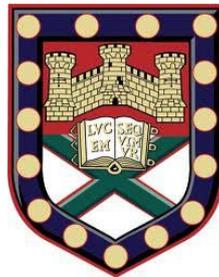# Why can't all males be attractive?

Inter-individual variation in male spotted bowerbird display.

Submitted by Jessica Rose Isden to the University of Exeter as a thesis for the degree of Doctor of Philosophy in Psychology in April 2014.

ABSTRACT

One of the greatest conundrums facing evolutionary biologists is how variation between individuals is maintained in situations where there is expected to be strong directional selection on an elaborate male trait. Sexual selection via female choice leads to the evolution of elaborate male traits, and consensus among females in their mate choice decisions can result in high reproductive skew. Such strong directional selection pressure may be expected to reduce genetic variation over time, yet high levels of inter-individual variation sustain such preferences. In this thesis I explored potential mechanisms that may maintain variation between individuals in one of the most unusual and exaggerated avian male traits; the bowers displayed by male spotted bowerbirds, *Ptilonorhynchus maculatus*. Choosy females exert strong selection pressure on males, yet males vary widely in their ability to exhibit a high quality display.

My results showed that male bower owners were remarkably consistent in their display of decorations, a trait expected to experience a high level of fluctuation due to variation in the ecological and social environment. Given the range of factors that may introduce inconsistency, my results suggest that males actively maintain consistent displays, although I found no evidence for the adaptive benefits of doing so. I then explored three mechanisms that may be expected to maintain variation in bowerbird display. I found that attending the bower imposed physical costs on males, but these costs were only apparent in seasons of environmental stress. Males varied in their cognitive and problem-solving abilities, but I found no impact of higher cognitive performance on a male's reproductive fitness. The final mechanism I tested was the impact of the social environment on male mating success. I found that males actively engage in marauding, a form of intrasexual competition targeting the bowers of rival males. Marauding was highly targeted and non-random within the population, and predominantly occurred between neighbouring bower owners. However, I was unable to determine what factors predicted these non-random interactions, and found no impact of the marauding rates experienced on male mating success.

In the final part of this study, I looked at the novel occurrence of collaborative display between male bower owners and other non-bower-owning males. I found that these auxiliary males may gain delayed benefits from attending the bowers of experienced males, but was unable to determine what impact contributions from auxiliaries had on bower owning males and females attempting to assess them. I conclude by discussing the implications of my results for models of sexual selection.

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DECLARATION

This thesis contains five data chapters, each of which has been written as a manuscript for publication, and is therefore intended to stand alone; some information may be redundant or repeated. The substantial contribution to the manuscripts was made by the candidate. While the candidate is fully responsible for the work presented in this thesis, where the first person is used in the manuscripts it is used in the plural ('we') to reflect contributions from co-authors and/or field assistants. Contributions by co-authors are detailed for each manuscript below. My supervisor, Dr. Joah Madden was involved in designing the project, guided data collection and provided comments on drafts of all chapters.

Dr Joah Madden (1998-2000), Dr Rebecca Coe (2002-2003) and Dr Laura Kelley (2007-2008) kindly shared data which has been used as part of this thesis, including GPS coordinates of bower location, banding and bower ownership data and bower mapping data. Some measurements and monitoring techniques were adopted from those used in previous research to allow for direct comparisons across seasons.

Chapter 3: **The consistency of male spotted bowerbird display**

Isden J., Dingle C., Panayi C., Kelley L., Coe R. and Madden J.

The candidate contributed to field data collection between 2009-2011, analysed the data and wrote the manuscript. Dingle and Panayi also contributed to field data collection between 2009-2011 and commented on previous drafts of the manuscript. Kelley and Coe kindly shared data collected during previous projects between 2002-2003 and 2007-2008 respectively which was used in this analysis. Madden provided supervisory support throughout, and contributed data previously collected between 1998-2000.

Chapter 4: **The physical costs of male attendance at their bowers**

Isden J., Dingle C., Panayi C., Madden J.

The candidate substantially contributed to field data collection, carried out data analysis and wrote the manuscript. Dingle and Panayi also contributed to field data collection. Madden provided supervisory support throughout.

Chapter 5: **Performance in cognitive and problem-solving tasks**

Isden J., Panayi C., Dingle C. and Madden J. (2013)

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The candidate designed the fieldwork with guidance from Madden, substantially contributed to field data collection, analysed data and wrote the manuscript. Panayi and Dingle also contributed to data collection. All authors and two anonymous referees provided feedback on drafts. The manuscript was submitted to *Animal Behaviour* in March 2012 was accepted with revisions in April 2012, and finally accepted for publication in July 2012.

Chapter 6: **Competitive** s**ocial interactions**

Isden J., Griffiths, A., Madden J.

The candidate substantially contributed to field data collection, analysed the data and wrote the manuscript. Griffiths carried out all lab-based genetic testing and generated relatedness scores between individuals. Madden provided supervisory support throughout and contributed data previously collected (1998-2000). Dr. Rebecca Coe and Dr. Laura Kelley also contributed ownership and bower measurement records collected between 2002-2003 and 2007-2008 respectively.

Chapter 7: **The role of auxiliary males in collaborative display**

Isden J., Griffiths A., Panayi C., Dingle C., Madden J.

The candidate substantially contributed to field data collection, analysed field data and wrote the manuscript. Griffiths carried out all lab-based genetic testing and generated relatedness scores between individuals. Panayi and Dingle contributed to field data collection. Madden provided supervisory support throughout and contributed data previously collected, including blood samples from birds captured between 1998-2000. Dr. Rebecca Coe and Dr. Laura Kelley also contributed blood samples and owner and auxiliary records for data collected between 2002-2003 and 2007-2008 respectively.

Chapter One

General Introduction:

Why can't all males be attractive?

1.1. INTRODUCTION

Sexual selection, via female choice, can lead to the evolution and elaboration of extravagant male traits. Females pay close attention to male traits and preferentially mate with males exhibiting the most extreme examples, resulting in highly skewed mating success among males. This strong directional selection offers an explanation for how and why such elaborative traits evolve. However, strong directional selection is also expected to rapidly degrade variation in heritable trait quality between males. Chosen males with the most extreme elaborations contribute disproportionately to the next generation and mean trait value therefore increases, but, in the absence of confounding factors, the variance between males decreases. The logical conclusion to this process is that the lack of variation between males reduces the need for costly female choice and so selection lessens, with a consequent decrease in directional selection on trait extravagance. However, observations of natural populations contradict this conclusion: in systems where males exhibit extreme traits we still commonly observe strong skew in mating success with active choice by females. We also observe high variation in trait quality between males. This conundrum is known as the 'paradox of the lek' (**Section 1.2**), and indicates that heritable variation is either not being exhausted or that variance between males is being imposed or maintained by non-genetic factors (**Section 1.3**). Such environmental determinants of variation may be adaptive in resource-based mating systems where males provide choosy females with material benefits, but in non-resource based systems, where females only acquire genetic material from males, maintenance of variation demands a more detailed explanation (**Section 1.4**).

