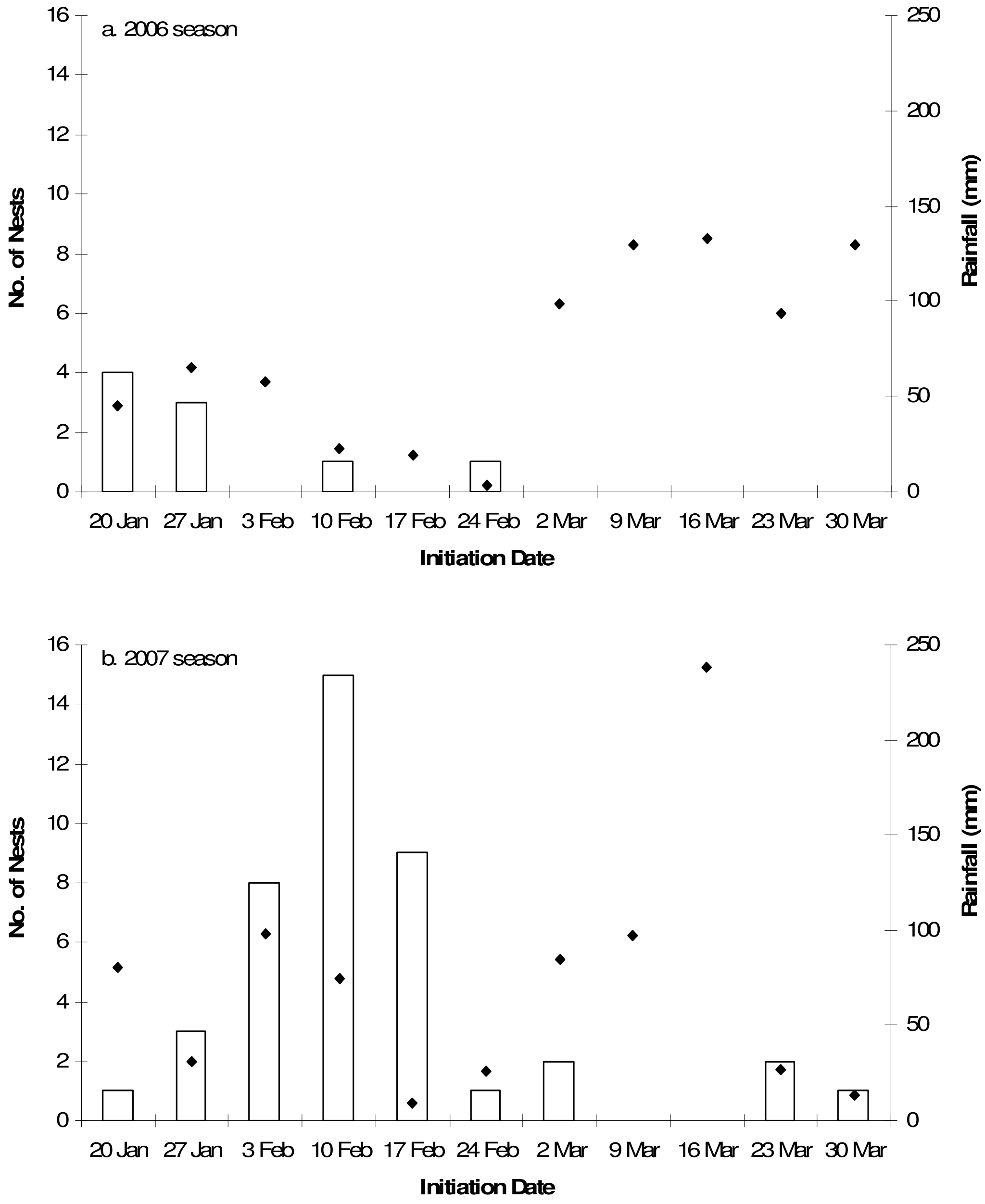


Fig. 1. Distribution of hooded parrot (*Psephotus dissimilis*) clutch initiation dates for two breeding seasons (a: 2006 and b: 2007), Katherine, Australia. Clutch initiation dates are grouped in 7-day intervals, beginning from the date indicated below each bar. Bars represent the number of

nests initiated in each week; points (diamonds) represent rainfall (sourced from the Bureau of Meteorology 2008).

Eight nests were found while the parent was still laying its clutch and for these nests, the period that the chick was in the egg could be calculated. Chicks hatched from these eggs a mean of 18.6 days (s.d. ± 1.95, range 16–22, n = 19, hereafter expressed as ± 1.95, 16–22, 19) after laying, though the actual incubation period was not recorded. Chicks hatched asynchronously, a mean of 1.5 days apart (± 0.74, 0–4, 102). There was, however, no effect of laying order on the likelihood of hatching ($\chi^2 = 5.17$, d.f. = 5, $P > 0.05$) or fledging ($\chi^2 = 8.56$, d.f. = 5, $P > 0.05$).

At the end of the nesting period, chicks from a given nest fledged over a mean period of 6.3 days (± 3.0, 3–12, 11). The sample size for this figure is low because eight nests fledged all of their chicks between nest checks, leaving only 11 nests for which the period is known. Chicks always fledged in the order in which they were hatched. Two broods fledged all of their chicks except for one within two days, the final chicks taking eight and 11 further days to fledge. Chicks were 29.2 days (± 2.9, 23–34, 62) old when they fledged, although they were younger in 2006 (mean 27.8, ± 2.88, 13–29, 20), than in 2007 (mean 29.8, ± 2.7, 24–34, 42).

Over the two seasons, 56.8% of the chicks were male (2006 68.2%; 2007 53.4%), which is not different to parity ($\chi^2 = 1.78$, d.f. = 1, $P > 0.05$). When hatch order is considered, males were no more likely to hatch later or earlier in clutches than expected by chance ($\chi^2 = 2.65$, d.f. = 5, $P > 0.05$). Further, there were no differences in the likelihood of fledging based on the sex of the bird ($\chi^2 = 0.26$, d.f. = 1, $P > 0.05$).

There was no significant difference in the number of eggs laid between seasons ($t = 0.94$, d.f. = 50, $P > 0.05$; table 1). However, significantly more chicks per nest hatched ($t = 5.16$, d.f. = 37.99, $P = 0.001$) and fledged ($t = 2.06$, d.f. = 50, $P = 0.045$) in 2006 than in 2007. This did not relate to the proportion of fledglings per nest once the eggs were hatched ($t = 0.48$, d.f. = 41, $P > 0.05$; table 1). Therefore differences in reproductive output are entirely due to the lower rate of hatching in 2007 compared to 2006. There was no difference between early and late nests in the numbers of eggs (*t* = -1.07, d.f. = 50, *P* > 0.05), chicks (*t* = 0.02, d.f. = 50, *P* > 0.05), fledglings (*t* = -0.92, d.f. = 50, *P* > 0.05) or the proportion of hatched chicks that fledge (*t* = -1.18, d.f. = 50, *P* > 0.05).

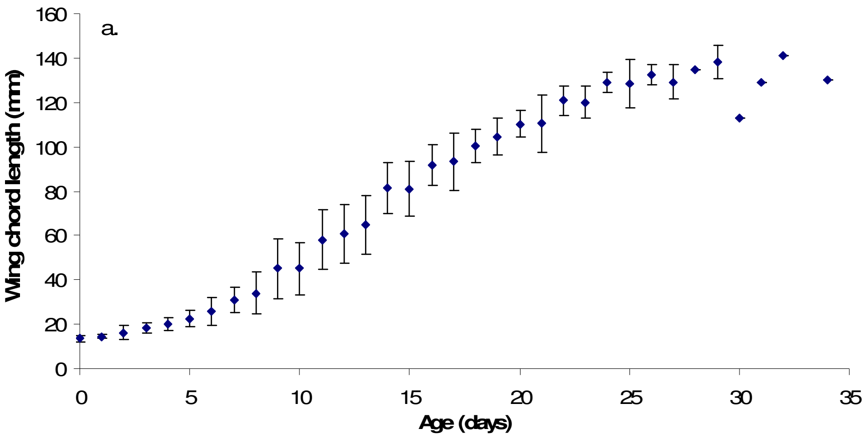
Hooded parrot eggs were 21.8 mm (± 0.1, 17.6–24.3, 179) long and 18.7 mm (± 0.6, 16.9–22.1, 179) wide and weighed 4.0 g (± 0.4, 2.3–5, 179; appendix 1). Eggs were the same width (*t* = -0.08, d.f. = 177, *P* > 0.05) and mass (*t* = 1.09, d.f. = 177, *P* > 0.05) in 2006 as they were in 2007, however they were significantly longer in 2007 than in 2006 (*t* = -2.37, d.f. = 22.09, *P* = 0.027). There was no difference in any these parameters based on either the sex of the chick within the egg (egg length *t* = -1.12, d.f. = 35.77, *P* > 0.05; width *t* = 0.86, d.f. = 52, *P* > 0.05; mass *t* = -1.16, d.f. = 36.29, *P* > 0.05) or the timing of the nesting attempt (late vs. early: egg length *t* = -1.16, d.f. = 177, *P* > 0.05; width *t* = -1.86, d.f. = 177, *P* > 0.05; mass *t* = 1.17, d.f. = 177, *P* > 0.05).

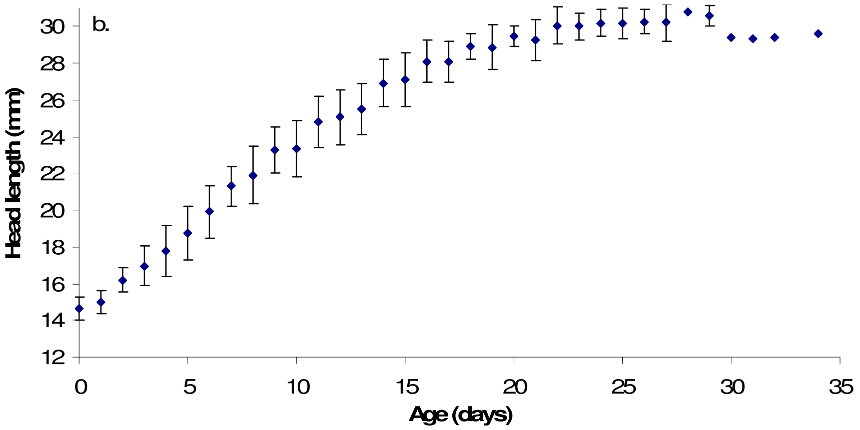
Table 1. Mean number (s.d., range, *n*) of hooded parrot (*Psephotus dissimilis*) eggs, chicks and fledglings per nest by breeding season. Prop. fledge is the proportion of chicks that fledge after they have hatched. * denotes significant differences between years (Student *t*-tests; see text).

	Eggs	**Chicks ***	**Fledglings ***	**Prop. fledge**
2006	4.7 (± 0.68, 4–6, 10)	4.5 (± 0.71, 4–6, 10)	3.1 (± 2.23, 0–6, 10)	0.68 (± 0.47, 0–1, 10)
2007	4.4 (± 0.94, 1–6, 42)	2.7 (± 1.79, 0–5, 42)	1.7 (± 1.89, 0–5, 42)	0.60 (± 0.48, 0–1, 33)
Total	4.5 (± 0.90, 1–6, 52)	3.0 (± 1.79, 0–6, 52)	2.0 (± 2.0, 0–6, 52)	0.61 (± 0.62, 0–1, 43)

Chicks hatched covered in pale grey down. They opened their eyes for the first time at a mean age of 5.4 days (± 1.62, 3–8, 96). Generalized linear modelling predicted that wing pins emerged after a mean of 11.0 days (s.e. ± 0.36), that wing feathers would be unsheathed after 18.9 days (s.e. ± 0.25) and that the bird would be fully feathered by 25 days (s.e. ± 0.40) (fig. 3).

Figures 2a and b show the growth curves for wing chord and head length. Both graphs predict that nestlings increase steadily in size to an asymptote at approximately 25 days, just prior to fledging. At this point they have a mean wing chord length of 127.5 mm (± 9.8, 102–151, 62) and a head length of 30.4 mm (± 1.0, 25.6–32.2, 62). Figure 3c shows the mass gain of the nestling parrots, which similarly increases to an asymptote before falling away, just prior to fledging. Mean mass of fledging parrots was 46.9 g (± 4.8, 33.5–61, 62). However, this did not remain static throughout the course of the breeding season.





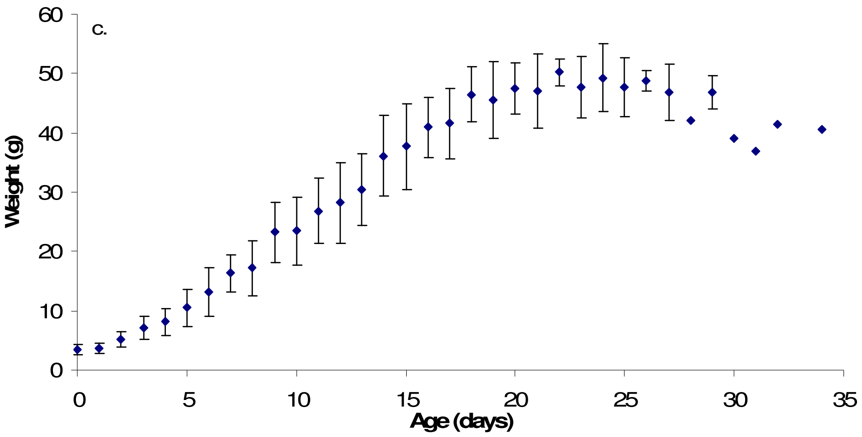


Fig. 2. Growth curves for hooded parrots (*Psephotus dissimilis*) at Katherine, Australia: wing chord (a), head length (b), and mass (c). Data are means ± s.d.

As the breeding season progressed, the overall trend was for chicks to fledge at a greater age (Fig. 3a). This resulted in longer wing chords at fledging (Fig. 3b), but these late fledging chicks had relatively small heads and light body masses (Figs 3c, d). That is, late fledging chicks had a normal wing length for their age but head length and body mass was low.

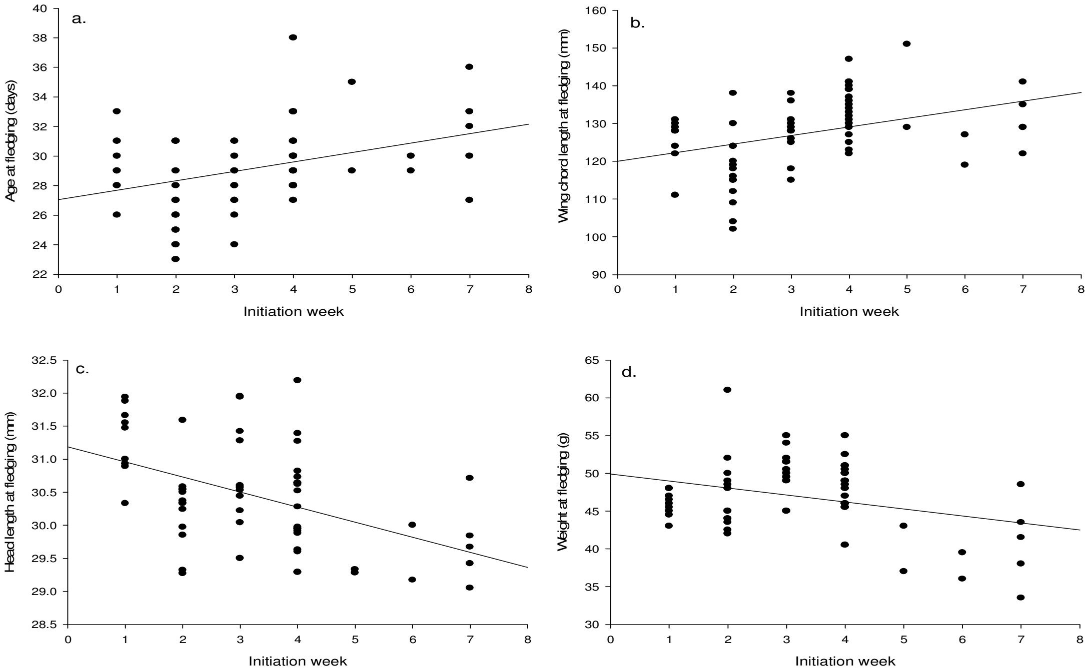


Fig. 3. The relationship between age and size at fledging and the week of clutch initiation in hooded parrot (*Psephotus dissimilis*) chicks, Katherine,

Australia. Week 1 is the week commencing 22 January 2006 and 21 January 2007. Regression lines of the fitted model are presented: a. Age of chick at fledging = 23.87 + 0.64 × Initiation week, Adj. R^2 = 21.1, F = 0.004. b. Length of wing chord at fledging = 108.65 + 2.28 × Initiation week, Adj. R^2 = 13.7, F = 0.002. c. Head length at fledging = 32.33 – 0.23 × Initiation week, Adj R^2 = 20.9, F = < 0.001. d. Mass at fledging = 51.61 – 0.82 × Initiation week, Adj R^2 = 8, F = 0.015.

The egg volume (calculated using the method of Hoyt 1979), clutch mass (mean number of eggs multiplied by the mean mass of an egg), incubation period and age at fledging of Australian termite mound nesting parrots were compared to other Australian parrots (Fig. 4). None of the variables measured showed differences between termite mound nesting and tree-cavity nesting parrots.

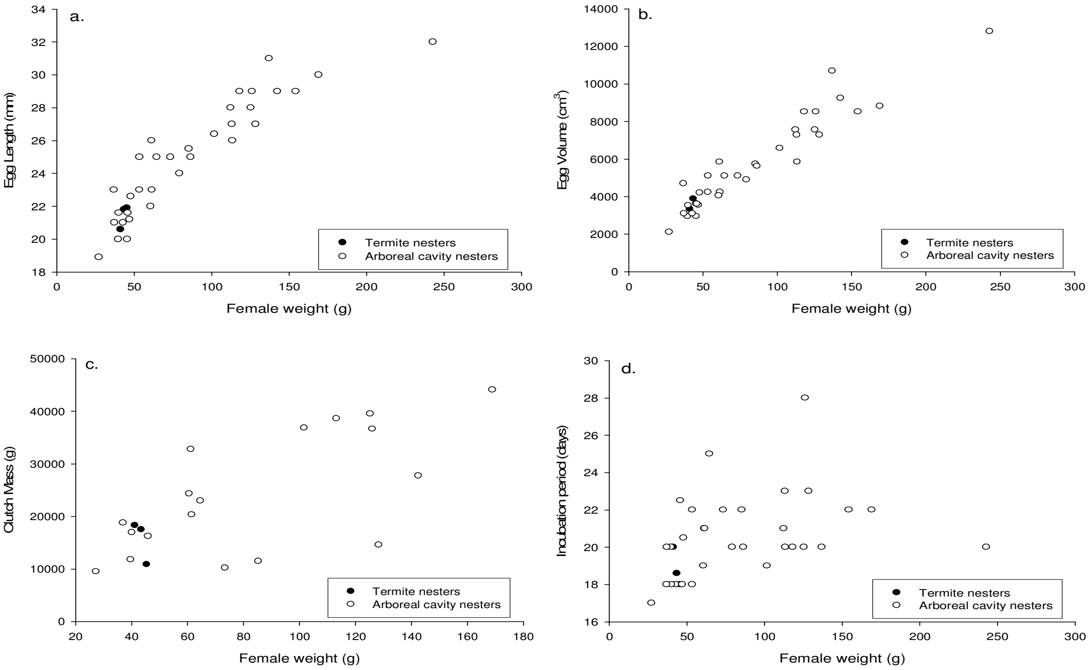


Fig. 4. Comparison of breeding data on Australian termite mound nesting parrots with that for all other tree-cavity nesting Australian parrots, excluding *Eclectus roratus.* Data based on Appendix 1. a. egg length; b. egg volume (calculated using the method of Hoyt 1979); c. clutch mass (mean number of eggs multiplied by the mean mass of an egg); and d. incubation period in days.

Discussion

In many respects, the breeding biology of hooded parrots is typical of other Australian parrots (Fig. 5). Adjusted for hen mass, egg size, egg volume, clutch mass and incubation period conform to the usual patterns exhibited by other Australian parrots. However, nesting success for hooded parrots was high for the two breeding seasons in this study; 11% higher than that reported by Reed and Tidemann (1994) in their study of hooded parrots 25 years earlier and higher than has been found for many temperate Australian parrot species (appendix 1).

The nesting period in this study matched that found by Reed and Tidemann (1994) at the King River site. Hooded parrots start nesting in January, however most breeding activity occurs in February, before tapering off to be completed by the end of April. In March of both years, high rainfalls coincided with a cessation of clutch initiation. In 2006 these rains continued and no further nests were found in these breeding seasons, however in 2007, three further nests were initiated once the heavy rain stopped. The greatest food abundance for hooded parrots occurs near the end of the wet season (around April-May; Woinarski and Tidemann 1991; Garnett and Crowley 1995), which coincides with the fledging of chicks and peak demand for food by hooded parrots.

In 2006, hooded parrots nested earlier, the chicks were bigger and nests were more successful than in 2007, which suggests that 2006 was a better, albeit shorter, breeding season. This may reflect the weather during the two seasons in which the study was conducted. Both seasons studied had extended dry periods in the middle of the wet season, however the dry period was more pronounced in 2006 than in 2007 (February rainfall for Katherine Aviation Museum, 14.44°S 132.27°E: 2006 62 mm; 2007 97.7 mm; 65 year average 239.8 mm; Bureau of Meteorology 2008). The extended dry period in 2006 may have promoted seed set in annual grasses earlier in the wet season, and therefore earlier in the breeding cycle of the parrot. The increased availability of food for parrots earlier in the nesting period may therefore have resulted in better nesting conditions in 2006 compared to 2007.

Nests that were initiated earlier in the season were able to fledge their chicks at a younger age and the chicks were bigger and heavier than those in later nests, although there was no difference in the wing length. This suggests that the use of energy to grow wings is constant, regardless of all but the most severe food shortage, and that the delays in fledging experienced by later broods are caused by shortages of food that result in these chicks fledging lighter and smaller.

The hooded parrot is one of three ‘antbed’ parrots, so named because of their habit of nesting in termite mounds. Almost nothing is known about the breeding biology of the extinct paradise parrot, however the golden-shouldered parrot has been studied extensively (see Crowley *et al.* 2004). Hooded parrots have been regarded as analogues for golden-shouldered parrots, especially in the ongoing management of golden-shouldered parrot populations (Garnett and Crowley 1995). Hooded parrots have smaller clutches than golden-shouldered parrots (4.5 vs. 5.5), but bigger eggs (21.8 mm x 18.7 mm vs. 20.6 mm x 17.8 mm; Higgins 1999), most likely as a result of their greater size. Hooded parrots, perhaps as a result of the bigger eggs, grow more quickly than golden-shouldered parrots and may fledge at a younger age (29 days for hooded parrots this study vs. 35 days for golden-shouldered parrots in Higgins 1999). However, accounts from captive birds record similar fledging ages for both species (Sindel and Gill 1996), suggesting that wild birds may fledge earlier.

In the hooded parrot population studied, reproductive losses were assumed to be the result of predation in the majority of cases, although no predator was seen taking chicks or eggs. In most cases the nest was left intact after the disappearance of the chicks, ruling out large goannas *Varanus* sp. (Crowley *et al.* 2004), however one nest was completely destroyed between visits and the chicks removed. There were three cases of apparent starvation. In one instance the condition of a chick declined after the loss of its siblings, before it too disappeared, and twice chicks were found dead in the nest. At one further nest, the hen was found dead in the nest and the eggs that were present on the previous visit had disappeared. Pied butcherbirds were assumed to be the main predators of hooded parrots and were abundant at the field sites, however these birds weigh close to 120 g (Higgins *et al.* 2006), more than twice the mass of adult hooded parrots (Higgins 1999) and it is not certain that they can gain access to the nest cavity. Conversely, at a cavity in one termite mound, a common tree snake

(*Dendrelaphis punctulata*) was found, although it was not known if this had been an active hooded parrot nest.

In birds, the sex ratio is typically close to parity (Clutton-Brock 1986). However, recent molecular techniques are revealing more cases of a biased sex-ratio in different species and under different conditions (Gowaty 1991; Heinsohn *et al.* 1997; Sheldon 1998). Parrots have been reported to manipulate the sex ratio of nestlings in response to nesting conditions (Heinsohn *et al.* 1997; Krebs *et al.* 2002; but see Budden and Beissinger 2004). Further, biased sex ratios are more common is sexually dimorphic birds (Clutton-Brock 1986) such as the hooded parrot, therefore it is possible that they are candidates for this behaviour. Indeed, in captivity one pair of parrots had extremely biased clutches resulting in 17 of 18 birds being male, before the following year producing seven out of eight female chicks (Sindel and Gill 1996). Despite this, no evidence of sex ratios that were significantly different to parity was found over the course of this short study.

This study adds to the growing literature about the breeding biology of tropical birds and in particular tropical parrots. With the decline of many species of parrot, information such as presented here will enable land and wildlife managers to make better informed decisions about hooded parrots so that the chances of them suffering the same fate as their congeners is lessened.

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CHAPTER III

Photo: S. J. N. Cooney

Nest-site selection of the hooded parrot *Psephotus dissimilis*—a primary cavity nesting species.

Abstract

Many species of bird nest in natural cavities or those they excavate. Whilst cavity nesters as a whole experience increased nesting success, the greatest success is experienced by species that can excavate their own nests. Certain arboreal cavity nesters, such as woodpeckers, require extensive morphological adaptation for this behaviour, but this has not occurred in Australia, despite competition among birds and a suite of arboreal mammals for naturally occurring cavities. Some species, however, have adapted their behaviour to make use of substrates that are not as hard as wood. Hooded parrots (*Psephotus dissimilis*) excavate nests in terrestrial termitaria, releasing them from competition for limited arboreal cavities. However, only termitaria with a high level of termite activity, and which are more than two metres tall, are suitable and the parrots exhibit a strong preference for the cathedral mounds of *Nasutitermes triodiae*. Nests placed in highly active mounds had a significantly higher success rate than those in mounds where activity was somewhat lower, suggesting that the behaviour is adaptive.

Introduction

The use of cavities for nesting is widespread among birds, with half the avian orders including cavity nesting species (Collias and Collias 1984). In Australia there is particularly high demand for cavities, as more than 119 bird species (15%) are obligate cavity nesters (Gibbons and Lindenmayer 2002), compared with only 5% in North America, southern Africa and Europe (Newton 1994). A range of other vertebrates also use hollows as both nest- and roost-sites, resulting in more than 300 species of vertebrate dependent on nest hollows in Australia (Gibbons and Lindenmayer 2002). Unless an animal can build its own cavity, there are a finite number of cavities in any given habitat and the large number of potential users puts a premium on the exploitation of this resource.

Avian cavity nesters are generally divided into one of two categories: primary cavity nesting (PCN) birds and secondary cavity nesting (SCN) birds. PCN birds are capable of excavating nests in trees unassisted; Piciformes (woodpeckers) being the prime examples of this behaviour. SCN birds, however, are reliant on other factors to form a cavity, such as degradation of a tree by other birds, fungi, bacteria, or wood-boring insects (Newton 1994; Gibbons and Lindenmayer 1996; Gibbons and Lindenmayer 2002). Some SCN birds modify the size and shape of a cavity by chewing or lining the existing cavity and this may be seen as an intermediate step in the evolution of primary cavity nesting (Collias and Collias 1984). Most treatments of the phenomenon of cavity nesting focus entirely on arboreal cavity nesters and cite only woodpeckers as representatives of the PCN approach (see for example Newton 1994; Gibbons and Lindenmayer 2002). Yet, a range of species build cavity nests in softer substrates such as earth banks (e.g.: Meropidae; *Pardalotus* sp; Higgins 1999; Higgins and Peter 2002) and both terrestrial and arboreal termite mounds (for review see Hindwood 1959). By considering all these species, an evolutionary pathway from opportunistic SCN birds, to a SCN bird that modifies its nest cavity, to PCN birds that can create their own nest cavity in soft substrates, to PCN birds that can burrow into hard wood is suggested (Collias and Collias 1984).