In this thesis I explore the unusual and extreme sexual displays exhibited by the spotted bowerbird, *Ptilonorhynchus maculatus.* Male bowerbirds build, decorate and maintain bowers, which act as a target of female choice. They operate non-resource based mating systems with choosy females creating high reproductive skew among males. Despite this choosiness, bowers vary markedly between males in terms of their size, composition and quality (**Section 1.5**). This may be because, as an extended phenotypic display, bower construction and decoration is shaped by external, ecological factors beyond the genetic control of their owners (**Section 1.6**). I investigate some of the potential mechanisms that might maintain variation between males, thus facilitating effective female choice. First, I ask whether males show consistency in the sexual signals they produce over short and long time

periods, and explore factors that may affect such (in)consistency (**Section 1.7**). I then ask whether variation between bowers reflects (i) differences between males in their ability to bear the physical costs of bower ownership (**Section 1.8**), (ii) differences in their cognitive abilities (**Section 1.9**), and/or (iii) differences in the level of competitive social interactions they experience as bower owners (**Section 1.10**). Finally, I report on a novel occurrence of collaborative display between bower owners and other non-bower-owning males, and ask whether variation may be a result of multi-male contributions to this elaborate sexual trait (**Section 1.11**). I conclude by summarising how this extreme example of a sexual trait, presumed to have evolved under strong directional selection, continues to act as a target of female choice (**Section 1.12**).

1.2. THE PARADOX OF THE LEK

Sexual selection can lead to the elaboration of male traits, with one sex (usually the female) exerting choice over members of the opposite sex (Darwin 1871). Competition between individuals for access to reproductive opportunities drives the evolution of traits that enhance an individual's ability to gain fitness benefits (Andersson 1994, Ryan 1997). As sexual competition is a zero-sum game, where males only succeed at another's expense, not every male can enjoy greater success by competing more efficiently. Females are often united in their decisions on mate selection, with males exhibiting the most extreme forms of a trait gaining disproportionate levels of mating success (Kirkpatrick and Ryan 1991, Johnstone 1995). Such preferences may arise because ornamentation indicates the additive genetic benefits mating with a particular individual can provide, and in many elaborate trait mating systems, high levels of reproductive skew mean that sexual selection is therefore assumed to be usually a directional, rather than stabilising, selecting force (Lande 1981, Tomkins et al. 2004, Kotiaho et al. 2008).

Strong directional selection pressure, however, gives rise to an evolutionary conundrum: how is genetic variation maintained given the concerted action of selection on particular traits? Traits under directional selection should endure a loss in genetic variance as a single genotype is favoured, leaving, over time, insufficient differences between males

to maintain female preferences (Borgia 1979, Taylor and Williams 1982, Kirkpatrick and Ryan 1991). Despite this expected erosion of additive genetic benefits, in many mating systems females remain highly selective and many elaborate traits show high inter-individual variation in their expression, with levels of genetic variance that can be comparable or higher to those found in traits under natural selection pressure (Pomiankowski and Möller 1995, Petrie and Roberts 2007). This is the challenge of the 'lek paradox' (Borgia 1979, Taylor and Williams 1982). This paradox predominantly applies to non-resource based mating systems where the female derives only indirect, genetic benefits from her choice, and has given rise to a multitude of theoretic models and, more recently, empirical tests (Grose 2011). Two potential solutions counteracting the depletion of genetic variance are prominent in the literature; first, sexual traits that are under selection may be multigenic, including modifier genes that may increase the number of genes contributing to a trait (Pomiankowski and Möller 1995) and/or mutation rates (Petrie and Roberts 2007). Second, traits may be condition-dependent with condition being under the influence of numerous genetic loci, again maintaining high genetic variation (Rowe and Houle 1996). Therefore, through selection, females gain 'good genes' from their mate choice either via direct variation in the genes that underlie the trait or through variation in condition which influences the expression of the trait (reviewed in Kokko et al. 2003, Radwan 2008, Grose 2011).

1.3. INTER-INDIVIDUAL MALE VARIATION

Inter-individual variation is essential for the ongoing process of sexual selection, and is maintained despite the contradiction posed by the lek paradox (Borgia 1979, Rowe and Houle 1996). Many non-genetic factors have been described which may influence male trait expression and thus function to maintain variation between populations (Jennions and Petrie 1997, Qvarnström 2001). How a species varies across its geographic range has received particular attention in the literature; geographically distant populations may differ in natural selection pressures acting on males, and/or the environmental conditions experienced during signalling transmission and reception (Endler 1992, Panhuis et al. 2001 Tomkins et al. 2004). Landscape-level variation in bird-song studies, for example, often focus

on the process of imitation and cultural evolution (e.g. Slabbekoorn and Smith 2002), and on the potential for trait divergence and, ultimately, speciation (reviewed in Baker and Cunningham 1985, Edwards et al. 2005). Female preference for male traits may also vary geographically, as has been demonstrated in guppies, *Poecilla reticulata,* where choice may be influenced by variation in water colour and predation intensity (Endler and Houde 1995). Differences in female preference can also lead to divergence in sexual traits and speciation; for example, female preference for white forehead patches shown in one population of pied flycatcher, *Ficedula hypoleuca*, was not replicated in a distance-separated population, where the same trait was small and male mating success was not influenced by its experimental alteration (nor was it replicated in a closely related species, the collared flycatcher, *F. albicollis*) (Dale et al. 1999).

High reproductive skew and variation in male trait expression within populations, however, suggests that the maintenance of variation between males may not always be accounted for by differences in wide-scale environmental conditions. Many species exhibiting highly exaggerated male traits experience strong female choice, creating skew for males within a population that exhibit the most elaborate examples. Classic examples include the male Jackson's widowbird, *Euplectes jacksoni,* that exhibits remarkable nuptial tail plumage, the extent of which predicts the chance of its exhibitor obtaining a copulation (Andersson 1989), the impressive train of the male peacock, *Pavo cristatus*, also selected for by females and attributes of which correlate with male body and muscle mass (Petrie et al. 1996), and the nest building ability and degree of tail ornamentation in barn swallows, *Hirundo rustica*, which predicts female reproductive investment and offspring viability (Soler et al. 1998 and Möller and de Lope 1994 respectively). Male traits may be indicative of and vary with current health, and directly influence a female and her offspring's resistance to disease (e.g. the bright male hypothesis, Hamilton and Zuk 1982) or signal the parasitic loads of their exhibitor (Borgia and Collis 1989, Thompson et al. 1997). A meta-analysis of the relationship between male traits and age indicated that typically males exhibiting the largest ornaments, weapons or courtship displays showed greater survivorship or longevity, suggesting that a male's ability to exhibit elaborate traits may not be fixed and can vary between and within individuals over time (Jennions et al. 2001).

1.4. CONDITION DEPENDENCE AND NON-RESOURCE BASED MATING SYSTEMS

In systems where males vary in the material benefits they offer, female preference for males offering the greatest advantage appears straightforward (Kokko et al. 2003). In some cases, a male's ability to offer direct benefits is immediately apparent; for example, the nuptial gifts that provide females with metabolic resources (Gwynne et al. 2008) or the ability to hold and defend a territory or nesting site (e.g. Hyman et al. 2004). However, in systems where males do not provide conspicuous direct benefits, but instead offer only genetic material to females, maintenance of variation may be more complex. In some cases, female preference can generate higher genetic mutation rates than would be expected under natural selection alone, thus indirectly reducing the rate at which mutator genes are lost and counteracting the reduction in genetic variance caused by directional sexual selection (Petrie and Roberts 2007). Alternatively, good-genes theories offer potential solutions when elaborate traits are considered to act as advertisements of male quality and condition (Grose 2011). Many elaborate traits impose signalling costs on males, and only males of high enough quality are able to carry that cost and signal at high levels (Nur and Hasson 1984, Johnstone 1995, Cotton et al. 2006). Such condition dependence on elaborate trait expression was an important addition to the original handicap principle proposed by Zahavi (1975), providing a predominant theory for the resolution of the lek paradox and an explanation for male trait variability and female selection (Pomiankowski 1987, Grafen 1990b, a, Iwasa and Pomiankowski 1994).

Evidence supporting the condition dependence hypothesis comes from a wide range of taxa (Johnstone 1995, Rowe and Houle 1996), but support across different elaborate traits is not unanimous (Cotton et al. 2004). For example, condition dependence in the expression of sexually selected traits has been reported for the throat patches of male house sparrows, *Passer domesticus*, (Griffith 2000), and plumage colouration in both male satin bowerbirds, *Ptilonorhynchus violaceus,* (Doucet and Montgomerie 2003c), and house finches, *Carpodacus mexicanus,* (Hill and Montgomerie 1994). In contrast, condition dependence of sexually selected traits was not found in a population of male collared flycatchers that showed a consistent lack of phenotypic plasticity (Hegyi et al. 2006), nor

was the sexually selected structural plumage colouration of the crown in male blue tits, *Cyanistes caeruleus*, related to the variation observed in their body condition (Peters et al. 2011). Additional explanations for variation in trait expression include the influence of stress (Peters et al. 2011), parasitic load (Hill et al. 2005) or developmental stress (e.g. Lachlan and Nowicki 2012). Mating systems characterised by the lack of direct material benefits gained by females require that the traits selected bring genetic benefits that can be inherited by offspring, or increase fitness outcomes of reproduction. Female choice for correlates of male social position, dominance or status suggests that variation may be maintained through dynamic social factors (Kokko and Johnstone 1999). Thus, the maintenance of variation between individuals, and the mechanisms through which such variation is maintained, may depend on a wide range of environmental, physical and/or social factors, or changing female preference over time.

1.5. BOWERBIRDS AND THEIR BOWERS

The sexual display traits of male bowerbirds, Ptilonorhynchidae, offer one of the most elaborate and unique systems for considering questions regarding the evolution and the maintenance of inter-individual variation. Male bowerbirds build highly exaggerated structures, bowers, which are intricately constructed and decorated with a wide array of coloured objects (Diamond 1982, Borgia 1985b, Borgia et al. 1987, Diamond 1987, Borgia 1995a, Frith et al. 1996, Madden 2002, 2003a, Madden and Tanner 2003, Endler et al. 2005, Endler et al. 2010). Their sexual displays are unique in the avian world, and their evolutionary pathway has long fascinated ornithologists, zoologists and behavioural biologists. Following Marshall's (1954) discovery that bowers acted exclusively to attract females and as the site of male sexual display, intense attention has been focused on understanding the mechanisms that drive selection for such an elaborate trait (Borgia 1985b, 1986a, 1995b, Humphries and Ruxton 1999, Uy and Borgia 2000, Madden 2003a, Madden and Tanner 2003, Patricelli et al. 2003, Coleman et al. 2004, Morrell and Kokko 2004, Coleman 2005, Keagy et al. 2009, Doerr 2010b, Kelley and Endler 2012). Bowerbirds, with the exception of the three catbird species, operate non-resourced based mating systems, with choosy females basing mate choice decisions on multiple aspects of male

display, including the size, symmetry and quality of the bower structure (Borgia 1985b, Doucet and Montgomerie 2003a, b, Robson et al. 2005, Endler et al. 2010), the numbers, types and positions of decorations (Borgia and Mueller 1992, Borgia 1995a, Uy and Borgia 2000, Madden 2003a, Coleman et al. 2004), vocal mimetic ability (Loffredo and Borgia 1986), plumage characteristics (Borgia and Collis 1989, Doucet and Montgomerie 2003c, Savard et al. 2011) and elements of their courtship displays (Frith and Frith 1993, Patricelli et al. 2002, Madden 2003b). Males provide no material benefits beyond copulation, and thus aim to maximise the number of copulations they can gain during each breeding season (Uy et al. 2000, Frith and Frith 2004). However, inter-individual variation in display quality, combined with highly choosy females, creates high levels of reproductive skew, and suggests that there are strong selection pressures acting on males (Borgia 1985b, Reynolds et al. 2007). Despite this selection pressure and variation in male traits being maintained, determining how selection acts on these highly complex, exaggerated male traits remains difficult to determine.