Overseas, PCN birds have been shown to influence the number and nature of cavities in a habitat, which affects the ability of SCN birds to nest in the area and therefore shapes the SCN bird community (Martin and Eadie 1999; Arsenault 2004). This ability to influence the SCN community suggests that nest-sites are rarely in abundance and are likely to be a limiting resource for many SCN birds. Suitable nest-sites have been shown to be limiting on populations of SCN birds overseas (von Haartman 1957; Pinkowski 1977; Scott 1979; Dobkin *et al.* 1995; but see Waters *et al.* 1990; Aitken and Martin 2004; Brightsmith 2005a), and suggested in Australia (Pell and Tidemann 1997; Legge *et al.* 2004). In Australia, the situation is potentially more critical, as there are few arboreal PCN birds (e.g., Australian fig-parrot (*Cyclopsitta diophthalma*), red-cheeked parrot (*Geoffroyus geoffroyus*); Higgins 1999) and the creation of new nest hollows in trees may take longer than 100 years before they are usable by some species (Disney and Stokes 1976; Nelson and Morris 1994). In addition, a higher proportion of birds are reliant on nest cavities, relative to other continents, which must increase the demand for these nest hollows.

Cavity limitation can not only arise from a dearth of cavities, but also because some cavities are unusable as a result of both inter- (Brawn 1990; Legge *et al.* 2004) and intra-specific competition (Gustafsson 1988). Furthermore, in many habitats, especially those managed for timber production, cavities are a declining resource (Saunders 1979; Brawn and Balda 1988; Smith and Lindenmayer 1988; Nelson and Morris 1994), exacerbating the shortage of suitable nest-sites for SCN birds.

Other studies have shown that secondary cavities are inferior to primary cavities as nest-sites, because secondary cavities have more parasites and are more prone to predation (Sedgwick 1997; Aitken *et al.* 2002). PCN birds can build a fresh nest and at an optimal location, which results in a higher success rate (Martin and Li 1992; Johnson and Kermott 1994).

Parrots are largely obligate secondary cavity nesters that, in Australia, account for 40% of the 119 cavity nesting birds (Gibbons and Lindenmayer 2002). Arboreal, and to a lesser extent, terrestrial termitaria also provide nest-sites for 36 parrot species (10.8% of parrots) worldwide and 7% in Australia (appendix 2).

Three closely related Australian parrot species, the hooded parrot (*Psephotus dissimilis*), golden-shouldered parrot (*P. chrysopterygius*; Crowley *et al.* 2004), and the extinct paradise parrot (*P. pulcherrimus*; Chisholm 1922), nest in terrestrial termitaria. The exterior of these structures is soft enough to allow the parrots to excavate cavities in the mounds, and the termites, once exposed to light, seal off the cavity so that bird and insect do not co-habit the nesting cavity (Hindwood 1959). Exploitation of this resource can be expected to alleviate some of the problems usually associated with nesting in secondary cavities. In particular, termitaria are assumed to be an abundant resource in many habitats, especially where trees are scarce. This should mean that suitable nest-sites would no longer be limiting for a population of parrots that build their nests in these structures, and indeed, this prediction is supported for some species that use arboreal termitaria (Brightsmith 2000; Kesler and Haig 2005b).

The hooded parrot nests in terrestrial termitaria of various termite species, but most commonly in the 'cathedral' shaped mounds of the spinifex termite

Nasutitermes triodiae, which are visually prominent in the tropical savannahs of northern Australia. However, our perception of a suitable nest-site may not accord with that of the bird and despite their number, many termite mounds may not, in fact, be suitable nest-sites.

A basic determinant of the location of hooded parrot nests is the distribution of termite mounds within the landscape, and the factors that influence this pattern. In some termite species, distribution of colonies appears to be random (Collins 1981; Lepage 1984), however competition, food resources, predation, temperature and moisture and habitat characteristics have all been shown to influence termite populations (reviewed by Lepage and Darlington 2000). The variable mounds built by *Nasutitermes triodiae* suggest that it is a generalist termite that can adapt to many different habitats, however these forms are not related to either soil type or vegetation (Lee and Wood 1971). *Nasutitermes triodiae* mounds are absent from areas with shallow soils, and instead favour areas of valley or flat where large mounds, with deep roots, can be constructed (Lee and Wood 1971). As its name suggests, the diet of *Nasutitermes triodiae* consists of grass tissue, often from the genus *Triodia* (Ratcliffe *et al.* 1952) and mounds are usually initiated within a clump of such coarse grass (Gay and Calaby 1970).

Between 1979 and 1982, Reed and Tidemann (1994) undertook a study of the nesting sites of hooded parrots at six localities in the Northern Territory and described the nature of the nests they found during this time. This study returns to one of their four study locations (King River) with three goals in mind:

1. to determine the factors that make a termite mound suitable as a nest-site for hooded parrots;
2. to determine the characteristics of termite mounds that make them more or less successful as nest-sites for hooded parrots; and
3. to determine the abundance of suitable nest-sites within this habitat.

Methods

Study Site

An area 30 kilometres east of Katherine, Northern Territory, Australia (S 14º 40' 08" E 132º 05' 27"), was searched for termite mound nests of hooded parrots between January and May, 2006 and 2007, spanning two full hooded parrot breeding seasons. The study area has a monsoonal climate, characterised by hot, wet summers and cool, dry winters. The work was based on a private cattle property (Manbulloo Station), and included both rocky ridge country, characterised by shallow gullies that form peripheral rocky ridges, and black soil country, characterised by well drained, sandy flats. The vegetation on Manbulloo Station is an open tropical savannah, with an overstorey of northern salmon gum (*Eucalyptus bigalerita*) and Darwin stringybark (*E. tetrodonta*), and an understorey dominated by grasses from the genus *Sarga*.

Experimental protocol

To characterise a 'typical' termite mound, one random survey was conducted for every hooded parrot nest found: thus, 52 nests were found and 52 random surveys undertaken. Using randomly generated numbers to create longitudes and latitudes, which were located using a GPS (Garmin, GPSmap 60CS), 52 quadrats, extending to the north and east of these points, each measuring 50 m x 50 m (¼ hectare) were established. Within each randomly determined quadrat, a range of parameters was recorded to characterise the nature of the habitat within that quadrat (table 1). Then, every termite mound in excess of 1.5 m tall was measured and a range of parameters recorded, to determine the nature of the mounds in these quadrats (table 2). Termite mounds shorter than 1.5 m tall were excluded because previous evidence suggested that they are too small to host a hooded parrot nest (Reed and Tidemann 1994); the rest of the mounds were considered 'potential' hooded parrot nest sites.

Table 1. List of parameters, recorded at a quadrat level, used to examine the nature of the habitat in which termite mounds were found, Katherine, Australia, 2006–7.

Parameter	Variable name	Description
No. of mounds	NUMB	The number of termite mounds more than 1.5 metres tall.
Paddock name	PAD	The surveys were located in one of four paddocks: Redbank and Buntine (separated only by the Victoria Highway) were immediately east of the King River and DB Paddock and Conical Land (also separated by the Victoria Highway) were west of the river.
Location	LOC	Quadrats were classified as being in one of two sub-habitats: gully (within an extended erosion gully) or flat.
Cattle (Y/N)	COWS	The presence of cattle was determined through dung, recent footprints or by being sighted in the quadrat when it was approached.
Fire	FIRE	The period since fire was estimated on a three point scale: 1 a fire passed last dry season; 2 signs of fire but not in the previous dry season, and; 3 no signs of fire.

At the site of the 52 nests, a similar survey to the random survey was undertaken. In these quadrats the hooded parrot nest marked the middle of the 50 m x 50 m quadrat. All termite mounds taller than 1.5 m were measured and the variables listed in table 2 recorded. As well as the variables listed in table 2, some additional variables were recorded at the termite mound that housed the active nest (table 3). The success of these nests was measured as whether chicks fledged from a particular nest or not, which was determined as the nest finished for the season (i.e. through predation, abandonment or fledging).

Table 2. List of parameters used to characterise randomly selected termite mounds greater than 1.5 metres tall and without nests and mounds that housed nests of hooded parrots (*Psephotus dissimilis*), Katherine, Australia, 2006–7.

Parameter	Variable name	Description
Termite mound height	HEIGHT	The height of the termite mound in centimetres.
Circumference at base	CB	Circumference of the mound at its base, in centimetres.
Circumference at cavity	CC	Circumference of the mound, in centimetres, approximately two thirds of the way up the mound (where one would expect to find a nest entrance; Reed and Tidemann 1994). For measurements of nests, the actual circumference at cavity height was used.
Active	ACTIVE	Was the mound an active termite mound (i.e. currently inhabited by termites)? Y/N.
% Cover	COVER	Termites cover their galleries with a smooth surface. This weathers away over time. Cover was an estimate of the amount of smooth termite mound exterior, in 5%

Parameter	Variable name	Description
		increments and served as a measure of termite activity within the mound.
% repaired	REP	As an additional measure of termite activity, the base of the termite mound—likely to be the most active part of the mound (M. Lenz; Pers. comm.)—was scraped to expose the galleries. After 30 minutes, an estimation of the response by the termites was made.
Used	USED	Signs that the mound had been used by a vertebrate in current or previous years included holes in the walls and base of the termite mound.
Mound type	TYPE	Either a cathedral mound of *Nasutitermes triodiae* or a conical mound of *Amitermes vitiosus*.
Distance to nearest tree	NT	Distance from the mound to the nearest tree, measured in centimetres.
Tree height	TREEH	Height of the nearest tree in centimetres.
Location	LOC	Mounds were classified as being in one of two sub-habitats: gully (within an extended erosion gully) or flat.
Paddock	PAD	The surveys were located in one of four paddocks: Redbank and Buntine (separated only by the Victoria Highway) were immediately east of the King River and DB Paddock and Conical Land (also

Parameter	Variable name	Description
		separated by the Victoria Highway) were west of the river.

Table 3. List of parameters used to characterise hooded parrot (*Psephotus dissimilis*) nests, Katherine, Australia, 2006–7.

Parameter	Variable name	Description
Old/New nest	REUSED	The age of the nest was determined either by direct observation of parrot building activity or by examining the base of the nest for signs of freshly excavated termite mound material (after Reed and Tidemann 1994).
Nest height	NH	Height of the tunnel leading to the nest from the ground in centimetres.
Tunnel height	TH	Height of the tunnel in centimetres.
Tunnel length	TL	Length of tunnel from front of mound to the beginning of the nest chamber in centimetres.
Chamber length	CL	Length of the nest chamber in centimetres.
Chamber width	CW	Width of the nest chamber in centimetres.
Chamber height	CH	Height of the nest chamber in centimetres.

Parameter	Variable name	Description
Nest orientation	NO	Orientation of the nest entrance measured with a compass in degrees (to nearest 10° interval).
Distance to next nest	DN	Distance from existing nest to the nearest nest, by season, in metres.

Analyses

The null expectation for the suitability of a termite mound for use as a hooded parrot nest-site is provided by the binomial theorem, and can be analysed using a generalised linear model, using binomial regression that assumes a binomial distribution and logit link function. Several co-variates were incorporated in the models (table 2). A modelling strategy of initially including all variables in an all-subsets regression to determine the most parsimonious model that contained only significant terms, based on the model's Akaike Information Criterion (AIC) was adopted. AIC identifies the model that loses the least amount of information whilst retaining parsimony, is independent of the order of the variables and can be used to assess the likelihood of different models (Burnham and Anderson 2002). Differences in AIC values <2 indicate substantial evidence for alternative models, differences between values of 3–9 indicate that alternative models are less likely and differences between values >10 indicate that alternative models are very unlikely (Burnham and Anderson 2002). Once key variables are identified, a significant model is proposed that includes only significant variables. Only termite mounds from the nest-site surveys were included in this analysis because unmeasured factors may have prevented a parrot from nesting in otherwise suitable mounds in the random quadrats.

The same approach was used to explore the determinants of nest success, except that only mounds that housed hooded parrot nests were used and the analysis also incorporated the additional nest variables listed in table 3. Because of the large number of variables in this analysis, the process was undertaken in three steps. In the first iteration, ten randomly chosen variables were included in the analysis. From this, the five most significant variables were noted. In the second iteration, the remaining 10 variables were used and from these, the five most significant variables chosen. The third step involved the use of the ten variables identified in the previous two steps and it was from this model that the final model was drawn. Because all the nests were excavated in the year in which they were used, the variable REUSED was not included in the analysis.

To analyse the factors that predict the presence of suitable mounds (as defined by the first analysis), a similar approach to the first analysis was taken, however a Poisson distribution was assumed, with a logarithmic link. These data are combined with the results of the nest suitability modelling to predict the number of suitable nest mounds per ¼ hectare quadrat.

Rayleigh's Uniformity Test was used to analyse the circular data of the orientation of the nest entrance tunnel. This test calculates the probability of the null hypothesis that the data are distributed in a uniform manner (Zar 1998).

All regression analyses were fitted with Genstat 10.2 (Payne *et al.* 2007). Analyses of circular data were fitted with Oriana 2.02 (Kovach Computing Services 2004). Differences were considered significant at the 95% level.

Results

Two-hundred and two potential nest-sites (i.e.: termite mounds taller than 1.5 m) were measured in the 104 surveys (47 in random surveys; 155 in nest-site surveys). The mean number of mounds per quadrat was 1.9 (s.d. ± 1.93, range 0–10, n = 104, hereafter presented as ± 1.93, 0–10, 104; table 4). However, during 29 (27.8%) of the surveys no mounds greater than 1.5 metres tall were located. This meant that the remaining quadrats had a mean of 2.7 mounds (± 1.79, 1–10, 76). When only suitable mounds were considered (as defined by nest-site selection modelling: see below) there were 2.5 mounds/quadrat in the nest-site quadrats and 0.6 mounds/quadrat in the random quadrats, which is significantly different (t = 7.2, *d.f.* = 84.5, P = <0.001; table 4). This difference remains highly significant even when the nest mound that determined the quadrat's location is removed (1.5 vs. 0.6 mounds/quadrat; t = 3.5, *d.f.* = 85.3, P = <0.001).

Table 4. Number of termite mounds per 50 m X 50 m quadrat in randomly placed surveys and surveys conducted at the site of an active hooded parrot (*Psephotus dissimilis*) nest, to determine the abundance of hooded parrot nest sites. Potential mounds are termite mounds greater than 1.5 m in height. Suitable mounds, based on linear regression modeling (see text), are mounds taller than 2 m in height, with more than 30% coverage of recent building activity (see text). The nest survey necessarily had one termite mound in the quadrat, therefore 'nest survey (excluding nest)' shows the number of mounds excluding the nest mound. Katherine, Australia, 2006–7.

Survey type	Potential mounds	Suitable mounds
Nest survey	2.9	2.5
Nest survey (excluding nest)	1.9	1.5
Random survey	0.9	0.6
Total	1.9	1.5

Of all the potential nest mounds, 81% were cathedral mounds of the termite *Nasutitermes triodiae*, with the remaining mounds belonging to the conical mound termite *Amitermes vitiosus*. However, this varied by paddock; DB Paddock had no potential *Amitermes vitiosus* nest mounds; Redbank 13%; and Buntine 16%; while all of the potential nest mounds in Conical Land were of *Amitermes vitiosus*. The presence of cattle was noted in 38% of quadrats and fire was recorded in 27% of quadrats. However, the incidence of fire is likely to be underestimated (see below).

A total of 52 hooded parrot nests were found in the 2006 (11 nests) and 2007 (41 nests) breeding seasons (table 5). The difference in the number of nests can be attributed to the amount of effort in each field season. In 2007, with four field assistants, the area searched was larger than that searched unassisted in

2006. Forty-nine nests were in the cathedral mounds of the termite *Nasutitermes triodiae* and three were in the conical mounds of *Amitermes vitiosus*. All three conical mound nests were found in the Conical Land paddock, where there were no cathedral termite mounds.

Table 5. The number of termite mound nests of hooded parrots (*Psephotus dissimilis*) over two breeding seasons, Katherine, Australia. Conical Land and DB Paddock were not searched in the 2006 field season.

Paddock	2006 nests	2007 nests	Total
Buntine	6	14	20
Conical Land	–	3	3
DB Paddock	–	10	10
Redbank	5	14	19
Total	11	41	52

A further two cathedral termite mounds housed nests of red-backed kingfishers (*Todiramphus pyrrhopygia*) in the 2006 field season. 23 (11.4%) of the surveyed termite mounds had signs that they had been previously occupied, including four that were nest mounds for hooded parrots in the 2007 breeding season. Of these 23, 19 mounds met the criteria of suitability for hooded parrots nest sites (as defined by nest-site selection modelling: see below). Only cathedral mounds had signs of previous use.

The termite mounds chosen by hooded parrots were significantly taller and wider at the base than randomly surveyed termite mounds, however they were not significantly bigger at the site of the cavity (diameter at cavity height vs. diameter at 2/3 height of mound; table 6). On one measure of termite activity, hooded parrot nests were highly significantly more likely to choose very active nests (% cover), but on another (% repaired), there was no difference between parrot nests and the randomly sampled termite mounds (table 6). While there was a trend towards nests being closer to taller trees than were random mounds, the difference was not significant, and there was no significant difference in the distance to the nearest tree.

Table 6. Student t-tests comparing the mean (standard error, range, sample size) of variables used to characterise hooded parrot (*Psephotus dissimilis*) nest mounds and randomly selected, non-nest termite mounds, taller than 1.5 m over two breeding seasons in 2006 and 2007, Katherine, Australia.

Variable	Non-nest mounds	Nest mounds	T-test
Termite mound height (cm)	194.2 (± 46.9, 150–362, 150)	239.7 (± 61, 151–425, 48)	t = -4.73, 65.72 *d.f.* P < 0.001
Circumference at base (cm)	317.7 (± 146.2, 50–686, 150)	361.3 (± 88.8, 109–621, 51)	t = -2.53, 143.71 *d.f.* P = 0.013
Circumference at cavity (cm)	188.3 (± 101, 14–442, 150)	194.6 (± 59.3, 92–380, 46)	t = -0.52, 129.53 *d.f.* P = 0.604
% cover	66.27 (± 39.2, 0–100, 150)	84.49 (± 17.45, 40–100, 49)	t = -4.49, 179.56 *d.f.* P < 0.001
% repaired	28.17 (± 37.58, 0–100, 150)	21, (± 32.87, 0–100, 50)	t = 1.20, 198 *d.f.* P = 0.230
Distance to nearest tree (cm)	191.2 (± 179.6, 0–970, 150)	202.1 (± 155, 0–732, 51)	t = -0.39, 199 *d.f.* P = 0.697
Tree height (cm)	441.8 (± 229.5, 150–1300, 150)	539.1 (± 334.6, 40–1500, 47)	t = -1.86, 60.16 *d.f.* P = 0.067

Hooded parrot nests were placed at approximately 70% of the total termite mound height; 168 cm from the ground (table 7). All of the measures of the nesting cavity itself had a high degree of variability, with standard deviations suggesting size differences between cavities of approximately 25% (table 7). No nest was reused in the study period, and nests were a mean of 540 m from their nearest neighbour (table 7).

Table 7. List of variables used to characterise hooded parrot (*Psephotus dissimilis*) nests over two breeding seasons in 2006 and 2007, Katherine, Australia.

Variable	Mean (± s.d., range, sample size)
Nest height (cm)	168.4 (± 46.0, 92–287, 48)
Tunnel height (cm)	6.9 (± 1.07, 5–9, 48)
Tunnel length (cm)	21.7 (± 6.7, 10–41, 47)
Chamber length (cm)	26.0 (± 5.9, 9–41, 46)
Chamber width (cm)	20.0 (± 4.79, 6–31, 46)
Chamber height (cm)	12.7 (± 3.34, 7.5–21, 45)
Distance to next nest (m)	540.4 (± 476.1, 109–2810, 52)

The mean vector of the orientation of the nest entrance tunnels was 150.9° (circular s.d. ± 112.9°), however the orientations of the nests were not significantly different from a uniform distribution ($Z = 1.009$, $P > 0.05$; figure 1).

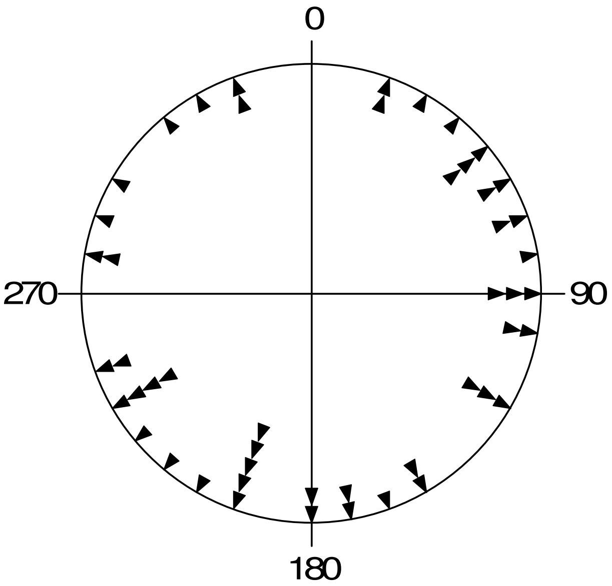


Figure 1. Orientation of nest entrance tunnels of hooded parrots (*Psephotus dissimilis*), Katherine, Australia, 2006–2007. Each triangle represents one nest and numbers are in degrees.

Modelling nest-site selection

Selection of a termite mound as a nest site is a factor of the variables TYPE, TREEH, COVER and MH (residual deviance = 50.1, *df* = 4, *P* = 0.001; table 8). REP was also identified as a significant factor, but it was correlated with COVER and dropped from the analysis. AIC also suggested that USED was important, however it was a non-significant variable and, given the small difference in AIC values between models 5 and 6 ($\Delta_i = 0.85$), it too was removed. Hooded parrots nested in the mounds of *Nasutitermes triodiae* more frequently than in the mounds of *Amitermes vitiosus,* regardless of the influence of other factors. Therefore, to determine the characteristics of a preferred nest site, nests of *Amitermes vitiosus* were dropped from further analyses. Thus the final model included the variables TH, COVER and MH (residual deviance = 34.4, *df* = 3, *P* < 0.001).

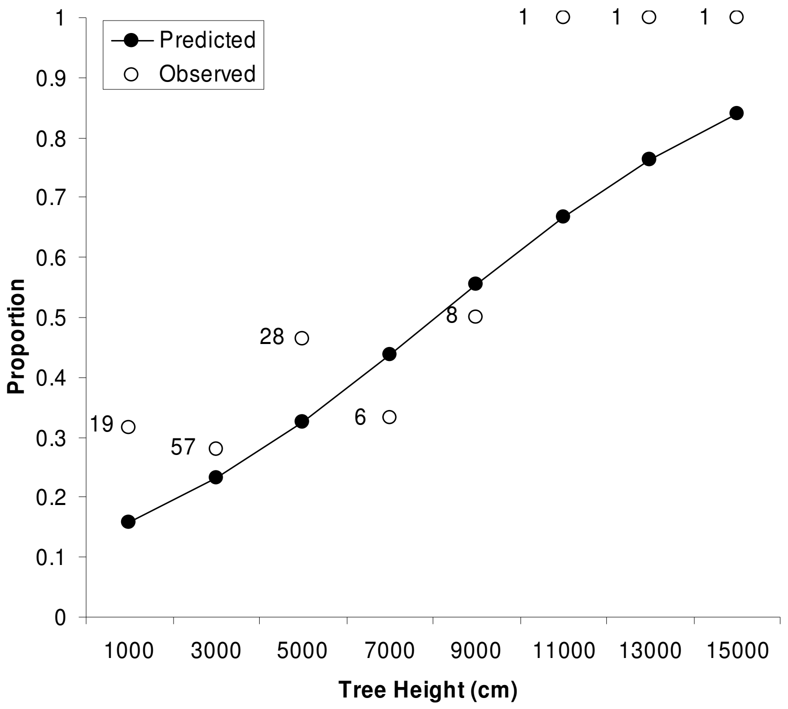
Table 8. Akaike's Information Criterion (AIC) analysis of variables used to predict the characteristics of termite mounds used as nest-sites by hooded parrots (*Psephotus dissimilis*).

Model	Variables	K	AIC	Δ_i
1	HEIGHT	2	186.85	34.45
2	HEIGHT+COVER	3	178.14	25.74
3	HEIGHT+COVER+TREEH	4	172.91	20.51
4	HEIGHT+COVER+TYPE+REP	5	162.02	9.62
5	HEIGHT+COVER+TYPE+REP+TREEH	6	153.25	0.85
6	HEIGHT+COVER+TYPE+REP+TREEH+USED	7	152.40	0.00
7	HEIGHT+COVER+TYPE+REP+TREEH+USED+ACTIVE	8	152.99	0.59
8	HEIGHT+COVER+TYPE+REP+TREEH+USED+ACTIVE+DT	9	153.71	1.31
9	HEIGHT+COVER+TYPE+REP+TREEH+USED+ACTIVE+DT+CC	10	154.72	2.32
10	HEIGHT+COVER+TYPE+REP+TREEH+USED+ACTIVE+DT+CC+CB	11	155.99	3.59
11	HEIGHT+COVER+TYPE+REP+TREEH+USED+ACTIVE+DT+CC+CB+LOC	12	157.99	5.59
12	Full model	13	163.00	10.60

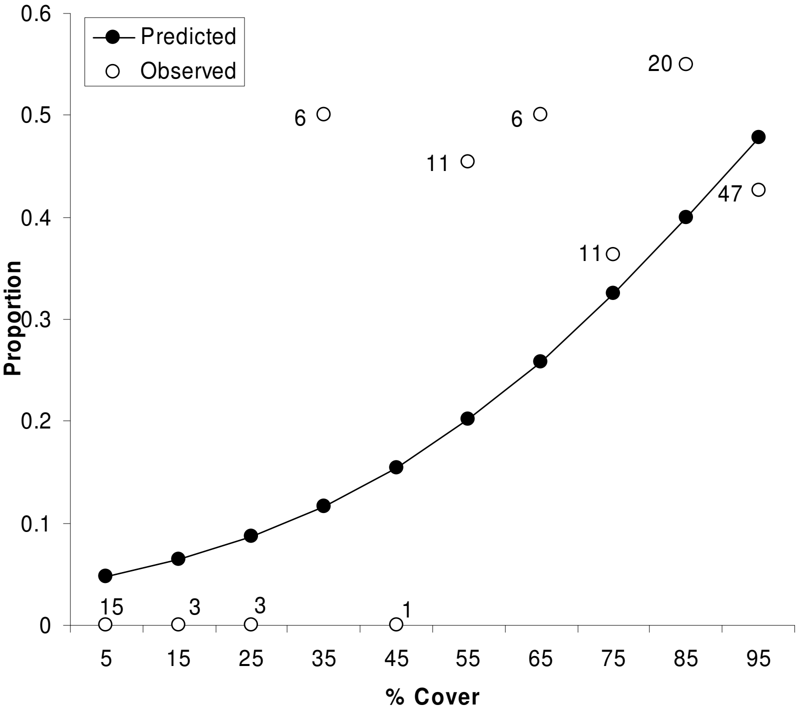
HEIGHT, height of mound; COVER, estimated cover of mound; TREEH, height of nearest tree; TYPE, type of termite mound; REP, level of repair of termite mounds; USED, was the termite used in the previous year; ACTIVE, is the termite mound an active mound?; DT, distance to the nearest tree; CC, circumference at cavity height or 2/3 the height of the mound; CB, circumference of the termite mound at the base; LOC, location of the mound—either on a flat or in a gully. K is the number of parameters in the model. Delta AIC (Δ_i), is the AIC value of the model, minus the minimum AIC value obtained.

Nests were situated more often in the proximity of larger trees, than smaller trees (figure 2a), which is indicative of open woodland with a grassy understorey, rather than woodland with a bushy middle canopy. The final two variables, COVER and MH, did not respond well to normal methods of analysis. These two results showed a stepwise increase in the probability of hosting a nest, not a logistic function (figures 2b, c). Nest-sites had a minimum level of 30% cover, a proxy for termite activity (figure 2b) and a height in excess of 200 cm (figure 2c); these are hereafter referred to as 'suitable' termite mounds for hooded parrot nesting.

a.