In the seventeen species of bowerbird that produce bowers, these bowers differ greatly in their type, size, composition and quality. Three different bower structural types have been identified; the court, avenue and maypole bowers (Frith and Frith 2004). Court bowers are relatively simple, lacking any structural element and consisting of a cleared area sparsely decorated with natural materials (Frith and Frith 1995). The avenue bowers consist of a structure forming two parallel walls, with a central aisle between, and an extended platform area which is decorated with an array of objects (Borgia 1995b, Frith and Frith 2004). The complex maypole bowers, such as those built by the MacGregor's, *Amblyornis macgregoriae*, and Vogelkop, *Amblyornis inornata*, bowerbirds are described as architecturally complex with sophisticated decoration arrangements (Diamond 1982, Diamond 1986a, Frith and Frith 2004). Coupled with the variation in bower display types, there are also species differences in the courtship displays performed by males. For example, vocal mimicry differs in function across species; mimicry forms an integral part of bowerbird courtship display in satin, *P. violaceus*, (Loffredo and Borgia 1986, Keagy et al. 2011) and toothbilled, *Scenopoeetes dentirostris*, (Frith and Frith 1993). In contrast however, male spotted bowerbirds, *P. maculatus,* do not use vocal mimicry in display, but instead produce mimicry in an alarming context (Kelley and Healy 2012).

Intra-species variation in male bowerbird display offers opportunities to investigate the influence of external factors that may cause and maintain variation between populations. Several studies strongly suggest that males in populations isolated from each other differ in multiple aspects of their display. Population-level variation may be explained by genetic variation, differences in environmental or ecological factors, by the influences of varying social pressures, by arbitrary changes through the cultural transmission of behaviour (Diamond 1986b, Uy and Borgia 2000, Westcott and Kroon 2002, Madden et al. 2004b, Madden 2006, 2008). For example, the use of, and male preference for, different decoration types varied between two populations of Vogelkop bowerbirds. These differences, which could not be attributed to any measured difference in environmental, ecological or predation risk factors, were demonstrated both observationally and experimentally (Diamond 1987, 1988, Uy and Borgia 2000). Similarly, males in two geographically isolated populations of spotted bowerbirds differed in numerous aspects of their display characteristics; the construction and orientation of their bower avenues, the decorations displayed, the vigour of male courtship displays and the levels of intra-sexual competition all showed markedly different expression between the two populations (Madden 2006).

Inter-individual variation between males within a population has led to numerous hypotheses that explain why strong directional selection pressure may not have led to the degeneration of additive genetic benefits (Jennions and Petrie 1997). Males within relatively short geographical distances can vary widely in their ability to produce high quality bowers (Madden 2006). Although relatively few species have been subject to consistent long-term investigation, a wide range of mechanisms that maintain variation in various aspects of male display have been suggested. Inter-individual variation in measured display traits may relate to male parasitic load, which functions to signal differences in male health (Borgia and Collis 1989, Doucet and Montgomerie 2003c). The decorations exhibited on bowers have been subject to intense scrutiny, often focusing on patterns of decoration use. Mechanisms proposed to determine variation in decoration use include the physical costs of decoration acquisition, especially for favoured objects that are rare in the natural environment (e.g. the use of blue feathers in satins (Borgia et al. 1987) and bird-of-paradise feathers in Archbold's bowerbirds, *Archiboldia papuensis* (Frith and Frith 2004)), or decorations that may impose

significant transportation costs (Doerr 2009a). Male spotted bowerbirds that cluster their bowers in close proximity tended to use more similar suits of decorations than males further away, despite low variation in environmental factors between them, suggesting localised cultural transmission mechanisms may maintain differences (Madden et al. 2004c, Madden 2008). Similar mechanisms have been proposed to explain the differences in structural properties of bowers. Differences in bower traits can predict female choice, but may be susceptible to change over time. For example, the use of *Solanum* fruits on bowers predicted male mating success in two consecutive breeding seasons (Madden 2003a), but data collected when revisiting the same population a decade later indicated a shift in predictive power towards the use of silver foil (Dingle et al. *in prep*). In this thesis, I explore four main mechanisms that might be expected to maintain variation between displaying male spotted bowerbirds; these are discussed in more detail in **Sections 1.7 – 1.11**.

1.6. EXTENDED PHENOTYPIC TRAITS

The bowers built by male bowerbirds are described as extended phenotypic traits, separated from the body of the male yet acting to influence male fitness (Schaedelin and Taborsky 2009). Although separated physically from the male, extended traits can potentially be costly to males and can act as important advertisements of male quality in a sexual context (Grose 2011). To act as honest signals, extended phenotypic traits should provide reliable information, which can be achieved through the common interests of the signaller and receive or through differential signalling costs (Pomiankowski 1987). Extended phenotypic traits that function in sexual signalling are generally dominated by (but not limited to) the elaborate display courts built by male bowerbirds (Borgia et al. 1985, Frith and Frith 1993, Lenz 1994, Frith et al. 1996, Frith and Frith 2004), the mating craters constructed by male cichlids, Cichlidae (e.g. McKaye 1991, Schaedelin and Taborsky 2006) and the nest-weaving abilities of male weaverbirds, *Ploceus spp.* (e.g. Collias and Collias 1984, Walsh et al. 2010). Extended phenotypic traits may be susceptible to increased levels of environmental and stochastic fluctuation compared to sexually selected traits which are intrinsically connected to the male, such as plumage or song. For example, in the season immediately following the damaging impact of Cyclone Larry, male toothbilled bowerbirds

commenced bower-building later in the season and used fewer decorations on their bowers compared with previous seasons, suggesting the influence of random events can be high (Freeman and Vinson 2008).

Extended phenotypic traits may provide signalling characteristics that are not possible to achieve with traits that are intrinsic to the male body or behavioural displays that occur at an instant point in time (Schaedelin and Taborsky 2009). For example, unlike behavioural displays that convey information on the immediate condition of a male, extended phenotypic traits can indicate long-term male physical quality if their persistence relies on ongoing energetic maintenance. The mating craters of Lake Tanganika cichlids, *Cyathophrynx furcifer*, are rapidly degraded by water currents, and the perishable decorations used on some male bowerbird displays both require regular male attention and physical input (Schaedelin and Taborsky 2006, Frith and Frith 2004). External traits that are physically separated from the male may also allow female evaluation to take place when the male is absent from his display; the chemical signals of male territory (e.g. Rich and Hurst 1998), as well as the decorated display courts of male bowerbirds, provide good examples of this process.

Extended traits may also increase inter-individual variation because they can indicate a high capacity for flexible behaviour. For example, male bowerbirds have incorporated novel experimental objects onto bowers (Diamond 1988), and populations in urban areas frequently adopt novel human objects onto their courts (for example, the blue plastic clothes pegs and cigarette packaging found on satin bowerbird bowers (Gould 2007). Choosy females may show preference for males that demonstrate such flexibility; male three-spined sticklebacks, *Gasterosteus aculeatus*, that incorporated novel colourful foil sticks and spangles into their nests were more attractive to females (Ostlund-Nilsson and Holmlund 2003). Extended traits that require a suit of different behaviours, or involve complex behavioural procedures could facilitate cognitive assessment of males by females (Madden 2001a, Schaedelin and Taborsky 2009, Madden et al. 2011). Additionally, extended traits also offer a novel system in which intra-sexual competition can operate to mediate the expression of a male's sexual signal. As traits that may not be constantly protected by their signaller, extended phenotypic traits may be especially vulnerable to disruption by rival

males (Pruett-Jones and Heifetz 2012). Intra-sexual interactions may help ensure the honesty of the signal to choosy females (Madden 2002).

1.7. CONSISTENCY IN MALE DISPLAY

Variation between males within a population has provided a framework for studies on sexual selection and the elaboration of male traits, with males exhibiting the most extreme forms of a trait often gaining higher mating success (Andersson 1994). However, less attention has been afforded to intra-individual variation and the ability of males to maintain or alter their sexual signal over different timescales (Griffith and Sheldon 2001). The repeatability of sexual signals exhibited by males may set the upper limit for trait heritability and determine the degree of condition dependence acting on those traits (Boake 1989, Griffith and Sheldon 2001). Sexual selection theory often assumes that traits which are the targets of female choice are consistently exhibited by males (Cornwallis and Uller 2010), and studies that measure the inter-individual variation in the expression of such traits often report levels of reproductive skew that are presumed to be stable over time (see Andersson 1994 for examples). Without knowledge of the long term repeatability of such traits, reports of skew in a population may inaccurately represent the directional selection of exaggerated traits, as predicted by the lek paradox, and incorrectly predict the strength of selection on traits within a population (Griffith and Sheldon 2001, Cockburn et al. 2008). The extent of inter-individual variation may influence the evolutionary pathway leading to trait exaggeration and have implications for female mate choice strategies (Boake 1989, Jennions and Petrie 1997).

In non-resource based mating systems, consistency over time in male trait expression may be expected to be high, reflecting the fixed genetic contribution males provide to females. However, for males that display via an extended phenotypic trait, we might expect that increased opportunities for trait disruption lead to lower levels of consistency in trait expression (e.g. Freeman and Vinson 2008). For male bowerbirds, sources of intra-individual variation in display come from a wide variety of potential causes, and the nature of such variation may have important consequences for females. For

example, aspects of male display that vary randomly due to stochastic events, or according to fluctuating environmental conditions may increase sampling costs for females or the risk of mate choice errors (Coleman et al. 2004, Bussiere et al. 2008). Male bowerbirds often display high numbers of perishable objects, such as fruit, flowers and leaves (Frith and Frith 2004), the production of which may fluctuate with rainfall and temperature, or vary in abundance on a local scale (e.g. Hunter and Dwyer 1997). Conversely, males also display high numbers of non-perishable objects that persist over time and are reused between seasons (Doerr 2009a, 2012), thus creating increased opportunity for the maintenance of trait consistency. Female satin bowerbirds make multiple visits to the same bowers across the breeding season, sampling the same male display over repeated events and time scales (Uy et al. 2000). It is unclear whether females may use such multiple visits to sample different components of male display, or to assess how consistent a male's display remains over time.

Alternatively, inconsistency in the expression of male traits may enhance female choice, through signalling aspects of male age or experience (e.g. de Kort et al. 2009). For example, the construction of bowers appears to develop over time, with young, inexperienced males selecting unsuitable construction materials or decorations (Pruett-Jones and Pruett-Jones 1983, Vellenga 1986). Younger males also build lower quality bowers (Frith and Frith 2000) and are less efficient at clearing display courts (Frith and Frith 1994), thus a high quality bower may indicate male age and/or experience. Whilst some of this variation could be explained through hormonal changes during development (see Collis and Borgia 1993), creating a high quality bower may also involve learning certain components of construction. For example, males may learn socially, through visiting the bowers of other males or practicing courtship display alongside other inexperienced males (Patricelli et al. 2002, Maxwell et al. 2004). Decorations used on bowers, particularly non-perishable objects such as stones, bones and plastic, are heritable across seasons and between male bower owners, and in great bowerbirds increase in number during the tenure of a male owner (Doerr 2012). Females may therefore use components of bower displays such as total numbers of decorations, to determine male age, experience or tenure. However, in order to fully determine the strength of selection, and the heritability, of traits that vary over the

lifetime of an individual, variation in their expression needs to be quantified and accounted for (Griffith and Sheldon 2001).

In **Chapter Three** I ask how consistent male spotted bowerbirds are in their use of display decorations. Decorations are an important element of spotted bowerbird display, and numbers of particular decorations have been shown to predict male mating success (Madden 2003a). Consistency in display may honestly reflect the fixed genetic benefits females gain from males, or indicate individual male preferences for bower aesthetics, whereas inconsistent displays may reveal male age, flexibility in behaviour or an individual's ability to acquire decorations in a fluctuating environment. Alternatively, inconsistency in display may signal male age or experience as bowers improve over time, or suggest that a male is not in good enough condition to cope with extenuating pressures affecting his display. Male spotted bowerbirds in this study population use a diverse range of decorations (up to 109 different types), experience long breeding seasons with fluctuating environmental conditions and males enjoy repeated ownership of their bowers between seasons (up to 10 years) (Frith and Frith 2004). Yet the consequences of male (in)consistency in decoration use over different time-scales has received little attention in the literature. I ask whether there are meaningful population-level fluctuations in decoration numbers, calculate individual male consistency scores for their decoration use within and between seasons and relate these scores to a male's mating success, in order to test whether consistency itself is a signal selected for by females.

1.8. PHYSICAL COSTS

Traits that act as handicaps can provide females with honest information regarding male genetic quality, with males in good genetic condition assumed to produce higher quality sexual traits (Zahavi 1975, Pomiankowski 1987). Sexual signals will act as handicaps when differential costs are paid by high and low quality males, and importantly, these costs should be condition dependent (Grafen 1990b, a, Grose 2011). Sexually selected traits that rely on condition dependent expression may maintain high genetic variation because of the high number of genetic loci involved (Tomkins et al. 2004). As well as genetic quality, male

condition can vary temporally with varying environmental conditions, therefore overall measures of male quality can have both genetic and environmental components (Iwasa and Pomiankowski 1999, Cotton 2004, Tomkins et al. 2004). Males of higher genetic quality may be able to better cope with fluctuating environmental conditions, thus paying less per unit cost than lower quality males. There is strong evidence in some species for the differential costs of condition-dependent expression of male genetic quality. For example, when the tail feathers of male barn swallows, *Hirundo rustica*, were artificially elongated, males with naturally longer tails pre-manipulation had higher survival rates than naturally shorter tailed males, whilst artificially shortening tail lengths only benefited males with already naturally short tails (Möller and de Lope 1994). These results suggest that tail length is more costly to males exhibiting the lower quality trait. In the stalk-eyed fly, *Cyrtodiopsis dalmanni*, whilst several individual body traits showed genetic variation in response to environmental stress, only the male sexually selected trait (eye span) revealed condition dependent genetic variation after differences in body size were corrected for (David et al. 2000). Thus, it was suggested that only male eye span showed a genetic basis to environmental condition dependence, in line with predictions made by the handicap model.