Predicted
Observed
Proportion
Tree Height (cm)
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
1000
3000
5000
7000
9000
11000
13000
15000
19
57
28
6
8
1
1
1

b.


Predicted
Observed
Proportion
% Cover
0
0.1
0.2
0.3
0.4
0.5
0.6
5
15
25
35
45
55
65
75
85
95
15
3
3
1
6
11
6
11
20
47

c.

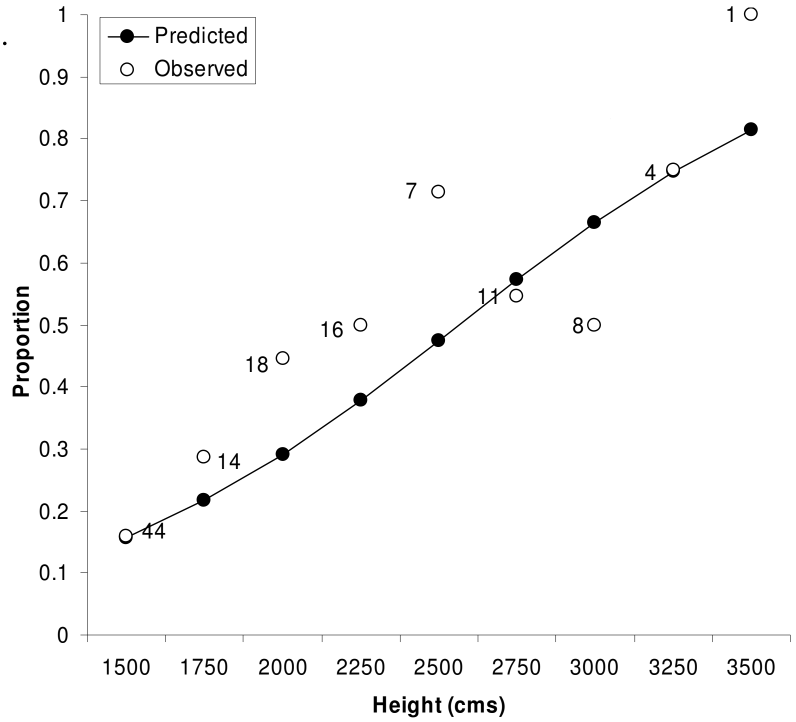


Figure 2. The observed proportions (points) and predictions (lines) of the best binomial regression model for the likelihood of a termite mound being a suitable hooded parrot (*Psephotus dissimilis*) nest site for a given range of: **a.** nearest tree heights; **b.** % cover, as a measure of termite activity; and **c.** termite mound heights. Numbers indicate sample sizes.

Modelling nest success

The higher the level of termite activity as measured by % REPAIRED, the more likely the nest was to succeed (residual deviance = 11.79, *df* = 1, $P < 0.001$; figure 3). Although the model with the lowest AIC score had five variables (table 9), only % REPAIRED was a significant factor in predicting nest success in the binomial logistic regression analysis that followed. The decision to use this single variable is further supported because the Δ_i between the five most parsimonious models is <2, suggesting small differences in the applicability of the models and the model with only two variables in it both measure termite activity within the mound (% REPARIED and COVER; table 9, model 22).

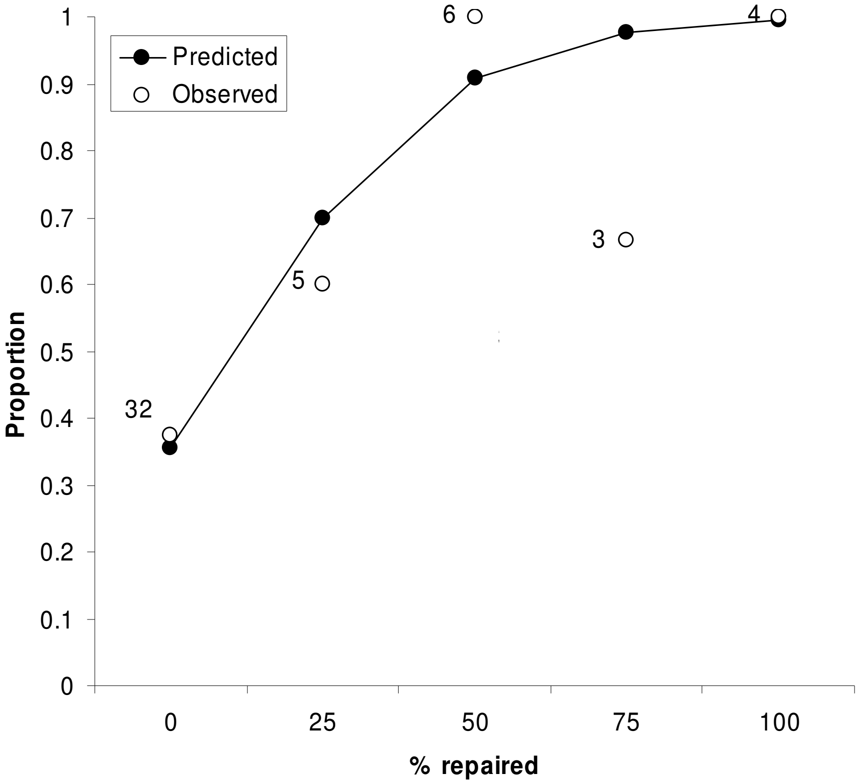


Figure 3. The observed proportion (points) and predictions (lines) of the binomial regression model for successful hooded parrot (*Psephotus dissimilis*) nest-sites, for a given range of repair by termites to their mounds when the mounds were experimentally disturbed. Percentage repaired is a measure of termite activity and the graph indicates that as termite activity increases within a mound, the proportion of nests that successfully fledge chicks also increases. Numbers indicate sample sizes.

Table 9. Akaike's Information Criterion (AIC) analysis of variables used to predict the characteristics of termite mounds, used as nest-sites by hooded parrots (*Psephotus dissimilis*) that make them more or less successful nests.

Model	Variables	K	AIC	Δ_i
Step 1				
1	CC	2	42.34	0.83
2	CC+ACTIVE	3	41.51	0.00
3	CC+ACTIVE+CL	4	42.66	1.15
4	CC+ACTIVE+CL+TYPE	5	43.79	2.28

Model	Variables	K	AIC	Δ_i
5	CC+ACTIVE+CL+TYPE+NH	6	45.54	4.03
6	CC+ACTIVE+CL+TYPE+NH+PADD	7	47.23	5.72
7	CC+ACTIVE+CL+TYPE+NH+NN+NO	8	51.05	9.54
8	CC+ACTIVE+CL+TYPE+NH+NN+NO+PAD	9	51.50	9.99
9	CC+ACTIVE+CL+TYPE+NH+NN+NO+PAD+ HEIGHT	10	53.01	11.50
10	Full Model	11	55.00	13.49
Step 2				
11	REP	2	38.24	0.36
12	REP+CH	3	37.88	0.00
13	REP+CH+CB	4	37.98	0.10
14	REP+CH+CB+LOC	5	39.55	1.67
15	REP+CH+CB+LOC+TH	6	41.36	3.48
16	REP+CH+CB+LOC+TH+CW	7	43.20	5.32
17	REP+CH+CB+LOC+TH+CW+COVER	8	45.11	7.23
18	REP+CH+CB+LOC+TH+CW+COVER+USED	9	47.02	9.14
19	REP+CH+CB+LOC+TH+CW+COVER+USED+ TREEH	10	49.01	11.13
20	Full Model	11	51.00	13.12
Step 3				
21	REP	2	46.80	3.20
22	REP+ACTIVE	3	43.97	0.37
23	REP+ACTIVE+CH	4	43.75	0.15
24	REP+ACTIVE+CB+TYPE	5	44.49	0.89
25	REP+ACTIVE+CB+TYPE+CH	6	43.60	0.00
26	REP+ACTIVE+CB+TYPE+CH+CL	7	44.39	0.79
27	REP+ACTIVE+CB+TYPE+CH+CL+CC	8	45.60	2.00
28	REP+ACTIVE+CB+TYPE+CH+CL+CC+NH	9	47.19	3.59
29	REP+ACTIVE+CB+TYPE+CH+CL+CC+NH+LOC	10	49.01	5.41
30	Full Model	11	51.00	7.40

CC, circumference at cavity height; ACTIVE, is the termite mound an active mound?; CL, length of the nesting chamber; TYPE, type of termite mound; NH, height of the nest from ground level; PAD, the paddock in which the nest was located; NN, the distance of the nearest nest from the current nest; NO, orientation of the nest cavity entrance; HEIGHT, height of mound; REP, level of repair of termite mounds; CH, height of the nesting chamber; CB, circumference of the termite mound at the base; LOC, location of the mound—either on a flat or in a gully; TH, the height of the nest cavity tunnel; CW, the width of the nest cavity; COVER, estimated cover of mound; USED, was the termite used in the previous year; TREEH, height of nearest tree. K is the number of parameters in the model. Delta AIC (Δ_i), is the AIC value of the model, minus the minimum AIC value obtained.

Modelling nest-site limitation

None of the measured variables (table 1) described the likelihood of there being a suitable termite mound for a hooded parrot nest within the habitat, except for the paddock in which the survey was done (residual deviance = 10.0, $df = 3$, $P = 0.022$; table 10). Using the model to predict the number of suitable nest mounds per hectare, the highest concentration would be found in the adjoining Buntine and Redbank paddocks, fewer in Conical Land—a paddock dominated by conical termite mounds—and fewer still in DB Paddock (table 11).

Table 10. Akaike's Information Criterion (AIC) analysis of variables used to predict the likelihood of a termite mounds that is suitable as a nest-site for hooded parrots (*Psephotus dissimilis*) (i.e.: greater than 2 m tall, with more than 30% fresh cover).

Model	Variables	K	AIC	Δ_i
1	PAD	3	106.89	0.00
2	PAD+COW	5	108.21	1.32
3	PAD+COW+LOC	6	109.66	2.77
4	Full model	8	112.00	5.11

PAD, the paddock in which the nest was located; COW, the presence of cows; LOC, location of the mound—either on a flat or in a gully. K is the number of parameters in the model. Delta AIC (Δ_i), is the AIC value of the model, minus the minimum AIC value obtained.

Table 11. Occupancy rate of termite mounds that are suitable as nest-sites for hooded parrots (*Psephotus dissimilis*) (i.e.: greater than 2 m tall, with more than 30% fresh cover), Katherine, Australia, 2006–2007.

Paddock	Suitable mounds per ha	Nesting birds per ha	Occupancy rate
Buntine	2.0	0.026	0.013
Conical Land	2.7	0.006	0.002
DB Paddock	0.4	0.013	0.031
Redbank	3.8	0.034	0.009

Discussion

Most parrots are SCN birds that nest in preformed cavities in the trunks and branches of trees (Brightsmith 2000) and are therefore dependent on natural processes and other species to create nesting opportunities (Gibbons and Lindenmayer 2002). Hooded parrots, however, have evolved the ability to excavate their own nests in terrestrial termite mounds, presumably releasing them from the potential shortages of suitable nest-sites facing arboreal SCN birds, eliminating competition with those birds for a scarce resource and allowing them to nest in otherwise unsuitable areas (e.g., savannahs). Termite mounds are a conspicuous component of the habitat of hooded parrots, however, this study demonstrates that not all mounds are resources available for nesting parrots. Furthermore, not all termite mounds are equal as nest-sites, and the termites themselves, not just their termitaria, are important to the outcome of a nesting attempt.

What are the characteristics of hooded parrot nests?

Hooded parrots build their nest approximately 2/3 of the way up the tallest classes of termitaria in their habitat. Reed and Tidemann (1994) reported a similar result for the King River region, however the nests that they found were even taller than those found in this study (239 cm this study vs. 285 cm), with a resultant increase in the height of the nests (168 cm vs. 193 cm). Despite this, on comparable cavity measurements, there was little difference in either the tunnel height (6.9 cm vs. 7.1 cm) or cavity length (combined chamber length and tunnel length 48 cm vs. chamber length 52 cm) between the two studies (Reed and Tidemann 1994).

Many species of cavity nesting bird orient their nests to suit prevailing weather conditions, and nest orientation has been shown to be an important determinant of nesting success (Inouye 1976; Inouye *et al.* 1981; Facemire *et al.* 1990). Despite this, the orientation of the nest entrance tunnels of hooded parrots, like those of golden-shouldered parrots (Weaver 1987), was not significantly different from random. It may be that the greater bulk surrounding the nest cavity of termite mound nesting species, compared to an arboreal cavity nesting species, and the moderation of internal temperatures by the termites (Korb and Linsenmair 1998; Korb and Linsenmair 1999), reduces the importance of nest orientation in determining the nest microclimate.

An active mound was also a pre-requisite for the establishment of a hooded parrot nest. Nests were never found in inactive termite mounds, or in mounds with low levels of activity as measured by the correlated variables % cover and % repaired. Further, increasingly active termite mounds improved the nesting success of the parrots. The termitaria used by other nesting animals are nearly always reported as being active (Hindwood 1951; Legge and Heinsohn 2001; Brightsmith 2004; Kalko *et al.* 2006; Knapp and Owens 2008; but see Chisholm 1922), however this is the first time that the level of termite activity has been correlated with the success of a nest. The reason that more active termite mounds make better nest-sites remains unclear. Active termite mounds may camouflage the nests from visual predators, although a dark cavity hole may be more obvious on the exterior of a smooth termite mound. They may mask the smell of nesting parrots or clean up the mound to make it less obvious to olfactory predators, or they may physically repel some predators from the nest-site. Despite the occurrence of predation during this study, none was directly observed, and the identity of the predators involved remains unknown. Termites moderate the temperature and humidity of termite mounds (Korb and Linsenmair 1998; Korb and Linsenmair 1999). In the absence of termites, the mounds may revert to temperatures that are less suitable for successful nesting attempts. A final possible explanation is that the nest cavity is more stable in the presence of termites. Mounds degenerate when termites leave the mound (Lee and Wood 1971), and the coarse nature of *Nasutitermes triodiae* mounds may lead to cavities becoming unstable as the birds damage the nest cavity in ways that are repaired when the termites are present.

Conical mounds of the termite *Amitermes vitiosus* were not chosen in three of the four study paddocks, despite being present in all of them (albeit only as small mounds in DB Paddock). The only paddock in which they were chosen, was the Conical Land paddock, so named because only conical mounds were present. It was also this paddock that had the lowest rate of occupancy, highlighting that the parrot only nests in conical mounds in the absence of other suitable nest-mounds. The preference for *N. triodiae* mounds was also found by Reed and Tidemann (1994), although the precise composition of termite species was not reported. By contrast, the closely related golden-shouldered parrot nests exclusively in conical and meridian mounds of the termites *A. scopulus* and *A. laurensis* respectively, on the Cape York Peninsula, even though cathedral mounds also occur in their habitat (Weaver 1982).

At King River, conical mounds were generally smaller than cathedral mounds in all respects, so that cavity walls were thinner and tunnels shorter. Smaller mounds have been shown to have poorer microclimatic moderation than other mounds (Weaver 1987), a supposed benefit of termite mound nesting (Kesler and Haig 2005a). As hooded parrots orient their nest tunnels randomly, it may be that critical temperatures are avoided more often in the larger cathedral mounds, than in the smaller conical mounds, by dint of their greater mass, which results in increased fecundity for birds nesting in cathedral mounds. Another difference between the two types of termitaria is the density of the mound itself. The mounds of *Nasutitermes triodiae* are softer and more friable than the densely packed mounds of *Amitermes vitiosus* (SJNC pers. obs.). The former mound would presumably be easier to excavate, however, the golden-shouldered parrot’s preference for conical mounds again sheds doubt on this as an explanation for the hooded parrot’s preference.

Nests were found closer to tall trees than shorter trees, suggesting more open woodland, with less of a mid-canopy. This pattern may occur because of the risk of predation. For example, when golden-shouldered parrot nests were placed in sites with thicker vegetation they were less successful than those placed in a more open habitat, as a result of increased predation (Crowley *et al.* 2004). Despite this, height of the nearest tree was not significantly different between successful and unsuccessful hooded parrot nests. It may be that successful nest sites, which are therefore suitable nest mounds, were more likely to be positioned near tall trees than small trees, which reflects the behaviour of the termite rather than the parrot.

Hooded parrots never nested in close proximity to another nest. Although three nest pairs were found within 200m of each other, two of these pairs were separated temporally within the same breeding season and may represent re-nesting attempts by the territory holders, however a third pair (138m apart) nested simultaneously. If only contemporaneous nests qualify as the nearest neighbour, the mean distance between nests will be even greater than the 540m recorded.

Unlike Reed and Tidemann's (1994) study, none of the nests in the current study were reused from previous years. In the former research, 40% of nests were reused, although which of the four study sites on which this occurred was not recorded (Reed and Tidemann 1994). The lack of nest reuse in this study may be an artefact of interference with nests in 2006, however the appearance of accumulated dirt at the base of nests in both seasons suggests that nest reuse was low and excavations were recent.

The factors that make a termite mound suitable as a hooded parrot nest-site are that they are active, tall termite mounds of the spinifex termite *Nasutitermes triodiae*, situated in open woodlands, 500 metres from the next nearest hooded parrot nest. Further, the main characteristic of successful hooded parrot nests is that they are excavated in termite mounds in which the termites are relatively more active than in randomly selected termite mounds.

How abundant are nest-sites for hooded parrots?

Despite being a primary cavity nesting bird, hooded parrots did not have an unlimited supply of nest-sites. When only 'suitable' termite mounds are considered as a nesting resource, hooded parrots are shown to nest in a non-random part of the landscape. The parrots nest in parts of the landscape where large, active mounds are much more common than in the surrounding landscape. In the random surveys at this study site, active *Nasutitermes triodiae* mounds greater than 1.5 metres tall were distributed at approximately 2.4/ha, however in the nest-survey plots, there was a far higher concentration of suitable mounds per hectare (10/ha). In the 52, ¼ hectare, random surveys, habitat with this density of suitable termite mounds was encountered only three times.

A review of the estimated number of arboreal hollows by Waters *et al.* (1990) found between 1 and 15 cavities per hectare in Europe and between 0.2 and 6.4 in North America. In Australia between 0 and 26.9 hollow bearing trees per hectare may be present (Gibbons and Lindenmayer 2002). However, where authors have looked at the specific requirement of their study species (rather than the total number of hollows), numbers below one suitable nest per hectare have been found for large Psittaciformes (Nelson and Morris 1994; Legge *et al.* 2004), and between 1–16 cavities/ha for a clade of avian hollow nesting species (Saunders *et al.* 1982; Pell and Tidemann 1997). Brightsmith (2000) found 15.8 suitable arboreal termitaria nest-sites per hectare for two species of parrot and black-tailed trogons *Trogon melanurus* in Peru, whereas Kesler and Haig (2005a) found only 3.2 suitable arboreal termitaria nest-sites per hectare for kingfishers in Pohnpei: the latter result similar to the one reported here (2.4/ha). Both authors of these studies concluded that their reported number of potential nest-sites was in excess of the number used by birds in any particular breeding season. However, both of these studies, and others (see for example; Legge and Heinsohn 2001) state that both intra- and inter-specific competition may have a role in rendering some nest-sites unavailable.

Two non-parrot nests were found concurrent with the hooded parrot breeding season (both red-backed kingfisher nests). Reed and Tidemann (1994) also found both a northern quoll (*Dasyurus hallucatus*) and a black-headed monitor (*Varanus tristis*) in hooded parrot nests. Both of these species are predators of hooded parrots (Higgins 1999), however neither were seen during the current study period (either in mounds or anywhere else), possibly as a result of the expansion of the introduced cane toad (*Bufo marinus*; SJNC pers. obs.). Nineteen suitable mounds had holes in them that suggested that they had been used as a nest- or roost-site in previous years by an unknown species; four of these mounds were used by hooded parrots as nest-sites in this study (although the parrot excavated a new cavity in each case), which suggests that previous use of mounds is not a restriction to later use. However, this level of previous use is likely to be an underestimation, given that one day’s expansion of the mound by the termites could easily cover any signs of previous use (Kesler and Haig 2005b). While hooded parrot predators would clearly displace a nesting attempt, it is not known what the outcome of agonistic interactions between hooded parrots and other, non-predatory termite nesters (such as red-backed kingfishers) would be. Thus the impact of interactions between hooded parrots and other potential termite mound users is largely unresolved, but does seem likely to have a small impact on the availability of suitable termite mounds.

In summary, only certain parts of the landscape are utilised by the parrots (where suitable mounds are concentrated), territoriality keeps nesting birds apart and, at least occasionally, some of the remaining potential mounds are used by other nesting species. Further, only three nests were found in conical mounds, despite the low occupancy rate in this paddock, suggesting a strong preference for the cathedral mounds of *N. triodiae* over the conical mounds of *Amitermes vitiosus.* However, although only a subset of termite mounds are available as nest-sites, the occupancy rate of these mounds remains very low. More work is required on these aspects of nest-site limitation before an argument can be made that suitable termite mounds are in short supply.

Crowley *et al.* (2004) found that suitable nest-sites for the golden-shouldered parrot may be limiting population growth, but for different reasons than considered here. They cite damage to existing mounds and slow recruitment of new mounds to a height usable by the parrots (Crowley *et al.* 2004). Whilst damage to mounds from cattle and at least partial loss of seven hooded parrot nest mounds either during or after the nesting season did occur, the mounds of *N. triodiae* can grow quickly, with a volume of approximately 20 cm^3 being added in one building session (SJNC pers. obs.). Therefore it is unlikely that an absolute lack of mounds is limiting for hooded parrots, but that the range of aforementioned factors leads to some mounds being unusable.

Inappropriate fire regimes are blamed for the loss of suitable nesting mounds for golden-shouldered parrots and the poor recruitment of termitaria generally (Crowley *et al.* 2004). Although the presence of fire in this study was measured, the rapid growth of vegetation following fire made these measures coarse and different topographical locations may have resulted in different estimations of time since fire. Given the frequency of fire in this habitat, it would be unlikely that fire did not have some bearing on the distribution of termites and therefore on suitable hooded parrot nest-sites, despite the ambiguous results presented here.

The shift from SCN to PCN is shown to benefit the parrot in a number of ways. Whilst the number of suitable mounds was not unlimited, a large number of mounds could be found in all four paddocks. Although the precise mechanism was not revealed, this study shows that nesting in active termite mounds improves nesting success for hooded parrots. It may be that the microclimatic benefits of nesting in a temperature moderated structure confer fitness advantages (Kesler and Haig 2005a; Kalko *et al.* 2006). Parasite loads have been shown to be lower in termite mound nests than arboreal cavity nests (Kalko *et al.* 2006), which can affect the fitness of both the parental birds and their chicks. Finally, it may be that ecological shifts to novel nesting niches may reduce the risk of detection by nest predators (Brightsmith 2005b).

While this study has characterised the nature of hooded parrot nests and gone some way to explore the abundance of suitable nest-sites for these birds, more work remains to be done. Hooded parrots do nest in other types of termite mound in other parts of their range (Reed and Tidemann 1994) and these parrots may have nest mound preferences that differ to those exhibited by the study population. Nevertheless, the results demonstrate that the benefits to the parrots of PCN, and of a commensal relationship with termites, may be both direct and indirect. The mechanism by which termites in improve nest success, however, remains an unresolved, yet intriguing, question.

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CHAPTER IV

Photo: Natalie Barnett

A new species of *Trisyntopa* Lower (Lepidoptera: Oecophoridae) associated with the nests of the hooded parrot (*Psephotus dissimilis*, Psittacidae) in the Northern Territory

Edwards E. D., Cooney S. J. N., Olsen P. D. and Garnett S. T. (2007). *Australian Journal of Entomology*. **46**, 276–280.

Abstract

Trisyntopa neossophila sp. n. (Lepidoptera: Oecophoridae), reared from the nest of the hooded parrot (*Psephotus dissimilis* Collett), is described using morphological characters. Aspects of its biology are reported and similarities to the biology of *Trisyntopa scatophaga* (White) found in the nests of the golden-shouldered parrot (*Psephotus chrysopterygius* Gould) are discussed and questions formulated to suggest further work on the parrot–moth relationship. The possibility that a moth was associated with the extinct paradise parrot (*Psephotus pulcherrimus* (Gould)) is considered in the light of the phylogenetic relationships between the parrots.

Introduction

The genus *Trisyntopa* Lower, 1918 was reviewed by Common (2000) who placed it in the *Chezala*-group of genera of the Oecophorinae and recognised two species, *T. euryspoda* Lower and *T. scatophaga* (White). Common's work was summarised by Edwards (2004) for the Oecophoridae part of the *Zoological Catalogue of Australia*. *Trisyntopa euryspoda* is found widely in Australia from coastal areas in New South Wales (NSW) and Western Australia (WA) to the arid zone in central Australia. It has been reared from the nests of the eastern rosella (*Platycercus eximius* (Shaw)) in coastal NSW and the mulga parrot (*Psephotus varius* Clark) in western Queensland (Qld) and is suspected to be present in the nests of other Psittacidae, Platycercinae, because it is found where neither of the two recorded bird species occurs. These parrots nest in hollows in trees. Further details of the association of *T. euryspoda* with parrots may be found in Hindwood (1951) and Common (2000). *T. euryspoda* seems to be an occasional inhabitant of nests, with most nests without moths. Most of the moths in collections have been taken at light. In contrast, the termite-mound-nesting parrots of the genus *Psephotus* Gould seem to be closely associated with different species of moths. Larvae of *T. scatophaga* have long been known to live in the nests of the golden-shouldered parrot (*Psephotus chrysopterygius* Gould) which is now found only in a limited area on Cape York Peninsula and is currently considered endangered. Further details of the association of *T. scatophaga* with the golden-shouldered parrot may be found in Turner (1923), Thompson (1935), Chisholm (1956), Garnett and Crowley (1995), Zborowski and Edwards (2007) and Olsen (2007). It is found in the great majority of nests of the golden-shouldered parrot, has never been taken at light, and all known specimens have been reared from cocoons collected from nest hollows. The larvae of both *T. euryspoda* and *T. scatophaga* feed on the faeces of the nestlings in all recorded cases.

In May 1979, IFB Common received a female moth for identification reared by MA Reed from a nest of the hooded parrot (*Psephotus dissimilis* Collett) near Katherine, NT. The female genitalia of Oecophoridae are usually less informative than the male genitalia, so the moth was identified on superficial characters as *T. scatophaga* and returned. But because only a female was known there remained some doubt as to the identity of the moth.

The remaining termite-mound-nesting *Psephotus*, the paradise parrot (*P. pulcherrimus* (Gould)), of south-east Queensland, is almost certainly extinct. In researching a book on the parrot, it became evident that it too was possibly associated with a moth. To add credence to that hypothesis, it was necessary that the uniqueness, or otherwise, of the hooded parrot moth was established. Hence, one of us (SC) has commenced a project to study the relationship between the hooded parrot and the moth. As a result, a series of moths reared from cocoons collected by two of the authors (SC and SG) is now available for study. These moths have proved to be very similar to *T. scatophaga* in appearance, although small differences can be found, but the male genitalia show clear specific distinctions.

This paper describes the moth using traditional morphological taxonomic criteria. Molecular, population and ecological studies are part of a continuing project. The term ‘close association’ is here used to indicate the situation where moths have only been found in the nests of one species of parrot and the majority of nests are inhabited by moths. But because so little is known of the details of the association, more precise terms are inapplicable without making unjustifiable assumptions about the nature of the association. The following abbreviations are used for the Australian National Insect Collection (ANIC) and for the Northern Territory Museum and Art Gallery (NTM).