Whilst most species will rely on favourable environmental conditions for the acquisition of metabolic resources, some will also need to acquire materials necessary for display. For extended phenotypic traits males often collect specific materials needed to construct elements of their sexually selected traits. The ability to collect materials could be indicative of aspects of male quality and subsequently affect female mate choice decisions and male fitness. For example, black wheatears, *Oenanthe leucura*, collect high numbers of stones and place them in nesting cavities, which imposes considerable transport costs (Moreno et al. 1994). These stones function in a post-mating sexual selection process, with females judging male stone carrying ability and adjusting their own reproductive effort accordingly. There has been extensive discussion on the relative costs associated with male bowerbird display, and whether bower quality is indicative of a superior genotype. Several aspects of the display may suggest a high physical cost of display. First, as males contribute only genetic material, the ultimate cost of display would be a loss or reduction of mating opportunity. Borgia (1993) tested the cost of display in satin bowerbirds using predictions from two good gene models (Zahavi's handicap model (1975) and Lande's quantitative

genetic model (1981)). Both models predict high absolute costs of display, however, such high costs were not found; bower owners were not at greater risk of predation, did not suffer a reduction in display vigour over the duration of the bower tenures and did not suffer any major loss of condition or mating opportunity (Borgia 1993, 1996). Similarly, aerobic capacity in male satin bowerbirds did not differ between bower-owning and non-bower-owning males, leading to suggestions that this measure of male vigour was not related to reproductive success (Chappell et al. 2011).

Second, males in many species collect high numbers of decorations from their local environment (e.g. Diamond 1987, Borgia 1995, Frith and Frith 2004, Doerr 2009). Decorations are often a mix of non-perishable objects, such as stones, bone, feathers, plastic and metal, and perishable objects, such as berries, leaves and fruits (Frith and Frith 2004). The costs of decoration acquisition, transport and replenishment may therefore indicate significant physical costs, with the numbers of decorations providing females with an advertisement of relative male quality. In some species, the decorations favoured by males and selected for by females are relatively rare in the environment; for example, the blue feathers used in satin bowerbird displays (Borgia and Gore 1986) and the rare bird-of paradise feathers collected by Archbold's bowerbirds, *Archboldia papuensis* (Frith and Frith 1990a). Exhibiting objects that are rare may enable females to assess male quality due to the acquisition and transport effort required to gather them (Borgia 1985b, Borgia et al. 1987, Diamond 1988, Hunter and Dwyer 1997, Madden and Balmford 2004). However, not all species exhibit rare decorations; spotted bowerbirds do not select decoration types that are rare or extremely costly (Madden and Balmford 2004). Despite this, high numbers of decorations displayed on bowers strongly suggests acquisition costs are involved in their attainment. Male great bowerbirds, *P. nuchalis,* may reduce some of these acquisition costs by re-using decorations across seasons (Doerr 2009), and/or inheriting them from previous bower owners (Doerr 2012).

A third way in which bowers can impose costs on males is simply through the proportion of time that males spend tending the bower (for some species, up to 60% of daylight hours; Donaghey 1981, Frith and Frith 2004). Spending time attending the bower may reduce opportunities for other activities, such as foraging or decoration acquisition,

and may in itself impose energy constraints, such as the costs associated with bower building and maintenance. If there is a cost to displaying a sexual signal, males may reduce the size of the signal when it no longer has a signalling function (e.g. the loss of sexually selected plumage traits in male house sparrows following female selection, Griffith and Sheldon 2001). Outside of the breeding season male bowerbirds abandon their bowers, which rapidly fall into a state of disrepair, suggesting there is a maintenance cost imposed on males. The level of investment male bowerbirds give to maintaining their bowers may be sensitive to fluctuating environmental conditions (Bussiere et al. 2008). The impact of environmental variation on mate choice can be ambiguous (Cockburn et al. 2008); environmental stress may increase selection pressure because fewer males will exceed the threshold for mating, thus each attracting a higher proportion of females. Alternatively, poor environmental conditions may decrease selection pressure because most males are no longer available to females (Cockburn et al. 2008). Thus, environmental effects on male condition could lead to a reduction in selection pressure, rendering choice ineffectual and potentially proving one mechanism for maintaining genetic variation (Kokko and Heubel 2008). In bowerbirds, whilst several studies have focused on the costs of male display in terms of absolute costs and material (mainly decoration) acquisition costs (Borgia 1993, Collis and Borgia 1993, Borgia 1996, Sheldon 1996, Madden and Balmford 2004), less is known about the physical costs of attending the bower itself.

In **Chapter Four** I examine one aspect regarding the physical costs of bower ownership, asking whether males pay physical costs for bower attendance behaviour, such that the bower may signal male physical condition. Whilst previous studies on the cost of display in bowerbirds have focused on decoration acquisition costs, or absolute costs of display, I focus on how a male's ability to remain at the bower is impacted by fluctuating environmental conditions. Males spend significant proportions of the day attending their bowers, which ceases outside of the breeding season, implying there are costs associated with this activity. I ask whether males reduce their attendance rates during times of low rainfall when natural resources are scarce, and explore whether these attendance rates can be increased through artificial provisioning. I then ask whether positioning the bower in an area with naturally high food resources allows males to attend their bowers for longer periods, which would suggest that bower attendance may be metabolically constrained, and

bower attendance represents a cost to males via losses in foraging opportunities. Finally, I test whether inter-male variation in bower attendance is signalled through aspects of the bower itself, thus asking whether females may use bower quality as an indicator of a male's ability to cope with the physical demands of bower ownership.

1.9. COGNITIVE ABILITIES

The role of cognition, defined as the acquisition, memory and use of information via processes such as learning, perception and decision making (Shettleworth 2010), in mate choice and sexual selection remains elusive (reviewed in Boogert et al. 2011b). In natural selection and life history traits, the role of cognitive processes has been widely examined (e.g. Balda and Kamil 2002, Pravosudov and Clayton 2002, Seed et al. 2009, Cole et al. 2012), and data across a wide range of animal taxa now show that, despite being phylogenetically distant, many species show consistent cognitive trends, suggesting convergent evolution of intelligence (Lefebvre and Sol 2008, Seed et al. 2009). Investment in cognitive strategies may be costly, leading to suggestions that increasing investment in both absolute and relative brain size have adaptive and cognitive performance benefits, such as enabling a species to cope with unpredictable environmental conditions (Seed et al. 2009), complex habitats (Shumway 2008), social interactions (Emery et al. 2007), adapting to new environments (Sol et al. 2005) or migratory behaviour (Möller 2010).