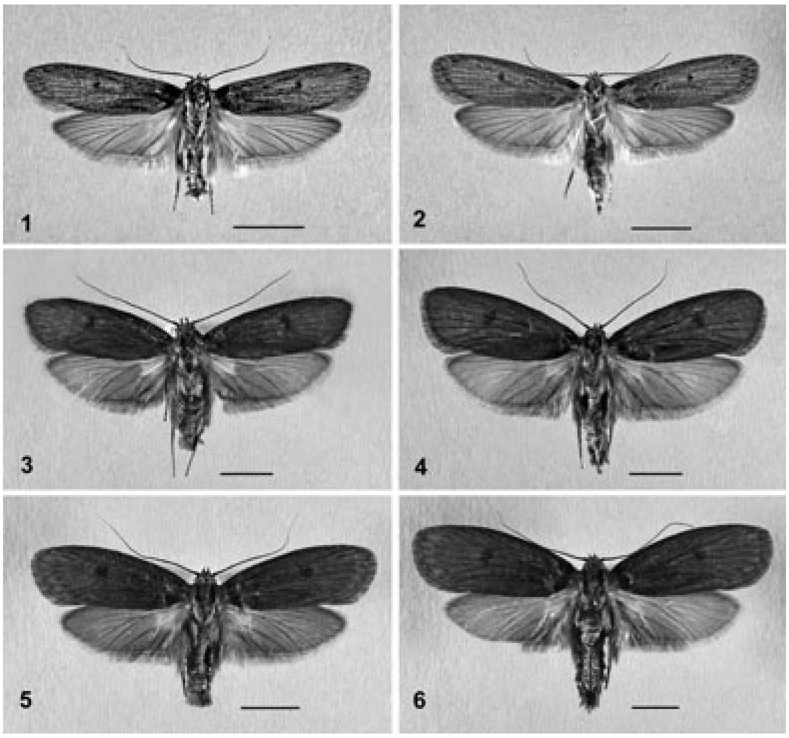
Systematics

Trisyntopa neossophila Edwards, sp. n.

(Figs 3, 4, 9, 10, 14)

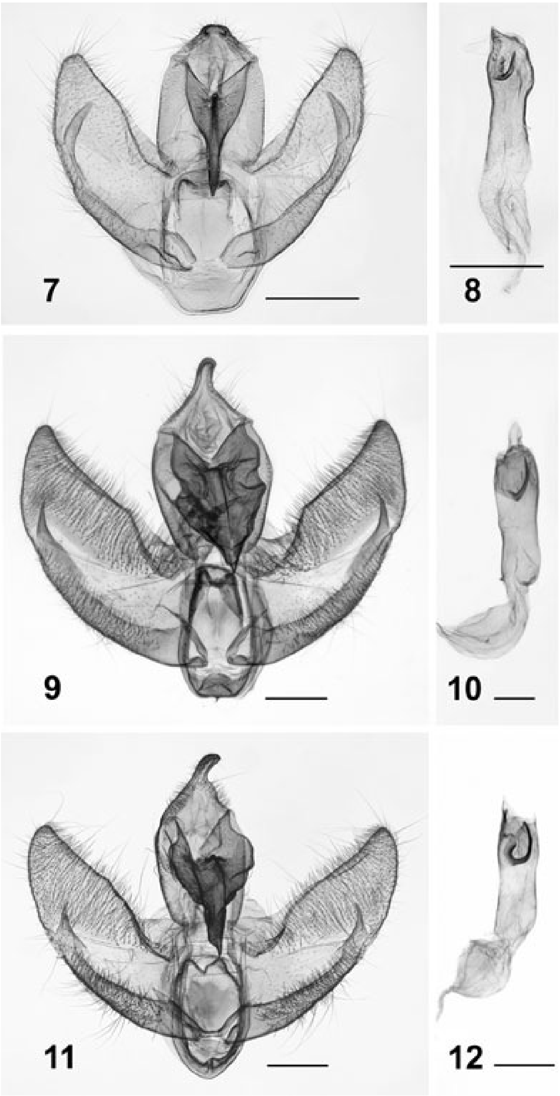
Types. ***Australia***. Holotype: male, Northern Territory, nr Katherine, 14°412S, 132°052E, 9 March 2006, S Cooney, S Garnett. Larva in cocoon in wall of hooded parrot nest in *Nasutitermes triodiae* mound (in ANIC). Paratypes: 9 males, 6 females same data and year as holotype but dated 5 February, 27 February, 6 March, 6 March, 13 March, 29 March, 29 March, 30 March, 4 April, 6 April, 6 April, 18 April, 20 April, 20 April, 19 May with genitalia slides ANIC 18586, 18590, 18592. In ANIC and NTM.

Diagnosis. Forewing uniformly dark grey with a darker spot at end of cell and an obscure darker spot in cell. Hindwing uniformly pale grey with hyaline area near base. Male genitalia with a broad winged gnathos narrowing abruptly to the tip.



Figs 1–6. Habitus of adult *Trisyntopa* species. Odd numbers, males; even numbers, females: **1, 2** *T. euryspoda*; **3,4** *T. neossophila* sp. n.; **5, 6** *T. scatophaga*. Scale bars = 5 mm.

Male. Forewing length 13–15 mm. Above. Head: proboscis vestigial; antenna simple, shortly ciliate; frons, vertex and antenna dark grey: thorax, legs and abdomen dark grey. Forewing costa gently, evenly bowed, termen slightly oblique gently rounded, inner margin almost straight; dark grey, a darker grey circular spot at end of cell, a poorly defined, faint darker spot halfway between base and end of cell, a faint dark streak along CuP, cilia dark grey. Hindwing apex rounded, termen slightly rounded, tornus rounded; pale grey, darker towards inner margin, a hyaline area at base extending outwards along CuP, cilia grey, paler in middle. Beneath, both wings silvery grey, a fine, slightly darker terminal line in forewing and around apex of hindwing but becoming paler around termen of hindwing, hyaline area at base of hindwing.

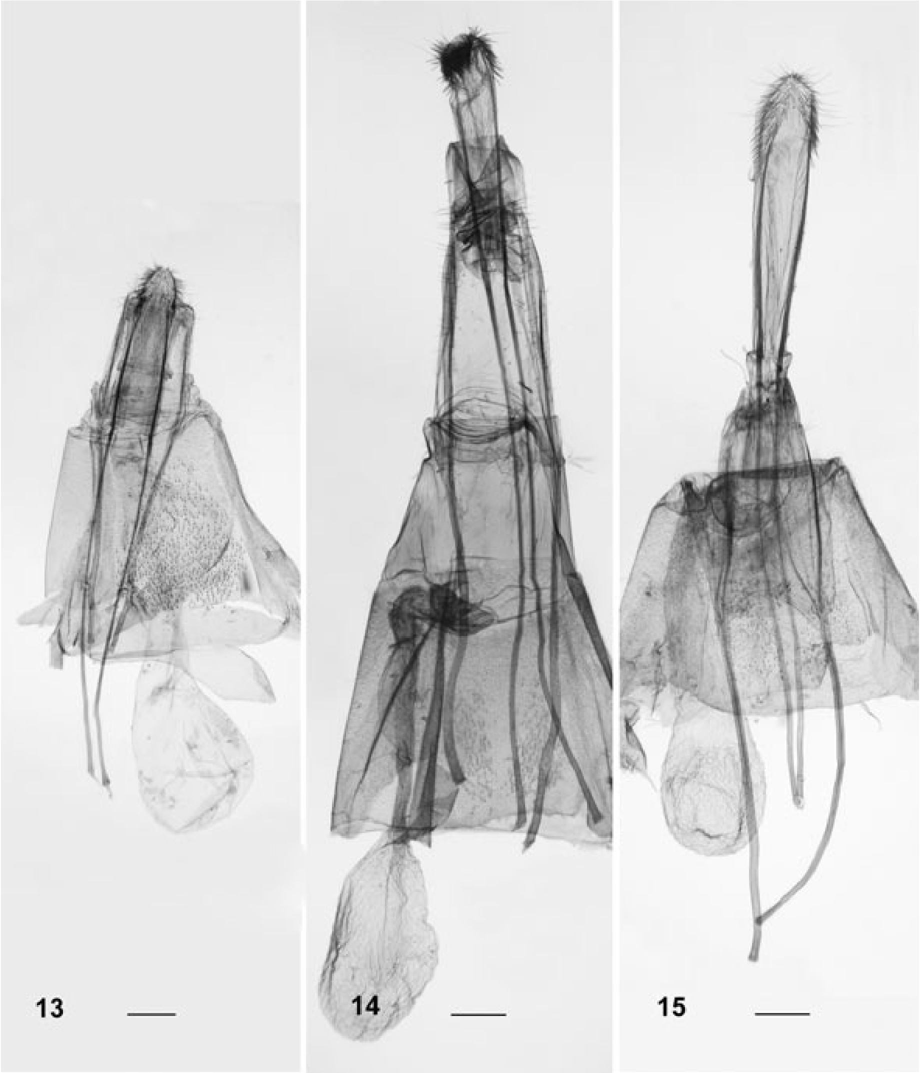


Figs 7–12. Male genitalia of *Trisyntopa* species. Odd numbers, genitalia; even numbers, aedeagus 7, 8 *T. euryspoda*; 9, 10 *T. neossophila* sp. n.; 11, 12 *T. scatophaga*. Scale bars = 0.5 mm.

Female. Forewing length 15–17 mm. Larger, similar to male, antennal cilia similar to male.

Male genitalia. Figures 9 and 10. Heavily sclerotised, uncus short, rounded at tip, gnathos large, with raised median ridge, greatly broadened laterally almost to tip, leaf-shaped, lateral margin waved, tapering abruptly to small tip, valva with saccular margin evenly and strongly convex, distal process at about three quarters, pointed, costa humped at about a third then gently concave to near tip, all sclerotised parts with numerous short setae, juxta sclerotised, with median dorsal indentation, almost twice as high as broad, vinculum rounded, aedaegus, short, stout, orifice oblique, with single curved cornutus.

Female genitalia. Figure 14. Abdominal segments 8 and 9 + 10 extensible, long narrow, papillae anales slender with numerous dorsal and lateral stout spines, ostium with a sclerotised, crescentic, ventral band within a broad pouch ventrally at posterior margin of segment 7, ductus bursae about same length as S7, corpus bursae spherical without signum.



Figs 13–15. Female genitalia of *Trisyntopa* species: 13 *T. euryspoda*; 14 *T. neossophila* sp. n.; 15 *T. scatophaga*. Scale bars = 0.5 mm.

Fully grown larva. Stout, pale bluish white, secondary setae absent, 25 mm long, 6 mm broad. Head hypognathous, heavily sclerotised, smooth, frontoclypeus longer than wide extending three quarters to epicranial notch. Prothorax with large heavily sclerotised plate; L group trisetose in triangle, thoracic segments with setal group L and groups situated more dorsally all on prominent sclerotised pinacula. Abdomen all setal groups L and above on prominent sclerotised pinacula; A1, A7 with SV group bisetose; A9 with D1 anterior to D2; prolegs short with crochets biordinal in circle.

Etymology

The species name is derived from the Greek; *neossos* meaning nestling and *philos* meaning fond of.

Biology

The known specimens of *T. neossophila* have been reared from a cluster of cocoons and carton removed from the wall of a nesting chamber of the hooded parrot. Larvae have been seen in the debris on the floor of an active nesting hollow and have been observed, like the larvae of *T. scatophaga*, to feed on the faeces of the nestlings thus keeping nesting hollows relatively clean. They eat the faecal part of the pellets, rejecting the uric acid. Small larvae live in loose debris in the bottom of the nest, but larger larvae form silken tubular shelters in the debris. Cocoons were formed on the inner wall of the nesting chamber. Adults have emerged from cocoons shortly after they were formed or after approximately 10–12 months. Those that emerged after about 10 months passed a resting period, presumably a diapause, as prepupal larvae. All 12 hooded parrot nests examined by SC in 2006 were populated by moth larvae although in a few they died because of the death of the nestlings. No alternative hosts for the moth are known. The evidence strongly indicates that *T. neossophila* has a similar close association with the parrot as that of *T. scatophaga*.

Discussion

Trisyntopa euryspoda (Figs 1, 2) is easily distinguished from the other species in the genus by having much narrower wings, much paler grey forewings and very pale grey hindwings. The forewings often have most veins darker and there is usually an ill-defined submarginal row of either darker or paler spots between veins. *Trisyntopa scatophaga* (Figs 5, 6) and *T. neossophila* are very similar to each other and perfectly preserved adults are needed to discern the differences. *Trisyntopa scatophaga* has slightly narrower wings and the dark marking between the discal spot and the base of the forewing is a poorly defined line rather than a spot. It also often has traces of a poorly defined subterminal row of slightly paler spots between the veins on the forewing which are not present in *T. neossophila*.

The male genitalia are depicted with the gnathos depressed to show the diagnostic differences, departing for the purposes of this paper from the Common (2000) standard slide preparation. The male genitalia of *T. euryspoda* (Figs 7, 8) are significantly smaller, less robust and less sclerotised than in the two other species. The uncus is shorter with a broader tip; the gnathos is long and tapering with a very prominent, raised, median ridge. The distal process of the valva is relatively larger and the juxta is dorsally broader with a wide indentation. *Trisyntopa scatophaga* (Figs 11, 12) and *T. neossophila* have more similar male genitalia but differ particularly in the shape of the gnathos which is widened or winged towards the base and tapers evenly and gradually to well before the tip in *T. scatophaga*. In *T. neossophila*, the gnathos is very broadly winged, waved and the wings taper more steeply to the tip and extend almost to the tip. The median ridge of the gnathos is prominent in *T. scatophaga* but much less prominent in *T. neossophila*. The juxta is shorter in *T. scatophaga* than in *T. neossophila* and the valvae are narrower with the distal process shorter and broader at the base.

The female genitalia of *T. euryspoda* (Fig. 13) have a tighter ostial band than the other two species and the corpus bursae, under high magnification, has a long narrow signum made up of many minute spicules. *Trisyntopa scatophaga* (Fig. 15) and *T. neossophila* have a more open ostial band and the corpus bursae is without traces of a signum. No differences could be discerned between *T. scatophaga* and *T. neossophila*. These species have only ever been reared and so the corpus bursae in the preparations is not expanded as it would be expected to be in wild-caught, mated females.

Limited information on the biology of the moths is available, but a significant behavioural difference is that the cocoons of *T. scatophaga* are formed in the thin wall of the nest hollow between the nest cavity and the exterior of the mound with the cocoons extending from the inner to the outer walls. William McLennan, who first discovered the nests of the golden-shouldered parrot, observed that the larvae always spun cocoons in the thinnest part of the nest wall (Turner 1923). On two occasions they have also been observed to spin cocoons in the nest entrance tunnel, resulting in the death of nestlings (SG pers. obs. 1993). It is thought that burrowing in the wall so that the cocoon abuts the outside of the mound allows the escape of the moths to the exterior should the termites, following the completion of nesting, repair the birds' entrance hole. The golden-shouldered parrot nests in the conical mounds of *Amitermes scopulus* (Mjöberg) and the 'magnetic' mounds of *A. laurensis* (Mjöberg), both fairly narrow mounds. Very rarely does the golden-shouldered parrot nest in mounds of *Nasutitermes triodiae* (Froggatt) (Higgins 1999). In contrast, the hooded parrot usually nests in the large and often bulbous mounds of *N. triodiae* and *T. neossophila* forms its cocoons on the inner wall of the nesting hollow. In this termite species, the walls of the mound are used to store harvested grass chaff and may be too thick for the larvae to penetrate to the outside, the grass stores may be too unstable as a substrate for cocoons or the cocoons may be too prone to being walled in by the addition of further storage bulges.

Biological studies on the moth are currently in progress but to date little is known. William McLennan (Turner 1923) observed mating moths in a nest with parrot eggs present. How do the moths find new active nests? Do the moths have alternative hosts? Do the moth larvae contribute significantly to nest hygiene? Do nests with moths, overall, have a different fledging success to nests without? Do the parrots ever eat moth larvae; a female golden-shouldered parrot was once filmed killing a *T. scatophaga* larva and feeding it to a chick (SG pers. obs. 2001)? Is the association between the moth and parrot commensal or mutualistic? Finally, do the answers to some of these questions have implications for the conservation of the birds?

Of the three termite-mound-nesting *Psephotus* one is almost certainly extinct, one is endangered and the third is threatened by overgrazing and inappropriate fire regimes (Garnett & Crowley 2000). Would it be prudent to attempt to introduce moths into aviary cultures of both hooded and golden-shouldered parrots to guard against the total loss of the moth species should either parrot become extinct in the wild? Moths would then survive and be available should reestablishment of the birds in the wild be contemplated.

The morphological evidence suggests that *T. scatophaga* and *T. neossophila* are more closely related to each other than they are to *T. euryspoda* (they share the enlarged, very heavily sclerotized male genitalia, the winged gnathos, broad wings and dark colour) and that *Trisyntopa* is monophyletic (Common 2000). The most parsimonious hypothesis is that the close moth association developed in a common ancestor to *T. scatophaga* and *T. neossophila*.

Did the paradise parrot also have a moth associated with it? A search of museum collections has failed to locate a preserved mound and nest hollow of the paradise parrot which could be checked for silken tunnels and cocoons.

If *T. neossophila* originated from a host switch of *T. scatophaga*, or vice versa, then this will provide no information on the likelihood that the paradise parrot had a close moth associate. If, however, the moths and parrots coevolved then some further information can be gleaned. It should be recognised that, even if the paradise parrot had a close moth associate, it could have been a now-extinct moth or one of the extant moths.

There seems little doubt that the three termite-mound nesting *Psephotus* form a monophyletic group. The unity of this group has never been questioned and the subgenus *Psephotellus* Mathews comprising just these three species was used in the *Zoological Catalogue of Australia* by Schodde (1997) who also stated that the phylogenetic relationships between the three species were in need of clarification. A molecular phylogeny of the species of *Psephotellus* has been investigated, but the results have not been published (J Norman & L Christidis pers. comm. 2006). However, preliminary results (Christidis & Norman 1996a, b) suggest that the paradise parrot and golden-shouldered parrot are the most closely related of the three. Should these preliminary results not be supported by future work it is notable that two of the three possible different phylogenetic trees showing the parrot’s relationships would support the hypothesis that the paradise parrot had an associated moth and the third is neutral.

Acknowledgements

I greatly indebted to David Britton and Walter Boles, Australian Museum, to Chris Burwell, Queensland Museum and to Peter Marriott, Museum Victoria for checking if their institutions held preserved nest hollows of the paradise parrot. Jak and Jade Irwin, managers of Manbulloo Station, allowed us access to the property. Don Sands and Brian Fletcher helped with specimens and information about *T. scatophaga* and Leo Joseph with parrot advice. Janette Norman kindly provided information on the progress of her molecular studies on parrot relationships. Natalie Barnett took the adult photographs, Robert Edwards for discussions on possible moth and parrot relationships and Vanna Rangsi took the photographs of the genitalia. Marianne Horak, Andreas Zwick and Vanna Rangsi provided constant help advice, and with John Trueman, helpful comments on the manuscript. SC would like to thank his supervisor, Andrew Cockburn, ANU, for his support and the Birds Australia Stuart Leslie Bird Research Award for funding.

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Accepted for publication 4 March 2007.

CHAPTER V

Photo: S. J. N. Cooney

Ecology of the coprophagous moth *Trisyntopa neossophila* Edwards (Lepidoptera: Oecophoridae)

Cooney S. J. N., Olsen P. D. and Garnett S. T. (In press). *Australian Journal of Entomology*.

Abstract

Trisyntopa neossophila (Edwards) (Lepidoptera: Oecophoridae) is an unusual moth whose breeding cycle is closely synchronised with a termite mound nesting parrot of northern Australia; the hooded parrot (*Psephotus dissimilis* Collet). *T. neossophila* is one of three coprophagous, nest dwelling moths in the genus *Trisyntopa* Lower 1918. True coprophagy is rare in the Lepidoptera, although some species occasionally consume faeces to gain rare nutrients. We present observations of the life cycle of *T. neossophila*, a moth that lays its eggs in the nest of a hooded parrot so that larvae hatch in synchrony with the hatching of the parrot's eggs. The larvae spend their larval period in the nest and exclusively consume the excrement of the nestling parrots. When the parrot chicks fledge, the larvae move to the walls of the nest cavity to pupate, emerging the following wet season to repeat the process during the next parrot breeding season.

Introduction

The majority of moth and butterfly species are phytophagous, with nectar feeding adults and plant tissue feeding larvae (Robinson 2004), although a range of other dietary niches are also exploited (Scoble 1992). One such variant, coprophagy, is extremely unusual among the Lepidoptera (Common & Horak 1994) and is most commonly noted in the Tineoidea. However, this diet has also been reported in a number of other phylogenetically disparate lepidopteran lineages and has evolved on a number of separate occasions (Waage & Montgomery 1976; Robinson & Nielsen 1993; Robinson 2004). Birds' nests are a common source of food for coprophagous lepidopterans. Despite this, recent research suggests that many of the species purported to be coprophagous are keratophagous, with a diet composed largely of feathers shed in the nest or nesting materials, rather than the avian hosts' faeces (Robinson 1988; Robinson 2004). An exclusively coprophagous diet is especially uncommon because lepidopteran larvae grow too slowly to compete for the resource in the presence of other coprophagous insects or are more sensitive to poor quality diets than other animals (Piñero & López 1998).

Where coprophagy does occur, it may be a means of providing nutrients important for reproduction. For example, nitrogen is required for egg production and is stored by larvae for that purpose (Labine 1968; Engelmann 1970; Gilbert 1972; Dunlap-Pianka *et al.* 1977). Coprophagous lepidopterans can supplement their larval reserves by consuming nitrogen rich foods, such as faeces. Coprophagous species also derive other nutrients for egg production from the uric acid or partly digested proteins in bird droppings (Dunlap-Pianka *et al.* 1977; Ray & Andrews 1980).

The family Oecophoridae is estimated to contain 5000 species of Australian moths, representing 20% of Australia's Lepidoptera (Common 1996; Common 1994). It includes only two genera that are known to be coprophagous (Common 1994). The genus *Telanepsia* comprises four species that feed on brush-tailed possum (*Trichosurus vulpecula* Kerr) and koala (*Phascolarctos cinereus* Goldfuss) dung. The dung contains undigested leaf litter, which is the most common diet of oecophorid moth larvae (Common & Horak 1994).

The genus *Trisyntopa* Lower, 1918 consists of three species that live in the nests of Australian parrots. All three species eat the excrement of parrots (Turner 1923; Thomson 1934; Hindwood 1951). The type species, *Trisyntopa euryspoda* Lower, 1918, was identified from the nests of eastern rosellas (*Platycercus exemius* Shaw) and subsequently found in mulga parrot (*Psephotus varius* Clark) nests and at light traps (Common 2000). These two parrots nest in cavities in the limbs and trunks of trees. The next species to be described was *T. scatophaga* (White 1922). This species was recovered from the nests of the golden-shouldered parrot (*P. chrysopterygius* Gould) which nests by excavating tunnels in termite mounds on the Cape York Peninsula, Queensland (White 1922). When similar looking larvae were noted in the termite mound nests of the hooded parrot (*P. dissimilis* Collett), the sister species to the golden-shouldered parrot, it was assumed that it too was *T. scatophaga* (Higgins 1999; Common 2000; Common 1994). It was not until 2005 that specimens of the larvae inhabiting hooded parrot nests were collected, reared and the adults subsequently described as a new species of moth, *T. neossophila* Edwards (Edwards *et al.* 2007). This recently described species is the focus of this study.

T. scatophaga and *T. neossophila* have only been recovered from the nests of golden-shouldered and hooded parrots, respectively, and studies of the breeding ecology of the golden-shouldered parrot indicate that moths are present at nearly all nesting attempts (Garnett & Crowley 1998). Early notes on the behaviour of *T. scatophaga* suggest that the appearance of the larvae is synchronised with the hatching of the parrot eggs (Campbell 1924). Once hatched, the larvae tunnel into the floor of the nest and build silken galleries, in which they gain protection from the movements of the parrot chicks (Turner 1923). When the chicks defecate, the larvae rapidly emerge from their tunnels and consume the faeces that fall on both the floor of the nest and on the chicks themselves (Turner 1923). In this way the nest cavity and nestlings are kept free from a build up of faecal matter. Prior to the parrots fledging, the moth larvae form a cluster of cocoons in the outer wall of the termite mound (Turner 1923), usually at the thinnest point (S. Shephard pers. comm.). The cocoons are arranged to resemble a honeycomb and line up horizontally across the cavity wall so that the imago can gain access to the exterior on emergence (Thomson 1934). Usually, the circular set of hexagonal casings is clearly visible from the outside of the mound, each moth having its own fibrous chamber (S. Shephard pers. comm.).

This study reports on the first observations of the behaviour of *T. neossophila* in the nests of hooded parrots. The observations were made during a study of the breeding ecology of hooded parrots, undertaken to determine the nature of the relationship between the moth and the parrots. Here we describe the unusual ecology of the larval stages of *T. neossophila* and contrast this behaviour with what is known about the closely related species, *T. scatophaga*.

Methods

Study Site

An area 30 kilometres east of Katherine, Northern Territory, Australia (S 14º 40’ 08" E 132º 05’ 27"), was searched for termite mound nests of hooded parrots during two field seasons between January and April 2006 and January and May 2007, spanning two full hooded parrot breeding seasons. In 2007 a volunteer workforce increased the survey effort, resulting in the location of more nests. The study area has a monsoonal climate, characterised by hot, wet summers and cool, dry winters. My work was based on a private cattle property (Manbulloo Station) and included both rocky ridge country, characterised by shallow gullies that form peripheral rocky ridges (nests = 34), and black soil country, characterised by well drained sandy flats (nests = 2). The vegetation on Manbulloo Station is an open tropical savannah, with an overstorey of Northern Salmon Gum (*Eucalyptus bigalerita*) and Darwin Stringybark (*E. tetrodonta*), and an understorey dominated by grasses from the genus *Sarga*. Mounds >1.5 metres high occurred at a density of approximately 7.8 termite mounds per hectare (S. Cooney unpub. data). Most (90%) termite mounds were built by the cathedral termite *Nasutitermes triodiae* (Frogatt); the remaining 10% were built by the conical mound termite *Amitermes scopulus* (Mjöberg) (S. Cooney unpub. data).

Nests were monitored every four days after discovery for the duration of the nesting period of the parrot. During this period, the behaviour of *T. neossophila* was also monitored.

Life cycle and behaviour

The dates at which moths and then larvae were first seen in each nest were recorded, as was the date of pupation. We collected some pupal cases in 2006, allowing the date at which the moths emerged to be recorded.

In 2006, larvae were removed from active nests and measured using digital Vernier callipers to the nearest 0.01 mm, however larvae have the consistency of a concertina and therefore the results were inconsistent. In 2007 we abandoned this measurement technique, and 5 randomly collected larvae were removed from active parrot nests and weighed to the nearest 0.01 g on digital scales. When all the larvae were removed from nests for an experiment on the nature of the relationship between moth and parrot, these larvae were also weighed. The mean of these weights was then calculated for each nest.

All of the larvae were removed from the nest cavity of ten randomly selected hooded parrot nests. The larvae were extracted by removing and sorting through the termite mound detritus at the base of the cavity. The detritus was then replaced. The larvae were then counted and weighed and the nest monitored for the appearance of more larvae that were also removed, counted and weighed.

Notes were kept of the behaviour of the larvae and moths on an *ad hoc* basis. Larvae could be observed when we accessed the parrot nest through a portal cut in the side of the termite mound, which was later plugged. We also used a video camera attached to a 22 mm diameter camera (Allthings Sales & Service: Bullet-DSP; 3.6 mm lens; 297 984 pixel ¼ inch Panasonic CCD sensor), lit by white LED lights, that was left to record the behaviour of the moths while the parrot chicks were being measured away from the nest.

Analyses

Logistic regression analysis and descriptive analyses of morphological measurements and dates were conducted with Genstat 8.1 statistical software. Dates were converted to Julian dates for analysis.

Results

Fifty three hooded parrot nests were found in the cathedral mounds of *Nasutitermes triodiae* and another three nests were found in the conical mounds of *Amitermes scopulus* (11 in 2006; 42 in 2007). All of these nests had been freshly excavated by the parrot for the respective breeding seasons. Nine nests were depredated while they contained only parrot eggs, and another two within 5 days of the parrots hatching. Moth larvae were not detected in these nests. Of the remaining 42 nests, 38 (90.5%) were found to contain larvae of *T. neossophila* (36 in *N. triodiae*; 2 *A. scopulus*). Four nests contained no moths, three of which were depredated approximately 14 days after the first chicks hatched, while the remaining nest successfully fledged a single chick. This last nest, however, had its cavity entrance pointed upwards, so the nest became wet during a monsoonal period, possibly affecting any larvae or moth eggs in this nest. The high frequency of this association is similar to the relationship between *T. scatophaga* and the golden-shouldered parrot. In nests checked for moths on Artemis Station, Queensland, *T. scatophaga* larvae were noted in 97.4% of nest cavities (S. Shephard pers. comm.).

Life cycle

Egg laying

An average of 2.3 (s.d. ± 0.87, range 1–4, n = 16) adult moths were seen in the nests of hooded parrots on 16 occasions (mean appearance date 16 February, range 13 February–17 February, with an outlier on 1 March). At ten nests, moths were seen once, while at three nests moths were seen on consecutive visits. Moths were only detected in nests during the laying period of the parrots; no moths were seen once the clutch was complete, nor when there were chicks in the nest. Likewise, up to three individual *T. scatophaga* moths have been seen in golden-shouldered parrot's nests early in the parrot's laying cycle, and some even prior to the commencement of laying (S. Shephard pers. comm.).

Nests were checked during the daylight hours of 6 am to 1 pm and moths could be detected at any time throughout this period.

Hatching

The mean date of the larvae being first detected, which was rigorously recorded only in the 2007 season, was 12 March (range 2 March–9 April). This was 10 days after the first chick hatched (± 3.9, 5–20, 24).

Growth

Larval weights ranged from 0.02 g at detection, to 0.62 g immediately prior to pupation, approximately 25 days later. During this period, larvae grew from approximately 0.7 mm to 35.6 mm in length, however at no stage was only one size class apparent, with both large and small larvae in the same nest suggesting progressive hatching of moth eggs. This was confirmed by the appearance of larvae in nests that had previously been cleared of larvae. Nonetheless, there was a strong correlation between the larva weight and chick age (Weight (g) = -0.0969 + 0.024 chick age (d), n = 48, Adj R^2 0.714, F < 0.001; Fig. 1).

Number of larvae

An average of 52.7 (± 15.6, 25–72, 10) larvae were removed from each of the 10 studied parrot nests (mean weight 0.2 g, ± 0.13, 0.05–0.40, 527). On three occasions, larvae were subsequently found in nests that had previously had the larvae removed. In one instance, a further 27 larvae (mean weight 0.12 g) were taken from a nest from which 71 larvae had been removed four days previously.

There was no evidence of a decline in the number of larvae as the nesting period progressed, as is suspected to occur in *T. scatophaga* (S. Shephard pers. comm.), although this was not specifically measured.

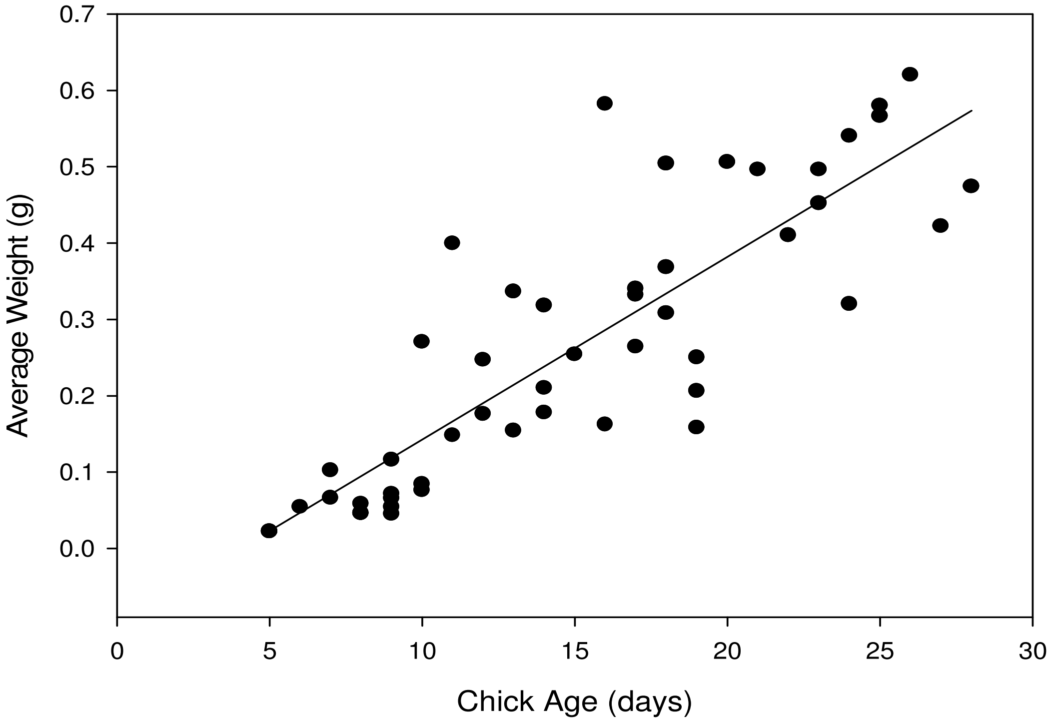

Fig. 1. Mean weight of *Trisyntopa neossophila* larvae plotted against age of oldest hooded parrot *Psephotus dissimilis* chick during 2006/7, Katherine, Australia.

Pupation

Unlike the cocoons of *T. scatophaga*, the cocoons of *T. neossophila* do not span the width of the walls of the termite mound, when they are placed in the termitaria of *N. triodiae*, because they are too short. However, no pupal casings were recovered from the two nests located in *A. scopulus* mounds, which is the usual nesting substrate for *T. scatophaga* (Weaver 1982; Weaver 1987; Crowley *et al.* 2004), nor are there records of *T. scatophaga* cocoons in *N. triodiae* mounds (S. Shephard pers. comm.). Therefore, it is unclear if the placement of the cocoons results from a difference in behaviour between *T. neossophila* and *T. scatophaga*, or merely from differences in nest site. The result of the placement of the cocoons, however, means that *T. neossophila* must emerge back into the nest cavity before flying free, unlike the moths of *T. scatophaga* that emerge on the outside of the nest cavity (Thomson 1934). This may make the moths of *T. neossophila* vulnerable to being sealed inside the termitaria as the termites become more active at the start of the dry season and newly built parts of the termite mound may cover the entry to the nesting cavity.

We determined the date of pupation on two occasions. In both cases the larvae pupated one day after the chicks had left the nest, 32 and 33 days after the first chick hatched.

Emergence

Two pupal casings collected during the 2006 season hatched on 9 March 2006 following anomalous late monsoonal rains in the region. These casings had been collected approximately one week before they emerged. In contrast, cocoons that were collected in June 2005, following that season's parrot breeding season, emerged between 5 February–19 May 2006 under laboratory conditions in Canberra, Australia (Edwards *et al.* 2007).

Behaviour

Once a nest is located by the moths, up to four male and female moths engage in courtship displays within the nest cavity, zigzagging across the walls of the nest chamber, and eggs are laid. During this display, the moths stay close to the walls and floor of the nest, walking and flying, rather than flying freely across the nest cavity. Should the nest chamber be disturbed, the moths retreat to exposed termite chambers for protection.

Once the moth eggs hatch, the larvae move about the nesting chamber eating the faeces of the parrot chicks and turning over the termite mound detritus at the base of the cavity. We observed the larvae eating only the dark faecal matter excreted by the chicks. The white uric acid component of the parrots' waste was avoided and therefore accumulated in the base of the nest. *T. scatophaga* has been reported to consume other organic matter within the nest, such as dead chicks, fallen feathers, egg shell and grass seeds (Garnett & Crowley 1992). The larvae of *T. neossophila* did not consume such material, nor did we observe the larvae eating faeces off the legs of chicks, as has been reported in *T. scatophaga* (Turner 1923; Campbell 1924).

As the larvae grow, they create a silken mass beneath the floor of the cavity and become more sedentary, emerging to eat and retreating when the nest is disturbed. The silken mass forms a dense mat of tubular chambers, with the silk binding the termite mound detritus in the nest cavity to create a barrier between the larvae and the growing chicks inside the nest.

Within days of the chicks leaving the nest, the larvae move to the walls of the nest cavity to pupate. The pupal casings are attached to the inner wall of the cavity in small, golf ball sized congregations, in contrast to the pupal casings of *T. scatophaga* that form one large mass (Edwards *et al.* 2007; S. Shephard pers. comm.).

Discussion

This is the first study of the ecology of either the recently discovered *T. neossophila* or *T. scatophaga*, however much remains unknown about key components of either moth's life-cycle. The critical stage of the life-cycle is immediately following emergence from the pupal casings. Given the large proportion of nests that house larvae, moths seem to be adept at finding the nests, however the mechanism by which they do this remains unknown. It is assumed that once moths emerge they immediately seek a suitable parrot nest cavity in which to find a mate and lay their eggs. Two factors make this process potentially life-threatening. Firstly, because adult moths have only a vestigial proboscis (Common 2000; Edwards *et al.* 2007), they are likely to have a very brief life-span and therefore a short time to find a nest. Secondly, both golden-shouldered parrots (Crowley *et al.* 2004) and hooded parrots (S. Cooney unpub. data) rarely nest in the same termite mound in consecutive years, which means that the moth must leave its natal mound to find a suitable nest. Furthermore, an abnormal weather pattern occurred late in the 2006 hooded parrot breeding season that triggered the emergence of some of the moths. Unless the same weather pattern stimulated the parrots to re-commence breeding, these moths would be unable to find a nest suitable for egg laying.

As yet we do not know how the moths find the nests of hooded parrots, at a suitable time, within the short life-span of the imago. Jalava (1980) suggested that the moths that live in the nests of Ural owls (*Strix uralensis* Pallas.) found their hosts by detecting urine and excrement from the birds. However, adult moths of *T. neossophila* and *T. scatophaga* (S. Shephard pers. comm.) have only been recorded in nests before the young birds hatch, so attraction by urine and excrement is not a possible explanation in this case as parent birds never defecate inside their nest (SJNC pers. obs.).

Moths from a pupal mass of *T. scatophaga* collected in 1994 and kept in Canberra, outside their usual tropical climate, emerged over a period of five years at different times of the year (Garnett & Crowley 1998; Common 2000). This is consistent with the finding that in 2007 even late hooded parrot nests, established 9 weeks after the first nests of the season, had been populated by *T. neossophila*. Based on the scant evidence presented here, one might hypothesise that the moths emerge from their cocoons in response to changes in barometric pressure associated with low-pressure weather fronts, characteristic of summer weather patterns, however that does not explain the asynchrony with which they emerge and other cues must be considered to explain the timing of their emergence.

Other questions remain. We do not know the genetic structure of the larvae within a given nest—do they consist of the descendants of one pair of moths or do several moths deposit their eggs in the one nest? Most intriguingly, we do not understand the nature of the relationship between the moths and the parrots. Is this relationship commensal, with benefit accruing only to the moths through the provision of a relatively safe and dry nest site and a constant and reliable food source, or does the relationship have an impact on the parrot, making the relationship mutual or parasitic?

Should the interaction prove to be a mutualistic relationship, conservation programs will need to take into account the survival of the moth when managing the parrot. This has immediate implications for the golden-shouldered parrot, which is considered endangered with fewer than 2000 birds in the wild (Garnett & Crowley 2000) and subject to intensive conservation management (Crowley *et al.* 2004). Indeed it is possible to speculate that the extinction of the paradise parrot *P. pulcherrimus* (Gould), Australia's only other obligate termite nesting parrot, also led to the extinction of a third species of *Trisyntopa* moth, perhaps through a synchronised and accelerated decline of moth and parrot as the nests became more isolated from each other (Edwards *et al.* 2007). Further, as demonstrated by the early emergence of *T. neossophila* moths in 2006, the relationship seems to be fragile and susceptible to collapse should weather patterns, as the most likely stimulus for moth emergence, change as a result of global warming. The nature of this relationship, then, becomes the priority for future work on this species.

Acknowledgements

We would like to thank Ted Edwards from CSIRO Entomology for his continued interest in and support of, our research into this unusual bird/invertebrate relationship; Jak and Jade Irwin, managers of Manbulloo Station, for giving us access to the property and Mrs Susan Shephard for her observations of *T. scatophaga*. Our field work was ably assisted by volunteers, without whom the project would not have succeeded: Kathryn Smith; Ona Alminas; Richard Milner; Isobel Booksmythe; and Murray Hunt. SJNC would also like to thank his supervisor Andrew Cockburn. SJNC received crucial funding from the following organisations for field work, they too, were indispensable: the Trust of the Late Violet Winifred Scott; the Norman Wettenhall Foundation Grant; the Cayley Memorial Scholarship; the Joyce Vickery Scientific Research Fund Grant; the Ethel Mary Reid Award, the Birds Australia Stuart Leslie Bird Research Award; and an Australian Postgraduate Award. Finally, Gaden S Robinson and Marianne Horak improved the clarity of the manuscript.

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Accepted for publication 30 July 2008.

CHAPTER VI

Photo: S. J. N. Cooney

Interactions between nesting birds and invertebrates—a theoretical framework

Abstract

Interactions between nesting birds and invertebrates have been documented for more than a century. An extensive list of birds nest in, or in close proximity to, structures made by invertebrates and avian nesting material provides a reliable shelter for many invertebrate species. However, despite their occurrence being well known, the nature of such relationships has rarely been experimentally demonstrated. I propose that in order to understand the nature of these relationships they need to be explored within the theoretical framework of community ecology. Putative mutual, commensal and parasitic relationships have all been documented in the bird/invertebrate nesting literature, yet researchers, with few exceptions, repeatedly overlook the impact that these relationships are having on the invertebrate, at best assuming the nature of its impact, but more often ignoring its impact entirely. Here I present a framework for formulating hypotheses to ensure that the nature of the relationship can be identified. Only by explicitly stating the level of organisation at which the experiment is to occur (individual or population), identifying the net cost or benefit of the interaction, the range of conditions under which such costs or benefits would apply and the spatial and temporal context in which they apply, can an investigator expect to recognise and describe the often complex nature of these relationships.

Introduction

Interactions between nesting birds and invertebrates are common and have been a source of interest to ornithologists for more than a century and half (Gosse 1847). The early accounts of bird/invertebrate nesting interactions reported opportunistic observations of this behaviour, with little attempt to understand the nature of the interaction (Le Souef 1898; North 1904; Lower 1918). As the number of observations grew, and the range of species involved in these types of interaction increased, a number of reviews summarised these accounts into lists of birds and invertebrates that engage in this behaviour in various parts of the world (Myers 1929; Alexander 1931; Myers 1935; Moreau 1936; Moreau 1942; Moreau 1943; Durango 1949; MacLaren 1950; Hindwood 1951a; Hindwood 1951b; Chisholm 1952; Hindwood 1955; Hindwood 1959; McCrae and Walsh 1974; Hockin 1979; Chattopadhyay 1981). Whilst these lists occasionally speculated on the effect of the relationship upon the birds, the invertebrate was invariably ignored, no experimental evidence was provided to support the claims, and the explanations were rarely explored within a theoretical framework.

The lists of birds and invertebrates that nest in association with each other reveal the ubiquitous nature of this behaviour and can take two main forms

1. Nests and nesting materials provide a reliable and accessible source of shelter and food for a range of arthropods including mites and ticks (Collias and Collias 1984), spiders (Hobbs 1990; Henschel *et al.* 1991), millipedes (Tajovsky *et al.* 2001), fleas (Christe *et al.* 1996), cimicid bugs (Brown *et al.* 1995; Brown and Brown 2002) and both the adult and larval instars of moths (Opheim 1973) and dipterans (Loye and Zuk 1991; Heeb *et al.* 2000). Sometimes the number and diversity of invertebrates in a nest can be extensive. Moreau (1942, p. 243) reports one nest of a silvery-cheeked hornbill (*Ceratogymna brevis*) that had '438 insects… mostly larvae… belonging to eight species'.
2. Birds frequently site their nests and modify their nesting behaviour in ways that maximise their reproductive potential (Clark and Robertson 1979). One approach to maximise reproductive output is for a bird to place its nest near the nest of a social insect. This can take one of two forms.
    a. The bird may excavate a nest cavity within a structure created by the insect (Smith 1985). The insects most commonly involved in this type of interaction are termites that build either arboreal or terrestrial termite mounds (Myers 1935; Hindwood 1959; Brightsmith 2000), although ant and wasp nests are also used (Hindwood 1959; Smith 1985). These structures are an apparently abundant resource in many habitats and the behaviour releases the bird from competition for cavities in trees (Brightsmith 2000; Brightsmith 2005a; Brightsmith 2005b).
    b. A less intimate relationship is created when a bird places its nest near the structure of a formidable insect species, such as stinging ants, wasps or bees, presumably to receive a measure of protection

from these species which provide a 'protective umbrella' around the nest (Dyrcz *et al.* 1981). More than 100 species of bird have been recorded in such a relationship, from a range of avian orders (Joyce 1993).

The nature of nesting interactions between birds and invertebrates can be evaluated within the framework of community ecology theory. Where these interactions involve two species living in close association for an extended period, the relationship is considered a symbiosis (Boucher *et al.* 1982; Douglas 1994). The term symbiosis does not imply that the relationship is beneficial to both or either party to the interaction (e.g. Begon *et al.* 1996) as it has come to be understood in popular language (Smith and Douglas 1987). Here, the term symbiosis refers to a range of intimate interactions from mutualism, through commensalism and predation/parasitism to competition (Bronstein 1994; Bradshaw and White 2006). This definition was clearly the intent of Anton de Bary who first used the term in 1878 (Goff 1982; Smith and Douglas 1987; Sapp 1994) and is the preferred definition used by workers in the field of symbioses (Hirsch and McFall-Ngai 2000; Thrall *et al.* 2007).

In a mutualistic interaction, a reciprocal exploitation occurs in which one species provides a good or service that the other cannot provide for itself and receives a good or service in return (Herre *et al.* 1999; Yamamura *et al.* 2004; McGill 2005). This type of interaction is commonly abbreviated to +/+ to denote that benefit is accrued by each party to the interaction. Commensalism (+/0) occurs when one party to the interaction derives a good or service from the interaction without having an impact on the other party. Predation/parasitism describes a relationship where one species benefits to the detriment of the other species (–/+; Boucher *et al.* 1982). Competition (–/–) occurs when two or more species reduce both their own fitness and the fitness of the other species (Boucher *et al.* 1982). It, along with amensalism (–/0) and neutralism (0/0; Bronstein 1994), are not reported in the bird/invertebrate nesting literature and will not be considered further. Despite the apparently clear distinctions between the categories that describe the effects of the interspecific interaction on each species, some studies suggest that both positive and negative interactions can occur at the same time (Haemig 1999) and apparently negative interactions can provide fitness benefits under certain conditions (Smith 1968) and vice versa (Weeks 1999). Furthermore, individual, spatial and temporal variation can alter the impact of the interaction (Haemig 1999) and therefore the range of interactions should not be seen as fixed, discrete categories, rather, they represent a continuum of effects and impacts (Bronstein 1994; Thompson 1994). The result of this variation is described as a conditional outcome, in that the costs and benefits involved are conditional on a range of external factors (Cushman and Whitham 1989; Bronstein 1994). In order to understand this sort of interaction, experimental protocols need to be able to deal with the fluid nature of the association, which highlights the importance of testing hypotheses concerning the nesting interactions within a theoretical framework.

Here, I examine the growing body of literature that documents instances of symbiotic bird/invertebrate nesting associations, to determine if the methods used to explore the nature of these interactions are framed within the theory of community ecology and can therefore ultimately explain the nature of the relationships between nesting birds and invertebrates.

Parasitism

The majority of invertebrate species found in the nests of birds are parasites. Parasites reduce the fitness of the host (Christe *et al.* 1996), therefore what follows is a discussion of research that explores a relationship between a nesting bird and invertebrate that benefits one member of the interaction to the detriment of the other. I do not discuss instances where a putative parasite is discovered not to have a negative impact on its host as, by the definition used here, these are not parasitic interactions.

Parasites represent a large proportion of extant species and most organisms will encounter them at some stage of their life-cycle (Heeb *et al.* 2000). Whilst most endoparasites, such as worms, haematozoa and viruses are widely recognised as having a detrimental effect on the health of a bird, ectoparasites, can have an equally profound effect on survival and fitness (Loye and Zuk 1991). Most nestlings share their nest with a suite of ectoparasites (Simon *et al.* 2003). The impact that a parasite has on its host is termed its virulence and this varies between individuals as well as spatially and temporally (Loye and Zuk 1991;

Johnson and Albrecht 1993; Heeb *et al.* 1998; Martin *et al.* 2001). Further, the type of ectoparasite will also influence its virulence and the nature of its relationship. For example, fleas feed intermittently on chicks in nests, whereas ticks attach for a prolonged period (Heeb *et al.* 2000).

Ectoparasites can have a detrimental effect on a range of life history parameters. Infestation of chicks by ectoparasites, such as mites and larval dipteran flies, has been demonstrated experimentally to result in slower growth rates (Johnson and Albrecht 1993; Bize *et al.* 2003). This can lead to reduced weight at fledging (Heeb *et al.* 2000; Weddle 2000; Berggren 2005; Fessl *et al.* 2006), poorer body condition (Hurtrez-Bousses *et al.* 1997) or result in delayed fledging while the chicks achieve the minimum required fledging weight (Bize *et al.* 2003). Infestation by blowfly larvae *Protocalliphora* sp., resulted in lowered haematocrit levels in blue tits (*Parus caeruleus*), which reduced the chick's ability to thermoregulate (Hurtrez-Boussès *et al.* 1997; Simon *et al.* 2004). Sleep can also be affected by parasite infestation (Christe *et al.* 1996), as chicks divert time from other activities to compensate for the irritation or energy lost to ectoparasites, impinging on sleeping time (Sheldon and Verhulst 1996; Simon *et al.* 2005). The ultimate cost of ectoparasites to birds can be an increased rate of mortality, and while this is not inevitable, there are many examples of parasite infestation resulting in the death of chicks in nests (see for example Whitworth and Bennett 1992; Brown and Brown 2004; Puchala 2004; Gwinner and Berger 2005; Fessl *et al.* 2006).

Parents are also subject to fitness costs as a result of parasitic infestation. Nests are a common source of parasites, such as feather lice, for adult birds (Møller and Rozsa 2005). Feather lice can have an impact on flight, metabolism (Møller *et al.* 2004) and sexual selection through damage to the feather (Hamilton and Zuk 1982; Clayton 1991). Such impacts can result in the late arrival of breeding birds to the breeding grounds, in poor condition (Møller *et al.* 2004), which can result in a delay in egg laying (Oppliger *et al.* 1994) and a shortened nesting period (Møller 2005). The presence of ectoparasites in the nest of a bird can also result in more time being spent on nest sanitation duties at the cost of provisioning (Hurtrez-Bousses *et al.* 2000). Often the impact of parasites is not manifested during the breeding season in which infestation occurs, rather, the impact is felt in terms of reduced future reproductive output (Brown *et al.* 1995; Bize *et al.* 2004). At a population level, parasites influence the evolution of clutch size (Møller 1991; Poiani 1993; Martin *et al.* 2001) and can result in biased sex ratios (Heeb *et al.* 1999). Finally, the presence of ectoparasites can result in the death of adult birds (Brown and Brown 2002).

There is little experimental evidence of birds nesting in a manner that parasitises invertebrates, although the regular phenomenon of birds nesting in termite cavities may provide examples of this interaction. These interactions will be discussed further in the discussion of commensal relationships. One documented example of this behaviour, however, involves the presence of caterpillars with stinging hairs in the nests of crested bellbirds (*Orieca gutteralis*) in Australia (Chisholm 1919; Higgins and Peter 2002). Up to 14 caterpillars, incapacitated but kept alive to ensure that they stay on the nest, have been observed in and on bellbird nests (Chisholm 1918; Chisholm 1919; Leach 1928; Ross 1930). The nature of the relationship between the birds and caterpillars is unclear, however it has been suggested that the caterpillars provide food for the parent and nestling birds (Milligan 1905; White 1918; but see Chisholm 1918). Others have suggested that the caterpillars, provide a measure of protection to the nest contents from their stinging hairs (Chisholm 1918; Chisholm 1919). As yet, no evidence has been presented that confirms the nature of this unusual relationship.

While there is unequivocal evidence of the negative impact of playing host to parasites, little experimental work has examined the positive benefits received by the invertebrate. It would reasonably be argued that the provision of food and shelter to the invertebrate constitutes a benefit to the fitness of that individual. Indeed some research suggests that there are direct benefits to populations of nest invertebrates of an increased brood size (Hurtrez-Bousses *et al.* 1999) and obligate avian parasites clearly derive benefit from their hosts (Brown *et al.* 1995). Despite this, detailed studies of the life cycle of many invertebrate nest parasites are lacking (Fessl *et al.* 2006) and the effect on the invertebrate involved is untested in most studies of avian nest parasitism, even where the data for such evaluations have been collected (see for example Heeb *et al.* 1998; Simon *et al.* 2003).

The literature that concerns invertebrate nest parasites is a discrete subset of the scientific literature that carries an important assumption that is rarely tested. Although there is good scientific evidence that some nest invertebrates reduce the fitness of their hosts, this is not always the case, and the *prima facie* investigation of 'birds and parasites' results in tautologies such as 'harmful parasites' (Gwinner and Berger 2005, p. 365). By definition, there can be no other type of parasite than a harmful parasite (Christe *et al.* 1996). More importantly, rarely is evidence provided that demonstrates the effect of this interaction on the invertebrate. It is assumed, often quite rightly, that the invertebrate is gaining a fitness advantage from the interaction, but the extent, variability within, and mechanism driving this assumption are not clear. Simon *et al*. (2004, p. 492) acknowledge that the effects of ectoparasites can be subtle and vary between individuals, yet state only that 'parasites should always have detrimental effects on their hosts', ignoring half of the definition of parasitism according to community ecology theory (i.e. that putative parasites must also benefit from the interaction). In many cases, this is the deliberate outcome of the experimental protocol, as the taxon of interest is the bird, however, the true nature of the interaction may be misjudged without an evaluation of the impact of the interaction on all members involved.

Commensalism

When nest parasite studies are structured within a framework of community ecology, some supposed parasites have been shown not to have detrimental effects on their hosts. This is not unexpected, as the evolution of tolerance to a parasite often results in apparent commensalism (Hirsch and McFall-Ngai 2000; Miller *et al.* 2006; but see Thompson 1994). Thus, haematophagous (Stamp *et al.* 2002; Berggren 2005) and feather-chewing lice (Blanco *et al.* 1997), as well as dipteran larvae that feed on the blood of nestling birds (Tompkins *et al.* 1996), have all been shown to have little effect on nestling growth or fledging success. Like the previous discussion about parasitism, however, in all of these cases the benefits to the invertebrate were assumed rather than tested. Granting the assumption of a benefit to the invertebrate, these interactions would be classified as examples of commensalism, with a benefit to the invertebrate at no cost to the nesting birds. Commensalism was also inferred from the observation of moths in the nests of Ural owls (*Strix uralensis*; Jalava 1980).