In bowerbirds, Madden (2001) showed a relationship between bower-building complexity and increased brain size, concluding with the suggestion that species building more complex bowers may have increased cognitive processing compared to species building less complicated bowers or non-bower-building species. However, the nature of the relationship between brain size, cognition and behaviour has not been without criticism (reviewed in Healy and Rowe 2007), and recent studies highlighting the cognitive abilities of insects (Chittka and Niven 2009) and reptiles (Leal and Powell 2012) may challenge existing beliefs on the complexity of neuronal and behavioural processed necessary for cognitive performances (see Roth and Dicke 2005). One approach that may help resolve such issues is to focus on specific areas of the brain that are known to function in particular tasks. For example, Day et al. (2005) found a strong positive association between bower complexity

and the size of the cerebellum, a region of the brain that functions in procedural learning and motor skills, but not in other brain measures (whole brain, telencephalon and hippocampus). They conclude that as bowers are a target of female choice, sexual selection may be responsible for the enlargement of the cerebellum in bowerbirds.

The basis of the handicap principle (Zahavi 1975) relies on a notion that if an individual shows superiority in one heritable aspect, then this superiority may be applicable to multiple aspects of his quality, which in turn provides benefits to females. If an exaggerated sexual trait relies on a cognitive input by males, it seems plausible that the same theory applies; males that are cognitively superior in one domain may have general cognitive skills enhancing their quality in other aspects (Phelps et al. 2006). This concept of general intelligence ('g') was first described by Spearman (1904) and arose from positive inter-correlations found in human mental processes. In humans this factor can account for 30-50% of the variance in performances across cognitive tasks, and is described as a highly heritable trait with a strong genetic basis, as well as being influenced by social and environmental factors (Jensen 1998, Plomin and Spinath 2002). There is evidence of underlying mechanisms controlling cognitive ability in numerous primate species (Reader et al. 2011), mice, *Mus musculus*, (Matzel et al. 2003), rats, *Rattus norvegicus*, (Anderson 1993), cotton-top tamarins, *Saguinus Oedipus* (Banerjee et al. 2009) and honeybees, *Apis mellifera*, (Chandra et al. 2000). In birds, evidence for a direct link between cognitive ability and mate choice is surprisingly scarce (Boogert et al. 2011b). Cognitive testing has typically focused on a problem-solving approach (e.g. Keagy et al. 2009, Cole et al. 2012, Cole and Quinn 2012, Cauchard et al. 2013). Cole et al. (2012) found that problem-solving performance in great tits, *Parus major*, indicated a positive covariance between problem-solving ability and the efficiency with which individuals exploited environmental resources. Where specific cognitive domains have been tested, evidence for general abilities across tasks has been mixed; Bouchard et al. (2007) found positive correlations in pigeons on performances in innovation and social learning tasks, but male song sparrows, *Melospiza melodia*, did not show consistent positive correlations in a range of cognitive tasks (Boogert et al. 2011a).

The current lack of empirical evidence for the role of cognition in sexual selection may be because selection for cognitive traits in nature is rare, and/or may potentially produce additional costs for females (Ryan et al. 2010). For example, females may have to learn preferences for complex trait discrimination, risking mate choice errors or time penalties (Riebel 2011). Alternatively, there may be difficulty in recognising when females are using cognitive traits to inform mate choice. Females rarely observe cognitive traits directly, but in controlled conditions often show preference for males with enhanced ability (e.g. Boogert et al. 2008, Keagy et al. 2009), even when this ability has not been observed and does not correlate with physical traits previously described as the targets of female choice. For example, in guppies, *Poecilia reticulate,* females showed preference for males that performed better in a learning task (unobserved by females), yet male performance did not correlate with body size and orange colour saturation, traits frequently cited as the targets of female choice (Shohet and Watt 2009). Finally, this role may have been neglected because of practical difficulties in observing and quantifying cognitive ability, and therefore also mate choice based upon it. An exception to this is in mate choice for song learning, which offers opportunities to test whether females are choosing traits that reflect male overall cognitive ability. In zebra finches, *Taeniopygia guttata*, males that sing more complex songs were also faster learners in a novel foraging task, suggesting selection via female choice is acting on a cognitive trait (Boogert et al. 2008). However, European starlings, *Sturnus vulgaris,* provide evidence of a more complex relationship, where variation in early developmental stress affected male song quality, but differentially affected their cognitive ability; males on *ad lib* food performed better on a spatial foraging task but worse in a social learning task (Farrell et al. 2012).

Tests utilising a species' natural behavioural repertoire, such as foraging, territorial or nesting behaviours, can be an effective method for targeting individual performance in cognitive domains; for example, testing the relationship between foraging and spatial memory in free-living rufous hummingbirds, *Selasphorus rufus* (Healy and Hurly 1995, Healy et al. 2009). A study on Zenaida doves, *Zenaida aurita,* utilised pair territoriality to repeatedly test learning ability in cognitive tasks as a measure of behavioural flexibility (Boogert et al. 2010) and Cauchard et al. (2013) developed methods for testing problem-solving in great tits by covering the entrance to nest-boxes with a string-pulling problem.

The first study to show a direct link between male problem-solving ability and mate choice was provided by an experimental test in wild satin bowerbirds (Keagy et al. 2009). The speed and degree to which males solved two problem-solving tasks was positively correlated with mating success, and combined with measures of other cognitively demanding traits (vocal mimicry and bower restoration) predicted mating success (Keagy (Keagy et al. 2009, 2011). However, the conclusions that can be drawn from Keagy et al.'s studies are limited by the lack of inter-correlations between tasks that fail to determine how the different tasks relate to one another, or how discrete selection on cognitive performance in these tasks relates to classically defined selection on bower-building behaviour. Keagy et al. (2009), Cole et al. (2012) and Cauchard et al. (2013) were all able to relate individual variation in performance to natural levels of reproductive success. However, the exact relationship between problem-solving ability and individual cognitive variability has yet to be determined, as problem-solving tasks do not target specific cognitive domains and therefore their outcomes cannot be measured against classically defined psychological predictions (Thornton et al. 2014).