Nesting associations between birds and Hymenoptera are common, with more than 100 bird species reported to place their nests near an active hymenopteran nest (Moreau 1942; reviewed in Hindwood 1955; Joyce 1990). Gosse (1847) first described such interactions from Jamaica, and observations from Africa (MacLaren 1950; Janzen 1969; McCrae and Walsh 1974; Dejean and Fotso 1995; Beier and Tungbani 2006), Australia (Campbell and Barnard 1917; Chisholm 1925), Central America (Wunderle and Pollock 1985; Young *et al.* 1990; Gilardi and von Kugelgen 1991; Joyce 1993), North America (Parker 1981), South America (Contino 1968), Europe (Haemig 1999) and the Indian subcontinent (Chattopadhyay 1981) provide further examples of the widespread nature of this phenomenon. Such interactions are generally considered commensal, with the birds benefiting from the protection afforded by aggressive stinging ants, wasps or bees, while the hymenopteran is not only unaffected by the presence of the nesting bird (Beier and Tungbani 2006), but seems to tolerate its existence (MacLaren 1950). However, few studies have demonstrated that the association increases the bird's nesting success (Smith 1968; Robinson 1985; Wunderle and Pollock 1985; Joyce 1993; Beier and Tungbani 2006; de Ita and Rojas-Soto 2006), and I am only aware of one study that explicitly examined the impact of the relationship on the invertebrate. This study found that there was no impact on the wasp involved (Beier and Tungbani 2006). Jackson and Burchfield (1975) examined nest site selection of barn swallows (*Hirundo rustica*) and found them to have a presumably commensal relationship with a wasp that builds its nests on concrete culverts. The swallow attaches its nest to the wasp nests and this increases the area available to the swallow for nesting. The effect on the wasp was assumed to be negligible, although the authors suggest that the swallow may prey upon predators of the wasp, making the relationship mutualistic.

Many species of bird nest in terrestrial or arboreal termite mounds; for some birds this behaviour is obligatory (Hindwood 1959; Brightsmith 2000). A feature common to such nest-sites is that the termites are active in their nest at the time that the birds excavate their nesting cavity (Hindwood 1959; Hardy 1963; Legge and Heinsohn 2001; but see Brightsmith 2000). Subsequently, the termites close the galleries that are exposed by the excavated cavity, leaving a sealed chamber in which the birds nest (Hindwood 1959). Clearly, the birds gain a fitness benefit from the interaction with the termites; nestling birds have a warm and sheltered site that may be freer from disturbance than similar tree cavities (Hindwood 1959). However, it should be noted that there have been no studies published that compare the nesting success of bird species that nest in both termitaria and other cavities to compare breeding success. The effect of this interaction on the termite is less clear and no study has explored the impact of a bird excavating a nest in a termite mound. A case could be made that the relationship is mildly parasitic. Energy is expended by the termites when they seal the excavated section of the termite mound, and the presence of a bird's nest may provide a portal for species that prey upon termites, such as ants or goannas (Moreau 1942; Hubbard 1877 cited in Hindwood 1959). Our current understanding of this behaviour suggests that the birds that nest in termite mounds do not eat significant numbers of the termites, even when, as a group, they include insects in their diet (Hindwood 1959). Therefore, whilst I have classified this interaction as a commensal relationship, on the assumption that birds benefit from the interaction through the provision of a nest site and the termites incur no significant cost in the interaction, an evaluation of the consequences of this behaviour is required.

Other presumed commensal interactions, in which the birds benefit, are associations with spiders. In such relationships, the spider's webs are used as nesting material and are transported to the nest when the birds are building (Henschel *et al.* 1991) or the bird nests in close proximity to a social spider's nest to gain protection from the biting or stinging arachnids (Bates 1936; Collias and Collias 1984; Hobbs 1990). Again, the effect that this has on the arachnids is unknown.

The aforementioned study by Beier and Tungbani (2006) is a notable exception in the literature on commensalism because it examines the effect of a nesting interaction between birds and wasps from the perspective of both parties to the interaction. Beier and Tungbani (2006) examine nest site preferences and nesting success of red-cheeked cordonbleus (*Uraeginthus bengalus*) in relation to the presence and absence of a wasp (*Ropalidia cincta*). Most significantly, Beier and Tungbani (2006) also examine the nest site preference and nesting success of the wasp in relation to the birds. This makes the study exceptional, the only study that fulfils its stated goal of determining the nature of the nesting association within the framework of community ecology, and the authors can confidently proclaim the relationship as commensal

Mutualism

Mutualistic interactions are thought to be extremely important at all levels of biological organisation (Herre *et al.* 1999). Despite this, experimental evidence that unequivocally confirms their existence is extremely rare (Boucher *et al.* 1982). Further, more than 90% of studies that document mutualisms involve a plant/animal pair that engage in pollination and/or seed dispersal (Weeks 1999). Studies that document mutualistic relationships between a bird and another vertebrate are extremely rare. Foraging associations between various species of bird and mammals provide some examples (see for example Rasa 1983; Ruggiero and Eves 1998). Other experimentally established mutualistic interactions that involve birds concern the nesting of two bird species in close proximity, such that one provides protection from nest predators for the other, which provides mobbing resources in return (Wiklund 1979; Wiklund 1982).

A possible bird/invertebrate mutualism is proposed by Blanco *et al.* (1997) between red-billed choughs (*Pyrrhocorax pyrrhocorax*) and feather mites (*Gabucinia delibata*). They demonstrate that the feather mites cause no harm to the choughs, which leads them to state that the relationship is commensal. They further surmise that the mites may even improve the feather cleaning efficiency of choughs making the relationship a mutualism.

While there are no studies that demonstrate mutualistic bird/insect nesting associations, some candidates for this behaviour exist. In 1922, McLennan discovered the larvae of a moth (*Trisyntopa scatophaga*), in the nest cavity of the golden-shouldered parrot (*Psephotus chrysopterygius*), feeding on the excreta of the nestlings (Turner 1923). It has since been assumed that the moth benefits from the symbiotic interaction through the provision of food and shelter, while the parrot derives benefit from having a clean nest (Thomson 1934). Indeed the life-cycle of the moth closely follows that of the nesting parrots, with the moth's egg-laying, hatching and pupation synchronising with the hatching and fledging of the parrot chicks (Turner 1923), indicating the closely coevolved nature of their relationship. Two other moths belong to the genus *Trisyntopa* and both have been recovered from the nests of parrots (Lower 1918; Edwards *et al.* 2007). Further, Myers (1935) discusses the case of the pyralid moth (*Caphys bilineata*) that is believed to behave in a similar manner to *T. scatophaga* in the nests of the brown-throated parakeet (*Aratinga pertinax*; Myers 1935). There may be as many as 100 species of Tineid moth that are found in birds' nests (Robinson 2004), some of which are not present in the absence of bird faeces (Hockin 1979), however the nature of their relationships with their avian hosts remains unknown. Many of these species are believed to be keratophagous and feed on the nest material or chick's feathers, rather than the faeces of the nestlings (Common and Horak 1994) and therefore may not confer a fitness advantage on their hosts.

Roberts (1940) and Morrison (1996) report a fly larva that behaves in a similar manner to the scatophagous moths. The maggots of this fly were observed to consume the excreta and dead siblings of eastern rosella (*Platycercus eximius*) chicks in their nest, leading Roberts to state that it was a 'perfectly efficient and beneficial arrangement' (Roberts 1940, p. 234). Hindwood (1951a), similarly reports a beetle (*Platydema pascoei*) that feeds on the excrement from nestling finches.

While it seems likely that these types of invertebrate/bird relationships represent a mutualistic relationship, other explanations are possible. The relationship could be commensal, with benefit accruing to the invertebrate, while the bird is unaffected, or the relationship could be parasitic if the invertebrate diverted resources from the nesting birds, or otherwise caused the nesting attempt to fail. Clearly, these interactions require further investigation, including experimental manipulation of the relationship in order to determine its nature.

Conditional outcomes and multiple associations

Smith (1968) describes a system in Panama in which birds suffered nestling losses from larval *Philornis* botflies that burrow into the chick's body prior to pupation. Giant cowbirds (*Scaphidura oryzivora*) also impose energetic costs on the birds by laying an egg in the host birds' nests. To mitigate these losses, the host birds adopted a number of strategies. To avoid both the botfly and the cowbirds, host birds could nest in the proximity of stinging bees or wasps. However, this meant that nests were built later in the season, the added weight of the nest might cause the branch to collapse and the nest might be devoid of protection if the bees or wasps left the nest site. Another strategy was to allow the cowbirds to parasitise the nest. The cowbird chick would preen the host nestlings and eat any botfly larvae. Thus, protection from botflies came at the cost of increased energy expended by the nesting bird on feeding the cowbird chick. Depending on when the cowbird laid its egg, however, sometimes this would lead to the host bird raising only the cowbird chick and none of its own. Smith (1968) found that the most successful strategy was to nest near the bees or wasps, unless the host only laid one egg, in which case there was a benefit to being 'parasitised' by the cowbird. He demonstrated that different birds had different strategies that were more or less successful at different times of the year or in different breeding seasons and that the gross costs and benefits of certain behaviours resulted in unpredictable net results.

Smith's (1968) description of the complicated and conditional outcomes of interspecific interactions highlights the importance of framing research on nesting interactions within a theoretical framework that allows the investigator to identify the potentially intricate nature of some bird/insect relationships. Rarely has this been done in a manner that would reveal such complexity, indeed, rarely has it been done in a manner that reveals the impact of the relationship on both parties to the interaction.

Other three-way interactions between birds and invertebrates are known. The relationship between *Psephotus* parrots, *Trisyntopa* moths and the termites that provide a nest site for them both, provide another example of the complicated ways in which relationships may manifest themselves. Many mounds used by golden-shouldered parrots collapse and die, conversely termites sometimes seal eggs of parrots to the floor of the nesting chamber or build across the nest tunnel after the first eggs laid, leading to nest failure (S. Garnett pers. com.). Therefore, from the point of view of the termites, the relationship with the parrots could be classified as parasitic, amensal or commensal with the outcome not determined until the relationship ends at the end of the breeding season. The influence of the moth on the relationship is not known in relation to either the termite or the parrot, but adds a further layer of complexity to this interaction.

Conclusions

Future work should consider multiple hypotheses within the framework of community ecology to determine the nature of nesting bird/invertebrate interactions (Blanco *et al.* 1997). The three basic hypotheses required to determine the impact on both species in the relationship are that the interaction is parasitic, commensal, or mutual. A fourth hypothesis is that the interaction is the result of a shared preference for resources and that costs and benefits accrue to each species because of those shared resources, rather than because of the interaction *per se* (Griffing 1974; Vermeer *et al.* 1992; Donázar *et al.* 1996).

I propose that these hypotheses are formed with respect to the following criteria:

1. At what level of organisation do we wish to assess the fitness consequences? It seems reasonable to assess changes in fitness at either the level of the individual (i.e. fecundity, growth rate, age specific mortality) or at the population level using Lotka-Volterra equations of competitive interactions (Boucher *et al.* 1982).

2. Changes in fitness need to be assessed in relation to a net cost or benefit in biologically realistic currencies (Herre *et al.* 1999). All net costs and/or benefits should be identified, quantified and evaluated in a biologically meaningful context (Herre *et al.* 1999). This is exemplified by the case of birds nesting in termitaria, where it seems unlikely (though not yet proven) that the interference by the birds results in a net loss of fitness to the termites.

3. Once the costs and benefits have been determined, it will be important to identify and quantify the range of conditions that are known to influence these outcomes (Bronstein 1994). A change in the presence and abundance of influential third parties, variation in host densities, changes in resource availability and broader changes in the physical environment

are all likely to have an impact on the nature of the interaction and change the observed costs and benefits (Herre *et al.* 1999).

4. The spatial, temporal and taxonomic context in which the relationship operates can also improve the understanding of the interactions (Herre *et al.* 1999). Phylogenetic approaches to understanding these conditions may be a useful tool for this process (Herre *et al.* 1999).

Interactions between invertebrate symbionts of nesting birds are potentially important factors shaping the life-history of each species in the association (Heeb *et al.* 1999). In other systems, these interactions have important conservation implications for either or both of the species involved (Fisher 1998; Robertson *et al.* 1999; Tellería *et al.* 2005). In the systems described here, the effect of parasites on host fecundity, the role of hymenoptera as protectors of birds' nests and the nest sanitation duties of the moths in parrot cavities may have the potential to inform our management of these species (Haemig 2001). However, unless we truly understand the nature of these relationships, and the influence of conditionality on them, any such management will be inefficient at best, and destructive, at worst.

Birds' nests continue to be a regular source for the identification of new invertebrate species (see for example Fessl *et al.* 2006; Majka *et al.* 2006; Edwards *et al.* 2007) and researchers should continue to note the nest fauna and nesting associations of birds. However, lists of nidilicous fauna will not explain the dynamics of the interactions between nesting birds and invertebrates and rigorous field experiments that examine the impact of the interaction on both species, within a theoretical framework, are required to advance our understanding of this behaviour. Hindwood (1955) called for such studies more than fifty years ago, yet it seems that few have heeded his call. By exploring the complicated interactions between nesting birds and their symbiotic invertebrates within community ecology theory, perhaps the next fifty years will improve our understanding of these fascinating relationships.

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CHAPTER VII

Photo: S. J. N. Cooney

An experimental investigation of the nesting relationship between hooded parrots (*Psephotus dissimilis*) and the moth *Trisyntopa neossophila*

Abstract

Interactions between birds and invertebrates are widespread. Parasitic and commensal relationships are commonly reported, however mutualisms between birds and invertebrates have not been reported. Despite this, candidates for this type of relationship exist. We experimentally examined one such candidate; the relationship between the hooded parrot (*Psephotus dissimilis*) and *Trisyntopa neossophila*, a moth that rears its young exclusively in nests constructed by the parrot. By manipulating the populations of moth larvae in a sample of hooded parrot nests, we sought to establish the impact of the relationship on each species. The moth depends on the parrot through provision of shelter and a reliable food source. The parrot however, was neither benefited nor harmed by the interaction in terms of short term reproductive output or chick growth, although differences between the treatment and control nests were noted. The relationship between the hooded parrot and *T. neossophila*, at least during the study period, is therefore concluded to be commensal.

Introduction

When two or more species interact, the outcome of this interaction can be described within the framework of community ecology theory. The impact of such encounters on an individual can range from beneficial to detrimental, however temporal, spatial and individual variation can alter the net effects of the interaction and result in interactions that can be both parasitic and mutualistic, depending on external conditions impinging on the relationship (Smith 1968; Haemig 1999; Weeks 1999). Therefore, interspecific interactions should be classified along a continuum of effects and impacts that are conditional upon the influence of external factors (Cushman and Whitham 1989; Bronstein 1994), rather than as discrete categories.

Birds provide many examples of interspecific interactions, particularly in respect to invertebrates. Invertebrates as parasites of birds are well studied and are known to profoundly affect all stages of a bird’s life (Loye and Zuk 1991; van Emden and Rothschild 2004). Commensal nesting interactions between birds and invertebrates are also well described in the literature. Many species of bird nest in close proximity to a range of invertebrate species, from which they derive protection or shelter at little or no cost to the invertebrate involved (see for review Hindwood 1955; Hindwood 1959; Ch VI). Mutualistic relationships between birds and invertebrates, however, are far less common. Whilst birds form mutualistic relationships as pollinators with plants (see for example Temple 1979; Robertson *et al.* 1999) and with mammals in foraging associations (Rasa 1983; Ruggiero and Eves 1998), no bird/invertebrate mutualisms have been reported in the literature, although contenders for such behaviour exist.

Jackson and Burchfield (1975) studied a population of barn swallows (*Hirundo rustica*) that could utilise a greater proportion of concrete culverts in the presence of the wasps *Trypoxylon politum* or *Sceliphron caementarium.* The wasps attach their nests to the culvert, onto which the swallow could then attach its own nest. While this is beneficial to the swallow, the effect on the wasp is unknown, although the authors speculate that the swallows may eat potential parasites of the wasps, shifting the interaction from commensalism to mutualism (Jackson and Burchfield 1975). Another potential mutualism is proposed by Blanco *et al.* (1997), who found that feather mites in red-billed choughs (*Pyrrhocorax pyrrhocorax*), not only caused no harm to the birds, but may improve the cleanliness of the bird's feathers. The authors were wary of drawing the conclusion that the relationship is an example of a mutualism, even though body condition was significantly positively correlated with mite abundance (Blanco *et al.* 1997).

A further, as yet untested, candidate for a mutualism between an invertebrate and a bird is found in the nests of parrots. The oecophorid moths *Trisyntopa scatophaga* and *T. neossophila* are found only in the nests of the golden-shouldered (*Psephotus chrysopterygius*) and hooded parrots (*P. dissimilis*) respectively. The nest cavities of the parrots are excavated into the side of a terrestrial termite mound and the moth lays its eggs in this cavity (Turner 1923; Thomson 1935). The arrival of the moth is synchronised with the laying of the parrot eggs and, once hatched, the larvae tunnel into the floor of the nest and build silken galleries in which they presumably gain protection from the movements of the parrot chicks (Turner 1923). When the chicks defecate, the larvae emerge from their tunnels and consume the faeces that fall on the floor of the nest (Turner 1923). In this way the nest cavity is kept free from a build up of faecal matter. When the parrots fledge, the moth larvae form a cluster of cocoons in the wall of the termite mound (Turner 1923), where they spend 10–12 months in a state of prepupal diapause before emerging at the beginning of the next year's parrot breeding season (Edwards *et al*. 2007; Ch V).

Two other, similar, moth-parrot relationships are thought to occur. *T. euryspoda*, is found in the tree cavity nests of south-eastern Australian parrots (eastern rosella (*Platycercus exemius*) and mulga parrot (*Psephotus varius*); Hindwood 1951), and the pyralid moth (*Caphys bilineata*) is found only in the termite mound nests of the brown-throated parakeet (*Aratinga pertinax*), in the Brazilian savannas (Myers 1935).

Most of the early researchers on the golden-shouldered parrot/*T. scatophaga* relationship believed that the relationship was mutualistic. They suspected that in keeping the nest cavity clean, the moths increase the success of the parrot's nesting attempt (Campbell 1924; Thomson 1934; Moreau 1943; Hindwood 1951). Few of these authors, however, explicitly explain how a clean nest cavity would improve nest success (Thomson 1934; Thomson 1935; Moreau 1942; Chisholm 1952). Hindwood (1951) states that a clean nest cavity reduces the number of parasitic flies at the nest site and other work on nest sanitation has demonstrated a link between the accumulation of faeces and an increased exposure to predation (Petit *et al*. 1989; Lang *et al*. 2002). Garnett and Crowley (1995), at the conclusion of a long study of golden-shouldered parrots took the opposite view, stating that the relationship should best be described as parasitic because the pupal casings occasionally cause the failure of some nests. None of these authors have experimental evidence to support their conjectures.

There is little doubt that moths benefit from the relationship with the parrot. The close synchrony of the moth's life-cycle to the parrot's breeding cycle, the quick death of the larvae when parrots left a nest prematurely (Cooney *et al*. In press; Ch V), the reliance on parrot faeces for food and that *T. neossophila* has never been recovered away from the nests of a hooded parrot, all indicate that the benefit received by the moth from the parrot is likely to be obligate and in the absence of nesting hooded parrots, the moth would become extinct. As larvae, the moths live in the base of the nests of the parrots. This provides them with a reliable and abundant source of food throughout larval development. The nest also provides shelter from the weather and is likely to afford a measure of protection from potential predators. When the larvae pupate and enter diapause for the duration of the dry season (May–Nov), temperatures reach a mean daily maximum of 33.7ºC, a minimum of 18.3ºC and mean 3 pm relative humidity falls to 29.3% (Bureau of Meteorology 2007). The termite mound nest cavity provides a more moderate microclimate that reduces the amount of desiccation that would be experienced if cocoons were in a less sheltered position (Hindwood 1959; Crowley *et al*. 2004; Kesler and Haig 2005).

Understanding the nature of interspecific interactions is important because these relationships potentially affect all components of a species' life cycle, including nutrition, reproduction and survival (Boucher *et al*. 1982). Many intimate relationships, such as those involving gut bacteria in ruminants (Boucher *et al*. 1982) and the pollination of some plants by insects (Fisher 1998) are obligate to one or both parties in the interaction, hence the survival of one species is intimately linked to the other. Further, of particular interest in this system, unlike the hooded parrot, the golden-shouldered parrot is endangered and subject to careful conservation management (Garnett and Crowley 2000; Crowley *et al*. 2004), however conservation management of the moth is not currently undertaken and the effect of this is unknown. Given the close taxonomic relationship between the hooded and golden-shouldered parrots, future conservation management of the latter will be informed by the results obtained in this study, using the hooded parrot as a proxy.

This makes the hooded parrot/*T. neossophila* interaction an ideal study system. Here we experimentally explore the nature of the relationship between the hooded parrot and *T. neossophila* to determine the impact of the interaction on the parrot, given that the moth clearly benefits from the relationship.

Methods

Study Site

An area 30 kilometres east of Katherine, Northern Territory, Australia (S 14º 40' 08" E 132º 05' 27"), was searched for termite mound nests of hooded parrots between January and May 2007, spanning one full hooded parrot breeding season. The study area has a monsoonal climate, characterised by hot, wet summers and cool, dry winters. My work was based on a private cattle property (Manbulloo Station), and included both rocky ridge country, characterised by shallow gullies that form peripheral rocky ridges (nests = 40), and black soil country, characterised by well drained, sandy flats (nests = 2). The vegetation on Manbulloo Station is an open tropical savannah, with an overstorey of northern salmon gum (*Eucalyptus bigalerita*) and Darwin stringybark (*E. tetrodonta*), and an understorey dominated by grasses from the genus *Sarga*. Mounds >1.5 metres high occurred at a density of approximately 7.8 termite mounds per hectare (Ch III). Most (83%) termite mounds were built by the cathedral mound termite *Nasutitermes triodiae*; the remaining 17% were built by the conical mound termite *Amitermes vitiosus* (Ch III).

Experimental protocol

When an active hooded parrot nest was located it was allocated to either an treatment group or a control group. The nest contents of both groups were accessed by removing a square plug from the side of the termite mound. Once the visit to the nest was complete, the plug was replaced and the portal resealed with mud.

Nests in the treatment group, had the crushed termite mound at the base of the nest removed. This material was then placed in a sorting tray and all visible larvae were removed. The material was then placed back into the nest cavity and arranged to form a flat base on which the chicks were returned. Any other nest fauna, bird debris or plant material was also returned to the nest. At subsequent visits to the treatment nests for measurements of chick growth, the cavity was checked for the presence of more larvae and these were also removed. The base of the control nest was left intact so that we did not disturb the creation of the web by the larvae.

Both the treatment and control nests were monitored every four days. At each nest visit, the chicks were removed from the nest. Flattened wing chord, from carpal joint to the end of the primary feathers, was measured using a butt-ended ruler and the birds were weighed to the nearest 0.5 g using Pesola scales, before being returned to the nest. At a mean age of 17 days (3.09, 12–25, 64) approximately 0.05 mm of blood was taken from the chicks' brachial vein. A drop of the blood was then placed on a glass slide, thinly spread over the slide and air dried before storage. Within 5 hours this slide was immersed in 100% ethanol for 10 minutes before being dried and stored for later endoparasite load analysis. Parameters relating to the condition, size and success of the entire brood were recorded.

To analyse the endoparasite intensity of the parrots, the blood smears were stained with Giemsa's Stain Improved R66 solution Gurr (Merck Pty Ltd, Kilsyth, Vic). 10 drops of concentrated stain were mixed into 100 ml of tap water and slides immersed for 1 hour, then removed, rinsed with distilled water and air-dried before examination. Each blood film was examined under a compound microscope for 15 minutes at 40x objective with a 10x eyepiece (magnification = 400x) and 10 minutes under oil immersion at 100x objective with a 10x eyepiece (magnification = 1000x). At both magnifications only single cell layers, edges and tails of films were examined, sites where blood cells infected with haematozoan parasites (e.g. hepatozoons) or larger parasites outside blood cells (e.g. trypanosomes, microfilariae) accumulate.

Analyses

Differences between treatments in the condition, size and success of broods were analysed using student *t*-tests and differences in condition and success by treatment using likelihood chi-squared values.

A logistic growth curve model was used to model weight gain and wing chord growth over time (Lee and Nelder 1996; Lee and Nelder 2001). The basic growth curve model (Model 1), for modelling weight gain that does not account for a possible treatment effect, takes the form:

$$weight\ (X) = A + \frac{C}{1+\exp(-B\times(X-M))} + Z + \varepsilon$$

where X is the age of the bird, A and C are constants that control the horizontal asymptotes of the logistic growth curve, B is a constant controlling the steepness of the curve and M is the inflection point. Z is the random effect corresponding to the nestling, nested within brood effect and ε the error term. A model of the same form was used to model wing chord growth.

Three variations to these models were considered to account for the possibility of different growth patterns between treatment groups. The second set of models had the same form, but allowed each treatment to have a different steepness coefficient (B_T). This was a more complex model that required one additional parameter to be estimated. Model 3 had the same form as Model 1, but estimated initial and final values (A_T and $A_T + C_T$) for each treatment. This more complicated model required two additional parameters to be estimated. Model 4 allowed for differences in both the asymptotes and the steepness coefficient.

Differences between models 2 vs. 1, 3 vs. 1, and 4 vs. 3 were assessed using change in the deviance. Under the null hypothesis, the difference in the deviance is distributed as χ^2 with 1, 1 and 2 degrees of freedom respectively.

Subsets of the data were also analysed using the above models to see if the effect of removing moths from nests had different effects on subgroups within the sample. Subsets explored were; successful birds only; males only; females only; first chicks only; early chicks only (1st or 2nd hatched); late chicks only (3rd or later hatched); early season birds only (excluding two nests that were started 3 weeks after the next latest nest); and excluding fully feathered birds (to explore differences only during the growth phase of nesting).

All data were analysed using GenStat 10 statistical software. Differences were considered significant at $p < 0.05$.

Results

Forty two hooded parrot nests were located in the 2007 field season. Nine of these nests failed to hatch any eggs and were therefore excluded from further analysis. After moth larvae appeared in the nest, 10 of the remaining 33 hooded parrot nests were randomly assigned to the treatment group, whilst the remainder of the nests were assigned to the control group. One further nest was also included in the treatment group, as early flooding apparently prevented development of moth larvae, presumably through drowning. These 33 nests produced 147 eggs that resulted in 112 hatchlings and 71 fledglings. The 11 treatment nests accounted for 47 eggs, 38 hatchlings and 23 fledglings. Reliable weights and ages were only recorded for 28 fledgling parrots in the control group and only these birds were used in the analysis (table 1).

An average of 52.7 (s.d. ± 15.6, range 25–72, n = 10, hereafter presented as ± 15.6, 25–72, 10) larvae were removed from each of the 10 treatment parrot nests in which larvae were present. The larvae appeared in the nest a mean of 10 days after the first chick hatched (± 3.9, 5–20, 24), which was when the treatment was applied. The result of this delay meant that 10 nests were either abandoned or depredated before the larvae appeared and were thus excluded from further analysis in the control group. In seven cases, larval removal achieved permanent elimination of the moths. On the remaining three occasions, 27, 6 and 7 larvae respectively, were removed from nests that had the larvae removed on the previous visit. In each case, the first larvae removed were heavier than the subsequent larvae and none were found after the second visit.

There were only two effects of removal of the moth larvae. First, dipteran maggots were found in 5 nests. The maggots were likely to have been *Passeromyia steini* (A. C. Pont pers. comm.), though they could not be reared to adulthood. Maggots were more common in treatment nests (4/11), than in control nests (1/22; $\chi^2 = 3.97$, df = 1, $p = 0.046$). Second, chicks were more likely to be dirty and caked in drying mud in treatment nests (6/11), than control nests (1/22; $\chi^2 = 6.8$, df = 1, $p = 0.009$). Two treatment nests had both maggots present and dirty chicks.

Despite these differences, removal of moth larvae had no effect on the mean number of chicks that fledged, mean percentage of chicks that fledged or the mean number of chicks lost between hatching and fledging (table 1, fig. 1). Nor were there differences in the age, weight or wing chord length of individual chicks at fledging (table 1). Separate analyses for subsets of the data set did not reveal significant differences between treatments. There was no difference between the number of total or partial brood losses or complete successes between treatments ($\chi^2 = 0.89$, df = 2, $p = 0.64$).

There was no evidence of a treatment difference in the growth patterns in either bird weight or wing chord length. In all six nested model comparisons (2 vs. 1, 3 vs. 1 and 4 vs. 3 for each of bird weight and wing chord length), the small change in deviance from the simpler to the more complex model indicated that the addition of a treatment effect did not result in a significantly better model (table 2, fig. 2).

No haematozoan parasites or larger extracellular parasites were located in red blood cells, white blood cells or free in the plasma, in either the samples from nests with moth larvae present or those where the moth larvae were experimentally removed.

Table 1. Results of student *t*-tests that compare hooded parrot (*Psephotus dissimilis*) nesting success between nests with *Trisyntopa neossophila* larvae present and those where the moth larvae were experimentally removed. Only nests in which chicks hatched are included. Katherine, NT, 2007.

	Treatment				
Measure	Moths present Mean (se, n)	No moths Mean (se, n)	Treatment difference Mean	95% CI of difference	p-value
Brood success					
# chicks that fledge/brood	2.1 (0.42, 22)	2.2 (0.54, 11)	-0.05	-1.48, 1.38	0.95
% chicks that fledge/brood	57 (0.10, 22)	65 (14, 11)	-7.6	-4.3, 28.7	0.67
# Chicks lost between hatching and fledging/brood	1.2 (0.35, 22)	1.3 (0.51, 11)	-0.05	-1.30, 1.21	0.94
Parrot success					
Age fledging (days)	26.1 (0.50, 28)	25.2 (0.41, 23)	0.89	-0.46, 2.24	0.19
Final weight (g)	47.45 (0.87, 28)	48.13 (0.87, 23)	-0.68	-3.19, 1.82	0.59
Final wing chord (mm)	129.8 (1.21, 28)	130.9 (1.65, 23)	-1.08	-5.12, 2.95	0.59

Table 2. Comparisons of growth curve models to determine differences in growth rates between nests of hooded parrot (*Psephotus dissimilis*) with *Trisyntopa neossophila* larvae present and those where the moth larvae were experimentally removed. The columns Weight and Wing Chord, list the change in deviance between the models in the left hand column.

Model number	**df**	**Change in deviance; Weight**	**χ2 p-value**	**Change in deviance; Wing Chord**	**χ2 p-value**
4 vs 3	1	0.16	0.69	1.68	0.20
3 vs 1	2	0.04	0.98	0.00	1.00
2 vs 1	1	0.02	0.89	0.31	0.58

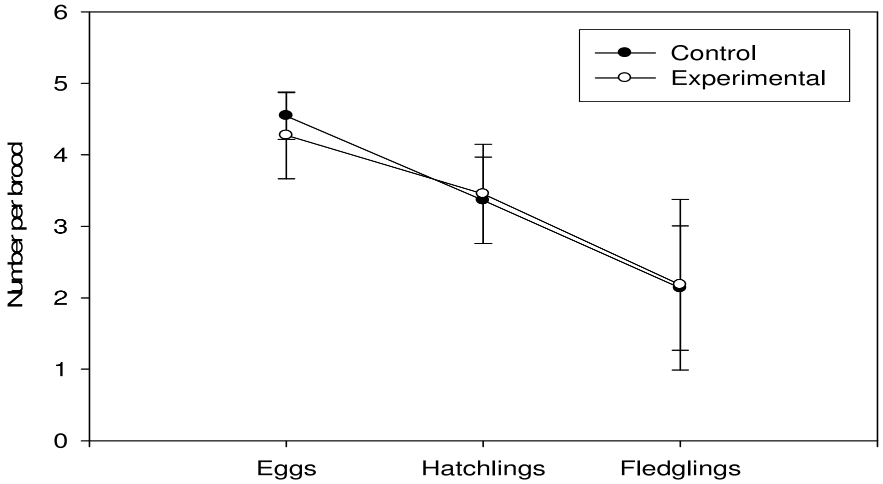

Fig. 1. Mean number of hooded parrot (*Psephotus dissimilis*) eggs, chicks and fledglings by treatment, with 95% confidence intervals. 11 nests had the larvae of *Trisyntopa neossophila* removed during development or were naturally devoid of larvae, while another 22 nests were left with their nest attending larvae intact.

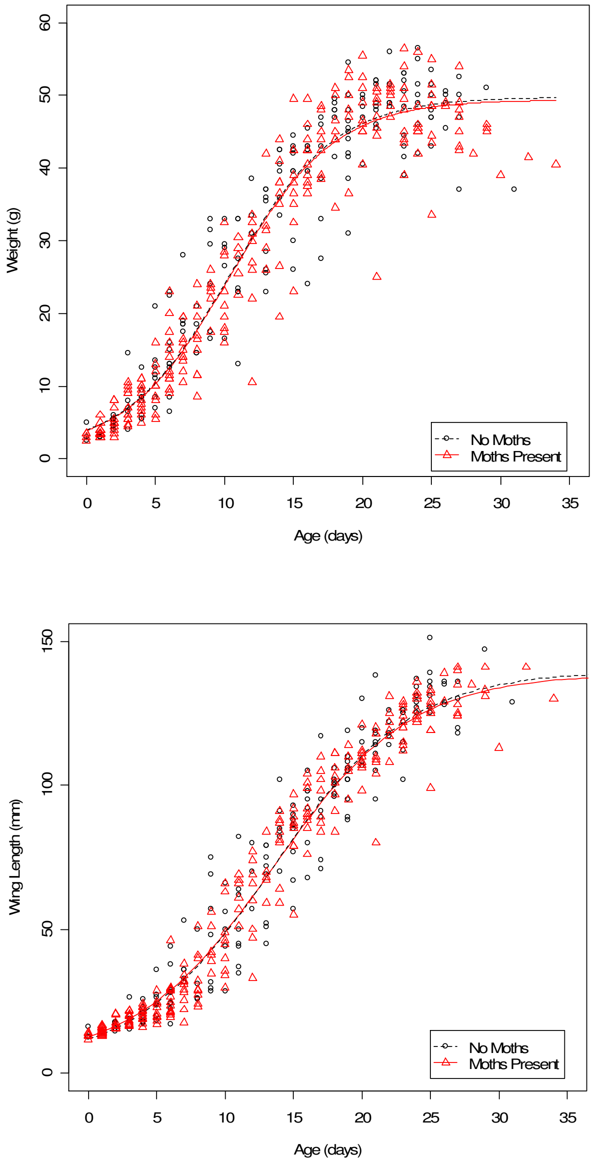

Fig. 2. Growth curve modelling of weight gain and wing chord growth of hooded parrot (*Psephotus dissimilis*) nests with *Trisyntopa neossophila* larvae present and those where the moth larvae were experimentally removed. The curve describes the result of model 2.

Discussion

The relationship between the moth, *T. neossophila*, and the hooded parrot is commensal for the nests observed. The moth benefits from the interaction during most stages of its life-cycle, while the parrot is unaffected by the interaction, neither gaining fitness benefits nor incurring fitness losses.

Despite this, there is evidence of an effect on the parrot arising from the relationship. When moth larvae were experimentally removed, there was an increased probability of the occurrence of dipteran maggots, and that chicks would become soiled and caked in mud. The reason that chicks become dirty is likely to be because, as moth larvae grow, they build a silk web at the base of the nest (Edwards *et al*. 2007; Ch V). The web provides protection for the larvae from the growing chicks, but also allows water to drain away from the base of the nest, removing it from the vicinity of the chicks. The experimental results indicate that the presence of maggots in the absence of moth larvae is likely to be causal. *Passeromyia steini* is an Australian dipteran that spends its larval stage as a free-living parasite of cavity nesting birds and is not known to affect nestling survival, although almost nothing is known of its biology (Roberts 1940; Pont 1974). No maggots were recorded in unmanipulated nests in 2006 (a wet year) and only once in 2007 (when the rainfall was close to average: 760.4 mm 65 year mean vs. 814.4 mm 2007 vs. 1024.2 2006; Katherine Aviation Museum rain data; S 14° 26' 24", E 132° 16' 12"; Bureau of Meteorology 2007). It seems likely that the *T. neossophila* larvae eat the eggs or the small *Passeromyia steini* maggots, or out compete the maggots before they were detected in unmanipulated nests.

Although mud caking and the presence of *Passeromyia steini* suggests that nests with moths would fare better than those without, this was not supported by the measures of nesting success. There was no effect of experimental removal of moths in either reproductive success at the nest level, nor were differences detected at the level of the individual bird in terms of endoparasitic load, weight gain, wing length, fledging chick size or nestling period. Parrots whose nests were experimentally without their moth larvae successfully reared chicks, and, in captivity, hooded parrots successfully raise broods without ever coming into contact with moths (Lendon 1950; Boyd 1985; Carr 1987; Boyd 1990; Hocking 1991; Julian 1992).

The first ornithologists to report on the relationship between *T. scatophaga* and the golden-shouldered parrot believed that the sanitary duties of the moth reduced the odour emanating from the nest (Campbell 1924; Thomson 1934). While parrot faeces did accumulate in the nests of the treatment group of nests, this was not associated with a noticeable increase in odour (from a human perspective), nor an increase in the rate of predation, therefore this is unlikely to be a source of benefit to the parrots.

Although the relationship appears to be commensal, the results ought to be interpreted with caution. Whilst a strong result of benefit or harm to the parrot, as a consequence of removing their nest attending moth, would be easy to interpret, the results as presented pose some difficulties. Differences were detected between the experimental treatments, however these differences did not translate into detectable differences in fitness and questions remain. Did we measure the relevant variables? Whilst we explored the effect of the moths at the level of the clutch's success and in relation to growth and endoparasite load, it may be that the moth affects other measures of nesting success. For instance, parasites are known to affect parental behaviour and fitness, affecting the amount of time that they spend on parental duties (Hurtrez-Boussès *et al.* 2000) and impacting future reproductive attempts (Brown *et al.* 1995; Bize *et al.* 2004). The nature of the field work also meant that we could not obtain sophisticated indices of chick health such as haematocrit (Hurtrez-Boussès *et al.* 1997) or leucocytes (Masello *et al* 2009), and the long term effect on both parents and chicks, raised with and without larvae is not known, yet such long term effects can be important factors contributing to the fecundity of a species (Hatchwell *et al.* 2004; Russell *et al.* 2007). This study also failed to account for temporal variation. One can postulate that the effect of having moth larvae in the nests manifests itself only occasionally, perhaps in abnormally dry or wet years, or years in which other parrot parasites have accumulated, maybe following wet (or dry) years. Finally, perhaps the sample size was too small to detect significant, yet subtle differences in fitness between the two groups (Russell *et al.* 2007). Garnett and Shephard (pers. comm.) found 2 of 600 golden-shouldered parrot nests in which chicks had become imprisoned by pupating *T. scatophaga* moths, representing just 0.3% of nesting attempts: hence, unlikely to have been noted here.

While conservation of *T. scatophaga* seems unlikely to be critical to the management of the endangered golden-shouldered parrot, the opposite is true if we are to secure the future of *T. scatophaga*. *T. scatophaga* is likely to be equally as dependent on the golden-shouldered parrot as *T. neossophila* is on its avian host, yet it does not receive the same level of protection afforded to the golden-shouldered parrot from any conservation organisations (Crowley *et al*. 2004). Indeed, *T. scatophaga* is even less secure than the golden-shouldered parrot because of its dependence on the parrot. The results presented here also support the speculation that, should the paradise parrot (*P. pulcherrimus*), a termite mound nesting congener of the hooded and golden-shouldered parrots, have had a nest attending moth, it would now be extinct given the highly dependent behaviour of the two extant moths (Edwards *et al*. 2007; Ch IV).

Although *T. neossophila* has an obligate and beneficial relationship with the hooded parrot, the parrot has a facultative and neutral relationship with the moth. This makes the relationship commensal in favour of the moth. Successful management of the parrot will ensure the persistence of *T. neossophila*, however the fate of the parrot is not tied to the moth.

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CHAPTER VIII

Photo: S. J. N. Cooney

Synthesis and future directions

Interactions between nesting birds and invertebrates are common and have been a source of interest to ornithologists for more than 150 years (Gosse 1847), however such interactions are generally poorly understood, with little experimental evidence to support conjecture about their nature. This thesis investigated the ecological interactions of the hooded parrot (*Psephotus dissimilis*). In particular, the focus of the research was to determine the nature of the nesting symbiosis between the hooded parrot and a moth reported to inhabit the nesting cavity of the parrot. In the course of this study, the breeding biology of the hooded parrot, as well as the specialised nesting requirements of the parrots were also investigated, both of which are of interest because of the susceptibility to extinction of the parrot's congeners.

Previous reference to the parrot-moth nesting symbiosis assumed that the moth was the same species that is found in the nests of the golden-shouldered parrot (*P. chrysopterygius*): *Trisyntopa scatophaga*. However this study described a new species of moth based on its morphological characteristics and named it *T. neossophila* (chapter IV). *T. neossophila* was found in all hooded parrot nests during the study and was concluded to be dependent on the hooded parrot during critical stages of its life-cycle. *T. neossophila* not only lays its eggs in the parrot's nest cavity, it also spends its larval period in the nests of the parrot (chapter V). During this time it builds a silken web at the base of the nest, from which it presumably shelters from the parrot chicks and emerges to eat the chick's faeces, which appear to comprise 100% of their diet. When the parrot's nesting attempt ends, the larvae move to the walls of the nest cavity. Here they build cocoons and enter a state of diapause before emerging, presumably during the next hooded parrot breeding season.

However, the results of the experiment to determine the impact of the relationship on the parrot were less clear cut (chapter VII). There was evidence that chicks that spent their nesting period with moths were less fouled with dirt, and less subject to other nest insects such as fly maggots. However, at least in the season in which the experiment was conducted, and on the measures of hooded parrot fitness recorded, the presence of the moth was not reflected in enhanced reproductive output or survival. Therefore, it was concluded that the relationship between the parrot and moth was commensal, with the interaction benefiting the moth, but neither harming nor benefiting the parrot.

The failure to discern effects on fitness means that questions remain. Although a large number of parameters were recorded to measure parrot fitness, it may be that the measure of fitness that is affected by the interaction was not examined, or that the effects of the interaction influence the long-term fitness of either the parent or the chick, which was not measured. Further, it may be that the benefit or harm resulting from the relationship only manifests itself in some breeding seasons, based on patterns of, for example, weather or predator abundance. In many interspecific relationships, temporal variation in the effects of the interaction is common (Haemig 1999). Therefore a long-term study that was conducted over multiple breeding seasons might reveal a relationship that was different to the one described here. These factors require further study in order to finally determine the nature of the relationship.

Despite having described *Trisyntopa neossophila* (chapter II) and provided the first description of its ecology, little is known about this species. The period in the moth's life history between emergence from one parrot nest to egg-laying in another has never been described. A key priority would be to determine how the moth finds hooded parrot nests that are at the right stage of development to receive the moth's eggs. Further, it will be important to understand the genetic diversity of the larvae within one hooded parrot nest, as it will give us insight into the population structure of the moth, and help to evaluate threats to both *T. neossophila* and by analogy *T. scatophaga*. It is also important to confirm that *T. neossophila* is only found in hooded parrot nests and not other avian cavity nests. A more extensive survey of cavity nesting birds in the range of hooded parrots would confirm that the moths are completely dependent on the parrot.

One further fascinating possibility concerning the termite nesting *Trisyntopa* species of moths remains. Given that both the hooded parrot and golden-shouldered parrots have nest attendant moths, did the third termite mound nesting parrot, the extinct paradise parrot *P. pulcherrimus*, also have such a relationship? Studies of paradise parrot termite mounds in museum collections have failed to find any evidence of the moth, and evidence in the field is likely to be very scant.

The specialised nesting associations of the hooded parrot, including its nesting symbiosis with *T. neossophila,* coupled with its restricted range, make it vulnerable to extinction, as reflected by the fate of its nearest relatives. This makes the investigation of the parrot's breeding biology relevant. The breeding biology of hooded parrots is, in many respects, typical of other parrots, both in Australia and worldwide (chapter II). However the parrot's choice of nest-site is unusual, both in its substrate and the nature of its construction (chapter III).

A key finding of this research is that hooded parrots rely on active termite mounds in which to nest. Further, when presented with the option of nesting in either the conical termitaria of *Amitermes vitiosus* or the cathedral termitaria of *Nasutitermes triodiae*, hooded parrots always chose to nest in cathedral termite mounds. However, the parrot excavates its nests only in a subset of these termite mounds. Suitable termitaria are always active and the parrots show a preference for taller mounds, than for smaller mounds. This preference for a subset of termite mounds, coupled with both intra- and limited, inter-specific competition, suggests that not all ostensibly suitable nest-sites are available as nest-sites for hooded parrots. Active termite mounds are not only a pre-requisite to nest-site selection, they also improve nesting success. The only measured variable that predicted the outcome of the nesting attempt was the level of activity of the termites within the mound. This suggests that the parrot's nest-site choice is adaptive.

In chapter VI, the biased nature of many studies of inter-specific relationships is discussed in a literature review. The review concludes that most studies ignore important aspects of many interactions between birds and invertebrates, by focusing on only one species in the relationship (usually the bird). Here, both the parrot and moth were examined in the symbiotic nesting relationship; however the parrot-termite nesting interaction was not examined to the same extent. The impact of the relationship between the hooded parrot and the termite *Nasutitermes triodiae* remains unknown. The relationship is assumed to be commensal, with benefit to the nesting bird at minimal cost to the termite (Ch III; Hindwood 1959). Clearly the termite is important to the parrot, as it provides a suitable nesting substrate for the bird. However the parrot's effect on the termite is unknown. Long-term monitoring of termite mounds that have been used as nest-sites is required to see if the birds are truly commensals, or if they parasitise termite communities by causing long-term damage. Furthermore, there are critical aspects of the life-cycle of the termites that are not well understood, such as the factors that influence the positioning of a termite mound, the growth rate of a termite mound and determining the mechanisms by which active termitaria influence the nesting success of the parrots. These are crucial questions if we are to fully understand the availability of nest-sites for hooded parrots.

Hooded parrots are not currently of conservation concern in the wild (Garnett and Crowley 2000). Nothing presented here challenges this view. However, this study was conducted in the core range of this bird (Crawford 1972; Higgins 1999; Barrett *et al.* 2003) and it found that parrots only nest in places that *N. triodiae* are particularly abundant and that only a subset of the ostensibly suitable termite mounds in this habitat are available as nest-sites. Therefore, changes in land management that make suitable termitaria less abundant would have an impact on the breeding population of hooded parrots. These changes may occur as a result of changes in stocking rates, fire regimes or the type of agriculture undertaken. Despite these potential threats, a large part of the current range of the hooded parrot is currently protected by national parks and is on Aboriginal land where grazing is minimal and fire regimes appropriate (Garnett and Crowley 2000). This safeguard should also protect *T. neossophila*, which is more vulnerable to extinction than the parrot, because of its reliance on the parrot.

Golden-shouldered parrots are endangered (Garnett and Crowley 2000) and have been intensively studied in an effort to save them from extinction (Crowley *et al.* 2004). What then, does this study bring to discussions about the management of golden-shouldered parrots? The provisional finding that hooded parrots have a commensal relationship with the moth *T. neossophila*, means that protection of *T. scatophaga*, which is found in the nests of golden-shouldered parrots, is not necessary for the protection of the parrot species. It does suggest that *T. scatophaga*, because of its reliance on the parrot, is endangered and should be afforded the same conservation status and protection as the parrot (Garnett and Crowley 2007). As a result of this study, a nomination has been made to redress this situation under the Environment Protection and Biodiversity

Conservation Act 1999 (EPBC Act; see Appendix 3). Further, as stated previously, the effect of the moth on parrot breeding success may only manifest in certain years or under certain conditions. Therefore, this research re-emphasises the need for moths to be involved in any future golden-shouldered parrot relocation attempt.

This project set out to examine the remarkable ecological associations of the hooded parrot. The project has discovered and described a new species of moth. It has made contributions to our understanding of an unusual lepidopteran, with a coprophagous diet. It has explored the two-way nature of bird-insect interactions, through both the literature review and the experimental manipulation of one such interaction. It has studied the availability of nest-sites for a primary cavity nesting species, and documented the reliance of hooded parrots on active termite mounds during the reproductive stages of its life-cycle. Finally, as a result of this study, an application has been made for the protection of an endangered species of moth and fruitful areas for future research have been identified.

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APPENDIX 1

Summary of nesting parameters of Australian parrots reported in Higgins (1999). Gaps in the data indicate that this breeding parameter was not reported for this species. Female weights are based on the largest single study of adult birds reported in Higgins (1999). Egg volume calculated using the method of Hoyt (1979); Volume = 0.51 × LB^2, where L is the length and B the breadth of the egg. * denotes the results from this research. ** The female weight for the paradise parrot is not known, therefore the weight used is an approximate weight based on the calculated weight:wing length ratio of both hooded and golden-shouldered parrots 1:2.765.

Common Name	Scientific Name	Female weight (g)	Number of eggs			Size of eggs (mm)			Laying interval (days)	Incubation period (days)	Feather Growth (days)			Eyes open (days)	Fledge age (days)	% hatch	% Fledge
			Mean	**Min**	**Max**	**Width**	**Length**	**Volume**			**Pins**	**Broken pins**	**Fully feathered**				
Rainbow Lorikeet	*Trichoglossus haematodus*	125	2			23	27	7284	2.5	23	22	30	45	14	58		
Scaly-breasted Lorikeet	*Trichoglossus chlorolepidotus*	75	2			21	25.5	5735	2.5	22	20			14	27		
Varied Lorikeet	*Psitteuteles versicolor*	55		1	2	19	23	4235		22	10		35		29		
Musk Lorikeet	*Glossopsitta concinna*	70	2			20	25	5100	2.5	22	14			12	48		
Little Lorikeet	*Glossopsitta pusilla*	40	4	3	5	17	20	2948	2	20	20		37.5	10	41		
Purple-crowned Lorikeet	*Glossopsitta porphyrocephala*	45		4	6	17	20	2948	2	18	22		45	12	30		
Eclectus Parrot	*Eclectus roratus*	550	2			33	42	23326	1	26							
Red-cheeked Parrot	*Geoffroyus geoffroyi*	140	3	2	4	25	29	9244			28		60		80		
Double-eyed Fig-Parrot	*Cyclopsitta diopthalma*	35		2	3	17	21	3095	1.5	20				6	35		
Australian King Parrot	*Alisterus scapularis*	240		3	6	28	32	12795	2	20	8		36		35		

Common Name	Scientific Name	Female weight (g)	Number of eggs			Size of eggs (mm)			Laying interval (days)	Incubation period (days)	Feather Growth (days)			Eyes open (days)	Fledge age (days)	% hatch	% Fledge
			Mean	Min	Max	Width	Length	Volume			Pins	Broken pins	Fully feathered				
Red-winged Parrot	*Aprosmictus erythropterus*	145		6		26	31	10688		20			35	8	35		
Superb Parrot	*Polytelis swainsonii*	145		4	6	24	29	8519		22					40		
Regent Parrot	*Polytelis anthopeplus*	175	5	3	5	24	30	8813	1.5	22	9	14	35	11	38		
Princess Parrot	*Polytelis alexandrae*	105		4	6	23	28	7554		21					38		
Green Rosella	*Platycercus caledonicus*	135		4	8	24	29	8519	1	20					35		
Crimson Rosella	*Platycercus elegans*	135	5.23	3	8	23	28	7554	2.1	20				4	33	66	50
Eastern Rosella	*Platycercus eximius*	105	5.6	3	9		22	6576	2	19	8				36	58	54
Pale-headed Rosella	*Platycercus adscitus*	105		4	8	21	26	5848		20					35	71	
Northern Rosella	*Platycercus venustus*	105		2	5	21	25	5623		20					35		
Western Rosella	*Platycercus icterotis*	65	5.6	2	7	21	26	5848		21					33.5	84	72
Australian Ringneck	*Barnardius zonarius*	165	4.3	4	6	24	29	8519		28					35	70	66
Red-capped Parrot	*Purpureicephalus spurius*	115	5.3	3	7	23	27	7284		23	12			10	33	54	27
Blue Bonnet	*Northiella haematogaster*	85		4	9	20	24	4896		20					30	70.4	
Swift Parrot	*Lathamus discolor*	65	4.5	4	6	20	25	5100	2	25					42		
Red-rumped Parrot	*Psephotus haematonotus*	60	4.8	3	7	19	23	4235	2	21	14				29	75	47
Mulga Parrot	*Psephotus varius*	55	6	4	7	19	22	4050	1.5	19	10	15	27	6	28		
Golden-shouldered Parrot	*Psephotus chrysopterygius*	55	5.5	4	7	17.8	20.6	3329	2	20	9				35	68	44
Hooded Parrot *	***Psephotus dissimilis***		**4.5**	**1**	**6**	**18.7**	**21.8**	3888	**1.5**	**18.6**	**11**	**18.9**	**25**	**5.4**	**29**	**75**	**61**
Hooded Parrot	*Psephotus dissimilis*	47	4.3	3	5	18.3	20.8	3553	1.8	20	10	18	30	10			
Paradise Parrot	*Psephotus pulcherrimus*	45**	3			18	21.9	3619									
Budgerigar	*Melopsittacus undulatus*	30	4.5	4	7	14.8	18.9	2111	1.5	17	5				34		40
Bourke's Parrot	*Neopsephotus bourkii*	45		3	5	17	21	3095	2	18	12	14	24	7	27		
Blue-winged Parrot	*Neophema chrysostoma*	55		4	6	19.1	22.6	4205	2	20.5	18		28	8.9	34		
Elegant Parrot	*Neophema elegans*	45		4	7	18.1	21.2	3542	2	18	10		28	7	30		

Common Name	**Scientific Name**	**Female weight (g)**	**Number of eggs**			**Size of eggs (mm)**			**Laying interval (days)**	**Incubation period (days)**	**Feather Growth (days)**			**Eyes open (days)**	**Fledge age (days)**	**% hatch**	**% Fledge**
			Mean	**Min**	**Max**	**Width**	**Length**	**Volume**			**Pins**	**Broken pins**	**Fully feathered**				
Rock Parrot	*Neophema petrophila*	55		4	6	20	25	5100		18	9	21	28	8	30		
Orange-bellied Parrot	*Neophema chrysogaster*	45	4.5	3	6	18.1	21.6	3609	2	22.5					32	94	71
Turquoise Parrot	*Neophema pulchella*	40	4.8	2	7	17.9	21.6	3530	2	18			21	7	30	74	60
Scarlet-chested Parrot	*Neophema splendida*	40	4	3	6	20	23	4692	2	18	7		25	7	30		
Ground Parrot	*Pezoporus wallicus*	80	3.8	1	6	21.5	27	6365	1.5	22.5	9	12	22	7	24	66.7	57.1
Night Parrot	*Pezoporus occidentalis*					19	25	4603									
	Mean	**99.4**	**4.2**	**3.2**	**6.2**	**20.8**	**25**	**6039**	**1.9**	**20.7**	**12.9**	**17.9**	**32.6**	**8.7**	**35.4**	**71**	**54**
	± Standard Deviation	**90.1**	**1.24**	**1.09**	**1.49**	**3.52**	**4.37**	**3676**	**0.39**	**2.35**	**5.91**	**5.74**	**9.85**	**2.82**	**9.89**	**10.2**	**13.3**
	Mode	**55**	**2**	**4**	**6**	**20**	**25**	**5100**	**2**	**20**	**10**	**14**	**35**	**7**	**35**	**75**	**N/A**

Additional sources of data: [1] Heinsohn and Legge 2003.

APPENDIX 2

List of all 36 Psittacidae species known to excavate nests in arboreal or terrestrial termitaria. 'A' denotes an arboreal termite mound nester: 'T' denotes a terrestrial termite mound nester. Nomenclature after Collar 1997.

Common Name	**Scientific Name**	**Arboreal or Terrestrial**	**Ref***
Red-flanked Lorikeet	*Charmosyna placentis*	A	3
Yellow-headed Pygmy-Parrot	*Micropsitta keiensis*	A	5
Geelvink Pygmy-Parrot	*Micropsitta geelvinkiana*	A	3
Yellow-breasted Pygmy-Parrot	*Micropsitta pusio*	A	5
Green Pygmy-Parrot	*Micropsitta finschii*	A/T	5
Orange-breasted Fig-Parrot	*Cyclopsitta gulielmitertii*	A	1
Hooded Parrot	*Psephotus dissimilis*	T	7
Golden-shouldered Parrot	*Psephotus chrysopterygius*	T	8
Red-headed Lovebird	*Agapornis pullaria*	A	6
Black-winged Lovebird	*Agapornis taranta*	A	3
Orange-fronted Hanging-Parrot	*Loriculus aurantiifrons*	A	3
Red-shouldered Macaw	*Diopsittica nobilis*	A	3
Green Parakeet	*Aratinga holochlora*	A	3
Red-masked Parakeet	*Aratinga erythrogenys*	A	3
Cuban Parakeet	*Aratinga euops*	A	3
Hispaniolan Parakeet	*Aratinga chloroptera*	A	3
Dusky-headed Parakeet	*Aratinga weddellii*	A	3
Olive-throated Parakeet	*Aratinga nana*	A/T	5
Orange-fronted Parakeet	*Aratinga canicularis*	A	4

Common Name	**Scientific Name**	**Arboreal or Terrestrial**	**Ref***
Peach-fronted Parakeet	*Aratinga aurea*	A/T	5
Brown-throated Parakeet	*Aratinga pertinax*	A	5
Green-rumped Parrotlet	*Forpus passerinus*	A	5
Blue-winged Parrotlet	*Forpus xanthopterygius*	A	3
Spectacled Parrotlet	*Forpus conspicillatus*	A	3
Canary-winged Parakeet	*Brotogeris versicolurus*	A	5
Grey-cheeked Parakeet	*Brotogeris pyrrhopterus*	T	3
Orange-chinned Parakeet	*Brotogeris jugularis*	T	3
Cobalt-winged Parakeet	*Brotogeris cyanoptera*	A	2
Golden-winged Parakeet	*Brotogeris chrysopterus*	A	3
Tui Parakeet	*Brotogeris sanctithomae*	A	2
Lilac-tailed Parrotlet	*Touit batavica*	A	3
Blue-fronted Parrotlet	*Touit dilectissima*	A	3
Sapphire-rumped Parrotlet	*Touit purpuratus*	A	3
Red-tailed Amazon	*Amazona brasiliensis*	A	3
Blue-fronted Amazon	*Amazona aestiva*	A	3
Yellow-crowned Amazon	*Amazona ochrocephala*	A	3

* References cited: [1] Bell and Coates 1979; [2] Brightsmith 2004; [3] Collar 1997; [4] Hardy 1963; [5] Hindwood 1959; [6] Moreau 1942; [7] Reed and Tidemann 1994; [8] Weaver 1982.

APPENDIX 3

Australian Government

Department of the Environment, Water, Heritage and the Arts

Threatened Species Nomination Form - For adding or changing the category of a native species in the list of threatened species under the *Environment Protection and Biodiversity Conservation Act 1999* (EPBC Act)

Nominator details **Note: Nominator details are subject to the provision of the *Privacy Act 1988* and will not be divulged to third parties if advice regarding the nomination is sought from such parties.**	
1. Full name	
Stuart J. N. Cooney[1], Stephen Garnett[2], Gabriel Crowley[2]	
2. Body, organisation or company name (if applicable)	
[1] Australian National University, [2] Charles Darwin University	
3. Contact details	
Email: **Stuart.Cooney@anu.edu.au** **Phone: 08 8956 9369** **Fax: 08 8956 9551**	**Postal address:** **Stuart Cooney, Department of Botany and Zoology, Australian National University, Canberra, ACT, 0200**
4. Declaration: I declare that the information in this nomination and its attachments is true and correct to the best of my knowledge.	
Signed (If available, please attach an electronic signature when submitting by email):	
5. Date signed:	

Nominated species - summary of eligibility

1. Name of species (or subspecies)

Trisyntopa scatophaga

2. Category for which the species is nominated under the EPBC Act

Current listing category	**Proposed listing category**
☐ Extinct ☐ Extinct in the wild ☐ Critically Endangered ☐ Endangered ☐ Vulnerable ☐ Conservation dependent ✓ Unlisted	☐ Extinct ☐ Extinct in the wild ☐ Critically Endangered ✓ Endangered ☐ Vulnerable ☐ Conservation dependent

3. Criteria under which the species is eligible for listing

For a species nominated as critically endangered, endangered or vulnerable, identify which of the eligibility criteria it meets (one or more) from the list below. Please note that the information you provide in this nomination form should support the criteria you select.

For further details on the criteria, please refer to the Threatened Species Scientific Committee guidelines attached to this form.

☑ Criterion 1 - It has undergone, is suspected to have undergone or is likely to undergo in the immediate future a very severe, severe or substantial reduction in numbers.

☑ Criterion 2 - Its geographic distribution is precarious for the survival of the species and is very restricted, restricted or limited.

☑ Criterion 3 - The estimated total number of mature individuals is limited to a particular degree and:
  (a) evidence suggests that the number will continue to decline at a particular rate; or
  (b) the number is likely to continue to decline and its geographic distribution is precarious for its survival.

☑ Criterion 4 - The estimated total number of mature individuals is extremely low, very low or low.

☐ Criterion 5 - Probability of extinction in the wild.

For species nominated as conservation dependent, identify which criterion the species meets (either criterion 1 or criterion 2).

☐ Criterion 1 - The species is the focus of a specific conservation program, the cessation of which would result in the species becoming vulnerable, endangered or critically endangered; or

☐ Criterion 2:

- The species is a species of fish; and
- The species is the focus of a plan of management that provides for management actions necessary to stop the decline of, and support the recovery of, the species so that its chances of long term survival in nature are maximised; and
- The plan of management is in force under a law of the Commonwealth

or of a State or Territory; and

- Cessation of the plan of management would adversely affect the conservation status of the species.

Important notes for completing this form

- Complete the form as far as possible. It is important for the Threatened Species Scientific Committee to have comprehensive information and the best case on which to judge a species' eligibility against the EPBC Act criteria for listing (Attachment A).
- To ensure you have the most up to date information, it is recommended that you contact the relevant Natural Resource Management authority. For details see: www.nrm.gov.au.
- Nominations that do not meet the EPBC Regulations will not proceed. Division 7.2 of the EPBC Regulations 2000 (www.environment.gov.au/epbc/about/index.html) specifies the required information. Note that, if after a search, relevant information is not available, please state this under the relevant question in the nomination form (as noted under sub-regulation 7.04(3)).
- Keep in mind that the purpose of the questions is to help identify why the species is eligible for listing in the nominated conservation category.
- Subspecies (or other taxa lower than the species level) may be nominated, but it is important to provide information on the full national range of the species to support the claims.
- The questions are separated into themes, which indirectly or directly relate to the criteria for listing. The Committee provides the following general description of what kind of information informs its judgements against the EPBC Act criteria for listing (Attachment A).
- For all facts and all information presented - identify your references and sources of information. Document the reasons and supportive data. Indicate the quality of facts/information and any uncertainty in the information. For example was it based on a peer-reviewed research publication or anecdote; or on observed data, an inference/extrapolation from the data, or a reasonable premise not yet supported by hard data.
- Personal communications - The opinion of appropriate scientific experts may also be cited (with their approval) in support of a nomination. If this is done the names of the experts, their qualifications and full contact details must also be provided at the end of this nomination.
- Confidential material – Identify any confidential material and explain the sensitivity.
- Tables – Can be included at the end of the form or prepared as separate electronic documents included as appendixes or attachments. Refer to tables in the relevant area of the text.
- Maps - If maps cannot be supplied electronically, please provide them in hardcopy.
- Cross-reference relevant areas of the nomination form where needed.

How to lodge your nomination

Completed nominations may be lodged either:

1. **by email to:** epbc.nominations@environment.gov.au**, or**
2. by mail to: The Director

Species Listing Section
Department of the Environment and Water Resources
GPO Box 787
Canberra ACT 2601

Further information

The Threatened Species Scientific Committee has developed guidelines to assist nominators. The guidelines are attached to this form. They include the statutory criteria for the 'critically endangered', 'endangered' and 'vulnerable' categories at Part A. Indicative thresholds, which may be used by the Committee to assess whether a species is eligible for listing against the criteria prescribed by the EPBC Regulations, are at Part B. It should be noted that the Committee does not apply these thresholds strictly, but has regard to them when making judgments about species in terms of their biological contexts, and on a case-by-case basis.

More detailed information on all categories for threatened species can be found in Section 179 of the EPBC Act and the statutory criteria can be found in Division 7.1 of the EPBC Regulations 2000. These are available at:
www.environment.gov.au/epbc/about/index.html

For questions regarding nominations contact:
The Director
Species Listing Section
Department of the Environment and Water Resources
GPO Box 787

Canberra ACT 2601
Telephone (02) 6274 2238
Fax (02) 6274 2214

Section 1 - Legal Status, Distribution, Biological, Ecological

Conservation Theme

1**. The conservation theme for the assessment period commencing 1 October 2008 (for which nominations close 31 March 2008) is** 'rivers, wetlands and groundwater dependent species and ecosystems of inland Australia'**.** ***How does this nomination relate to the*** *conservation theme****?***	*This species is endemic to the inland area of the Cape York Peninsula, Queensland and has critical ecological ties to an endangered species endemic to that area.*

Taxonomy

2. *What are the* ***currently accepted scientific and common name/s*** *for the species?* *Note any other scientific names that have been used recently. Note the species authority and the Order and Family to which the species belongs (Family name alone is sufficient for plants, however, both Order and Family name are required for insects).*	*The currently accepted scientific name is* Trisyntopa scatophaga *(White), it has also been called* Neossiosynoeca scatophaga*. It is a moth that belongs to the order Lepidoptera, family Oecophoridae (Common 2000).*
3. *Is this* ***species conventionally accepted****? If not, explain why. Is there any controversy about the taxonomy?*	*Yes*
4. *If* ***the species*** *is* ***NOT***	

conventionally accepted**, please provide:* *(i) a taxonomic description of the species in a form suitable for publication in conventional scientific literature; **OR *(ii) evidence that a scientific institution has a specimen of the species and a written statement signed by a person who has relevant taxonomic expertise (has worked, or is a published author, on the class of species nominated)**,** that the person thinks the species is a new species.*	
5. *Is this species **taxonomically distinct** (Taxonomic distinctiveness – a measure of how unique a species is relative to other species)?*	*Yes*

Legal Status

5. *What is the species' **current conservation status** under Australian and State/Territory Government legislation?*	*None*
6. *Does the species **have specific protection** (e.g. listed on an annex or appendix) under other legislation or intergovernmental arrangements, e.g. Convention on International Trade in Endangered Fauna and Flora (CITES), Convention on Migratory Species (CMS).*	*No*

Description

***7.** Give a brief description of the species' **appearance**, including size and/or weight, and sex and age variation if appropriate; social structure and dispersion (e.g. solitary/clumped/flocks).*	*Small grey moth, with ciliated forewings that are darker than the hindwings. Wingspan 26.2–36.7 mm. As larvae, off white with dark brown head; ~3 cm in length immediately prior to pupation.*
***8.** Give a brief description of the species' **ecological role** (for example, is it a 'keystone' or 'foundation' species, does it play a role in processes such as seed dispersal or pollination).*	Trisyntopa scatophaga *may provide nest sanitation for the Golden-shouldered Parrot* Psephotus chrysopterygius (*hereafter GSP), which is classified as endangered.*

Australian Distribution

***9.** Describe the species' **current and past distribution in Australia** and, if available, attach a map.*	*Endemic to southern and central Cape York Peninsula, Qld, between Weipa, Normanton, Bulleringa, Port Stewart and Coen (Garnett and Crowley, 2000). Moth larvae are found exclusively in the nests of GSPs, therefore the range of the moth has contracted with the parrot's contraction.*
***10.** What is the **extent of occurrence** (in km^2) for the species (described in Attachment A); explain how it was calculated and datasets used.*	*3000 km^2; this is the current accepted extent of occurrence of the GSP (Garnett and Crowley 2000).*
a. *What is the **current** extent of occurrence?*	*One sub-population Musgrave-Morehead Rivers, the other west*

	of Chillagoe, Qld.
b. *What data are there to indicate* ***past declines*** *in extent of occurrence (if available, include data that indicates the percentage decline over the past 10 years or 3 generations whichever is longer)?*	*Last parrot recorded in Coen to Port Stewart area was in 1920s, Musgrave-Morehead Rivers population in decline, with the last parrot nests on Violetvale station reported in the 1970s (Garnett and Crowley 2000). This contraction in the parrots' range will be paralleled by the moth's contraction.*
c. *What data are there to indicate* ***future changes*** *in extent of occurrence (if available, include data that indicates the percentage decline over 10 years or 3 generations whichever is longer (up to a maximum of 100 years in the future) where the time period is a continuous period that may include a component of the past)?*	*Without management for the protection of GSPs, inappropriate fire regimes and high levels of cattle grazing will continue to reduce the breeding populations of the parrots and therefore of the moth as well.*
11. *What is the* ***area of occupancy*** *(in km^2) for the species (described in Attachment A); explain how calculated and datasets that are used.*	
a. *What is the* ***current*** *area of occupancy?*	*1500 km^2; this is the current accepted area of occupancy of the GSP (Garnett and Crowley 2000).*
b. *What data are there to indicate* ***past declines*** *in area of occupancy (if available, include data that indicates the percentage decline over the past 10 years or 3 generations whichever is longer)?*	*See above (10b)*

c. *What data are there to indicate **future changes** in area of occupancy (if available, include data that indicates the percentage decline over 10 years or 3 generations whichever is longer (up to a maximum of 100 years in the future) where the time period is a continuous period that may include a component of the past)?*	*See above (10c)*
***12.** How many **natural locations** do you consider the species occurs in and why? Where are these located?* *The term 'location' defines a geographically or ecologically distinct area.*	*2; Musgrave–Moorhead Rivers region, Qld and west of Chillagoe region, Qld.*
***13**. Give **locations of other populations**:* *captive/propagated populations; populations recently re-introduced to the wild; and sites for proposed population re-introductions. Note if these sites have been identified in recovery plans.*	*None known*
***14**. Is the species' **distribution severely fragmented?** What is the cause of this fragmentation? Describe any biological, geographic, human-induced or other barriers causing this species' populations to be fragmented.* *Severely fragmented refers to the situation in which increased extinction risk to the taxon results from most individuals being found in small and relatively isolated subpopulations (in certain circumstances this may be inferred from habitat information). These small subpopulations may go extinct, with a reduced probability of recolonisation.*	*Yes, the moth has a limited time for dispersal because it does not feed as an adult moth and, because of its size, limited ability to disperse over larger areas, therefore the two sub-populations are unlikely to be interbreeding. The lack of GSP nests outside of the two identified breeding areas make these areas unsuitable habitat for the moth. Should one of the two sub-populations become extinct, it is highly unlikely that they*

	would be naturally re-populated.
***15**. Departmental Use Only:*	

Global Distribution

***16.** Describe the species' **global distribution**.*	*Endemic to Australia*
***17.** Give an overview of the **global population**'s size, trends, threats and security of the species outside Australia.*	*N/A*
***18.** Explain the **relationship** between the Australian population and the global population, including:*	*N/A*
a. *What **percentage** of the global population occurs **in Australia**;*	
b. *Is the Australian population **distinct**, geographically **separate** or does part or all of the population move in/out of Australia's jurisdiction (give an overview; details in Movements section);*	
c. *Do **global threats** affect the Australian population?*	

Surveys and Monitoring

***19**. Has the species been **reasonably well surveyed**? Provide an overview of surveys to date and the likelihood of its current known distribution and/or population size being its actual distribution and/or population size.*	*Yes, the population of GSPs is well known and* Trisyntopa scatophaga *is only found in the GSP nests.*
***20**. For species nominated as extinct or extinct in the wild, please provide details of the **most recent** known **collection**, or authenticated **sighting** of the species and whether additional populations are likely to exist.*	
***21**. Is there an ongoing **monitoring programme**? If so, please describe the extent*	*From 1993 to about 2000, GSP populations were monitored*

and length of the programme.	*annually on Artemis Station and every five years in more remote parts of the parrots range (Garnett and Crowley 2000), but monitoring has been less regular in recent years.*

Life Cycle and Population

22. *What is the species' total population size in terms of* ***number of mature individuals****? How were population estimates derived and are they reliable? Are there other useful measures of population size and what are they?* In the absence of figures, terms such as common, abundant, scarce can be of value.	*The ecologically similar moth* Trisyntopa neossophila *was found to have a mean of 53 larvae per Hooded Parrot nest (Cooney et al, In Press). If this is extrapolated to the number of breeding GSPs, it would result in a population size of 53,000 larvae, however only 2.3 adult moths were seen in any one nest, which would relate to an adult population size of 2300 moths during the critical period of reproduction.*
23. *Does the species occur in a* ***number of smaller populations****? How many? For each population give the locality, numbers and trends in numbers and tenure of land (include extinct populations). Can these be considered to be subpopulations and why?* **Subpopulations** are defined as geographically or otherwise distinct groups in the population between which there is little demographic or genetic exchange.	*Yes.* *Musgrave–Morehead Rivers region: 50% of population, decreasing, free-hold and lease-hold agricultural land.* *West of Chillagoe region: 50% of population, decreasing, free-hold and lease-hold agricultural land.* *These are sub-populations because of the lack of genetic*

	flow between the populations
***24.** Provide details on ages of the following:*	
***a.** sexual maturity;*	*~10 months*
***b.** life expectancy;*	*~1 year*
***c.** natural mortality.*	*~1 year*
25. Reproduction	
***For plants**: When does the species flower and set fruit? What conditions are needed for this? What is the pollinating mechanism? If the species is capable of vegetative reproduction, a description of how this occurs, the conditions needed and when. Does the species require a disturbance regime (e.g. fire, cleared ground) in order to reproduce?*	
***For animals**: provide overview of breeding system and of breeding success, including: when does it breed; what conditions are needed for breeding; are there any breeding behaviours that may make it vulnerable to a threatening process?*	*This moth lays its eggs in the nest of a GSP so that larvae hatch in synchrony with the hatching of the parrot's eggs. The larvae spend their larval period in the nest and exclusively consume the excrement of the nestling parrots. When the parrot chicks fledge, the larvae move to the walls of the nest cavity to pupate, emerging to repeat the process during the next parrot breeding season.*
***26.** What is the **population trend** for the entire species?*	
*a. What data are there to indicate **past decline** in size (if available, include data on rate of decline over past 10 years or 3 generations whichever is longer)?*	*As per the GSP, the moth has disappeared from parts of its former range and declined in abundance in its current range.*

b. *What data are there to indicate* ***future changes*** *in size (if available, include data which will indicate the percentage of decline over 10 years or 3 generations whichever in longer (up to a maximum of 100 years in the future) where the time period is a continuous period that may include a component of the past)?*	*As per the GSP, the moth will continue to decline without active management that implements appropriate fire regimes and lower rates of grazing by cattle.*
27. *Does the species undergo* ***extreme natural fluctuations*** *in population numbers, extent of occurrence or area of occupancy? To what extent and why?* **Extreme fluctuations** can be said to occur in a number of taxa when population size or distribution area varies widely, rapidly and frequently, typically with a variation greater than one order of magnitude (i.e. a tenfold increase or decrease).	*Yes, the moth has large numbers of young, but relatively low numbers of breeding adults.*
28*. What is the* ***generation length*** *and how it is calculated?* **Generation length** is the average age of parents of the current cohort (i.e. newborn individuals in the population). Generation length therefore reflects the turnover rate of breeding individuals in a population. Generation length is greater than the age at first breeding and less than the age of the oldest breeding individual, except in taxa that breed only once. Where generation length varies under threat, the more natural, i.e. pre-disturbance, generation length should be used.	*Emergence of moths from pupae under laboratory conditions can take several years (Ted Edwards pers comm.). Adult moths are between 10 and 12 months old when they reproduce (however this is poorly understood), therefore the generation length is 11 months.*
29*. Identify* ***important populations*** *necessary for the species' long-term survival and recovery? This may include: key breeding populations, those near the edge of the species' range or*	*Neither sub-population is more important than the other for the future survival of the species, however the Musgrave–Morehead*

those needed to maintain genetic diversity.	*population is currently being more intensively managed for the protection of GSPs and is more accessible for future conservation efforts.*
***30.** Describe any **cross-breeding** with other species in the wild, indicating how frequently and where this occurs.*	*None known*
***31.** Departmental Use only:*	

Populations in Reserve

***32.** Which **populations** are **in reserve systems**? Which of these are actively managed for this species? Give details.*	*None known*

Habitat

***33**. Describe the **species' habitat** (e.g. aspect, topography, substrate, climate, forest type, associated species, sympatric species). If the species uses different habitats for different activities (e.g. breeding, feeding, roosting, dispersing, basking), then describe each habitat.*	*The larvae are found in termite mounds on grassy areas within ti-tree* Melaleuca *spp. or eucalypt savannahs (Garnett and Crowley 2000).*
***34.** Does the species use **refuge habitat**, e.g. in times of fire, drought or flood? Describe this habitat.*	*None known*
***35.** Is the **extent or quality** of the species' habitat **in decline**? If the species uses different habitats, specify which of these are in decline.*	*Yes, both the extent and quality of habitat has declined as a result of fewer termite mounds suitable for GSP nests, and therefore natal habitat for the moth (Garnett and Crowley 1995).*
36.** Is the species part of, or does it rely on, a **listed	*It is completely reliant on the*

threatened ecological community*? Is it associated with any other* ***listed threatened species****?*	*GSP which is listed as Endangered in parts of its range.*

Feeding

37*. Summarize the species'* ***food*** *items or sources and timing/seasonality.*	*The moth exclusively eats the faecal matter of nestling GSPs as larvae and eats nothing as an adult.*
38. *Briefly describe the species'* ***feeding behaviours****, including those that may make the species vulnerable to a threatening process.*	*The moth's diet is entirely reliant on the breeding of GSPs*

Movement Patterns (fauna species only)

39. *Describe any relevant* ***daily and seasonal pattern of movement*** *for the species, or other irregular patterns of movement, including relevant arrival/departure dates if migratory.*	*After emerging, imagos leave their natal termite mound and seek a current season's GSP nest in which to lay eggs.*
40. *Give details of the species'* ***home ranges/territories****.*	*Larvae are confined to the GSP nest cavity, adult territories are unknown.*

Survey Guidelines

41. *Give details of the* ***distinctiveness and detectability*** *of the species.*	Trisyntopa scatophaga *is only found in GSP nests and is the only known moth in GSP nests. It is, however very similar in appearance to it congeners* Trisyntopa neossophila *and* Trisyntopa euryspoda, *which are allopatric.*
42. *Describe* ***methods for detecting species*** *including when to conduct surveys (e.g.*	*Surveys should be conducted during the GSP breeding season*

season, time of day, weather conditions); length, intensity and pattern of search effort; and limitations and expert acceptance; recommended methods; survey-effort guide.	*(Mar–Aug), by examining the nests of GSPs. GSP nests are likely to be dispersed and hard to find, however it requires little specialist knowledge to identify a nest and nest are currently monitored for management of that species.*

Section 2 - Threats and Threat Abatement

Threats

***43**. Identify **past, current and future threats**, to the species indicating whether they are actual or potential. For <u>each</u> threat, describe:*	*The most critical threat to* Trisyntopa scatophaga *is the continuing decline of the GSP.*
*a. **how and where** it impacts on this species;*	Trisyntopa scatophaga *is completely reliant on the parrot for the provision of a suitable nest site and food during its larval stages.*
*b. what its **effect** has been **so far** (indicate whether it is known or suspected; present supporting information/research; does it only affect certain populations);*	*The decline of the parrot has resulted in a concurrent decline in the population size of the moth.*
c. *what is its **expected effect in the future** (is there supporting research/information; is the threat only suspected; does it only affect certain populations);*	*Should the targets of the GSP recovery program be successful (recolonisation, pastoral management guidelines and down-listing the parrot to vulnerable within ten years), then the moth will also be more secure than it is now.*
d. *what is the **relative importance or***	*This threat is critical to the*

***magnitude** of the threat to the species.*	*survival of the species.*
***44.** If not included above, identify **catastrophic threats**, i.e. threats with a low predictability that are likely to severely affect the species. Identify the threat, explain its likely impact and indicate the likelihood of it occurring (e.g. a drought/cyclone in the area every 100 years).*	*None known*
***45.** Identify and explain any **additional biological characteristics** particular to the species that are threatening to its survival (e.g. low genetic diversity)?*	*None known*
***46.** Identify and explain any **quantitative measures or models** that address the probability of the species' extinction in the wild over a particular timeframe.*	*None known*
***47**. Is there **other information** that relates to the survival of this species that you would like to address?*	*No*

Threat Abatement and Recovery

***48.** Give an overview of how broad-scale **threats** are **being abated**/could be abated and **other recovery actions** underway/ proposed. Identify who is undertaking these activities and how successful the activities have been to date.*	*For the Golden-shouldered Parrot:* *1. Breeding biology, feeding ecology and analysis of threats have been studied.* *2. Causes of vegetation change impacting on the parrot on the Cape York Peninsula have been determined.* *3. The part of the Morehead sub-population that occurs on Artemis station was monitored annually from 1992 to 2000 and*

	has been partially monitored each year since then. *4. The remainder of the two populations were surveyed at five year intervals between 1996/7 and 2001/2 and were found to be stable.* *5. Supplementary feeding takes place on Artemis station.* *6. Fire regimes have been analysed.* *7. Fencing has been erected to allow modification of fire regime on leasehold land and a conservation agreement signed.* *8. Favourable fire regimes have been implemented over part of the current range of the Morehead population.* *9. Community and land manager participation has been facilitated through extension and interpretation.* *10. A Recovery Team was established, but is currently in abeyance and a Recovery Plan prepared.*
***49.** For species nominated as extinct in the wild, provide details of the locations in which the **species** occurs **in captivity** and the level of human intervention required to sustain the species.*	*N/A*

Mitigation Approach

***50.** Describe any **mitigation measures or approaches** that*	*None undertaken specifically for*

have been developed specifically for the species at identified locations. Identify who is undertaking these activities and how successful the activities have been to date.	Trisyntopa scatophaga, *however those planned for the GSP are likely to be successful at protecting the moth.*

***51.** Departmental use only:*	

Major Studies

***52.** Identify major studies on the species that might relate to its taxonomy or management.*	*The GSP has been the subject of an intensive study (Crowley, Garnett and Shephard 2004), as has* Trisyntopa neossophila *(Cooney 2009), which is believed to be an ecological analogue for* Trisyntopa scatophaga.

Management Documentation

***53.** Identify **key management documentation** available for the species, e.g. recovery plans, conservation plans, threat abatement plans.*	*Crowley G., Garnett S. and Shephard S. (2004). 'Management Guidelines for Golden-shouldered Parrot Conservation.' (Queensland Parks and Wildlife Service: Brisbane.)*
***54.** Departmental use only:*	

SECTION 3 – REFERENCES AND REVIEWERS

Notes:

- **The opinion of appropriate scientific experts may be cited (with their approval) in support of a nomination. If this is done the names of the experts, their qualifications and full contact details must also be provided in the reference list below.**
- **Please provide copies of key documentation/references used in the nomination**

55. ***Reference list***
Common I. F. B. (2000). Oecophorine genera of Australia III. The *Barea* group and unplaced genera. In 'Monographs on Australian Lepidoptera'. (CSIRO: Collingwood.) Cooney S. J. N. (2009). 'Ecological associations of the hooded parrot *Psephotus dissimilis*'. Unpublished PhD Dissertation, ANU: Canberra. Cooney S. J. N., Olsen P. D. and Garnett S. D. (In Press). Ecology of the coprophagous moth *Trisyntopa neossophila* (Edwards) (Lepidoptera: Oecophoridae). Australian Journal of Entomology. Crowley G., Garnett S. and Shephard S. (2004). 'Management Guidelines for Golden-shouldered Parrot Conservation.' (Queensland Parks and Wildlife Service: Brisbane.) Garnett S. and Crowley G. (2000). 'The Action Plan for Australian Birds.' (Environment Australia.)
57. ***Has this document been reviewed and/or have relevant experts been consulted? If so, indicate by whom (including current professional position).***
Yes, by authors.