In complex, multicomponent displays females may be basing mate choice decisions on structures that provide information regarding the cognitive quality of a potential mate. In **Chapter Five** I outline the potential benefits that could be gained from choosing cognitively superior males, and then use a battery of tests to gain a measure of male cognitive ability. As well as presenting males with a problem-solving task, I also measure four tasks that are independent of any natural behaviours and have specific, pre-defined cognitive domains, such that they mirror psychologically based tests classically used in measures of intelligence. These tasks were specifically designed to allow unforced cognitive testing on free-living individuals. Combining and contrasting the results of these I ask whether bower properties, and ultimately male mating success, can be predicted from cognitive performance scores, thus addressing the hypothesis that the complex male displays built by male bowerbirds may be limited by, and indicative of, general intelligence.

1.10. SOCIAL STATUS

The evolution of elaborate traits is driven by directional intersexual selection pressure, but can be mediated by intrasexual competitive processes (Andersson 1994, Berglund et al. 1996, Kokko and Johnstone 1999). The relative contribution of each can vary widely between species; in some, male-male competitions can determine mating outcomes without the need for further female discrimination. For example, in natterjack toads, *Bufo calamita*, the pitch of their advertisement call signals body size and fighting ability to other males, but females show no preference for pitch in experimental playbacks and are passive in their choice, suggesting that intrasexual competition is more important in determining male mating success (Arak 1983). In other species, female choice and intrasexual competition can act congruently, with competitive interactions between males enhancing female choice, for example, through gaining high quality territories, nesting sites or resources that enhance reproductive success (e.g. Kokko and Johnstone 1999). Alternatively, intrasexual competition may not always ensure the highest fitness benefits for females, and may require trade-offs between fitness components in order to maximise total outcomes (Kokko et al. 2003, Wong and Candolin 2005). For example, females may avoid interacting with harmful or aggressive males by selecting less dominant individuals, even when dominance determines access to other important resources (Ophir and Galef 2003). Social interactions can also function to maintain honest signalling; in three-spined stickleback, males that court females when in competition with other males adjust their red nuptial colouration so that it more accurately reflects parental ability (Candolin 2000).

Male bowerbirds exhibit one of the most distinctive forms of male-male competition. As both the bower structure and its decorations are targets of female choice (Borgia 1985a, Borgia and Mueller 1992, Lenz 1994, Borgia 1995a, Madden et al. 2004b), they also become the focus of competitive interactions between male bower owners. Males attempt to disrupt the sexual signals of their rivals by engaging in a behaviour known as marauding; the destruction of the bower structure through violent physical actions that rip up building materials (Borgia 1985a, Lenz 1994) and/or the theft of decorations (Borgia 1985a, Borgia and Mueller 1992, Lenz 1994, Madden et al. 2004b, Wojcieszek et al. 2006, Wojcieszek et al. 2007, Doerr 2009b). Decorations that are stolen are often incorporated onto the thief's bower (Borgia and Gore 1986, Borgia and Mueller 1992, Frith and Frith

2004). The effect of decoration theft is unusual in that it results in a two-fold impact on male attractiveness; stealing reduces the quality of the rival bower whilst simultaneously increasing the quality of the thief's (Morrell and Kokko 2004). Unlike many other forms of intrasexual competition, in this extended phenotypic trait competition acts to reduce the quality of the sexual trait without direct injury or impairment to the male himself (Borgia 1985a, Humphries and Ruxton 1999). Bower marauding has been the subject of extensive observational, theoretical and experimental analysis. The majority of these have focused on the theft of decorations, rather than destructions of bower structures, possibly due to the relative ease with which decoration objects can be marked and tracked throughout the population. Bower destruction activities require more intensive bower monitoring and identification of individuals in the population, but may represent a more significant disruption to the male's display.

Observational studies have shown that the theft of decorations, and in cases where observations allow, destruction activities, usually occur between nearest-neighbours, although almost never when owners are present at their bowers (Borgia 1985a, Borgia and Gore 1986, Lenz 1994, Madden 2004, Wojcieszek et al. 2007, Reynolds 2009, Doerr 2009). Patterns of decoration theft appear to vary between and within species, and studies indicate that bower marauding is not random and may target particular males or aspects of display (Wojcieszek et al. 2006). For example, male great bowerbirds appear to steal from bowers with fewest decorations (Doerr 2009b), and male spotted bowerbirds do not target other males with higher numbers of *Solanum* fruits, an important predictor of mating success (Madden 2002). In satin bowerbirds, the theft of decorations in two independently studied populations appeared to be mostly reciprocal in nature, with the most successful stealers stealing from other successful stealers (Borgia and Gore 1986, Wojcieszek et al. 2007). However, whilst Borgia (1993) reported that in one population of satin bowerbirds decoration theft was not correlated with the total number of decorations on a bower, Hunter and Dwyer (1997) report negative correlations between theft and decoration numbers in another. Marauding males may target certain aspects of display that function to maximise the increase in their own traits; Wojcieszek et al. (2006) show that certain decorations are stolen more frequently than expected given the relative availability of all other decorations. These preferred decorations have higher levels of ultraviolet reflectance,

and their theft may have an adaptive benefit to males as they function to increase contrast between decorations at the bower.

Optimum marauding strategies suggest that males should balance the time they spend at their bowers, guarding them from marauders, against time away from the bower to forage or maraud others, thus leaving their own bower open to attack, and that the relative ratio of these two activities differs (Morrell and Kokko 2004, Pruett-Jones and Pruett-Jones 1994). Modelling of such strategies would suggest that (i) males that frequently maraud are more often marauded themselves, and (ii) that males will target those bowers closest to them that represent the shortest distances and time away from their bowers. Modelling strategies of guarding versus marauding have provided important insights into which strategies may be best for species with different physical and social parameters (Morrell and Kokko 2003, Pruett-Jones and Pruett-Jones 1994, Pruett -Jones and Heifetz 2012). For example, investing in marauding may be advantageous for a male that is unlikely to receive copulations compared to his rival, whereas successful males should invest more in bower defence (Pruett-Jones and Heifetz 2012). Borgia and Mueller (1992) found that rates of marauding in spotted bowerbirds were markedly lower than in the congeneric satin bowerbird, and inter-bower distances were significantly greater. However, within-species differences in marauding behaviour can also be substantial between populations. Madden (2006) reports marauding levels in two populations of spotted bowerbirds that appear to contradict previous assumptions; in the population with lowest inter-bower distance marauds were significantly lower than in the population where bowers were more widely spaced.

Why certain males, bowers and/or decoration types are targeted by other males may help explain how variation between males is maintained through intrasexual competition. Experimental manipulations have offered some insight into the specific functions marauding may serve. Male spotted bowerbirds whose bower decorations were manipulated to signal above natural levels of decorations displayed suffered higher destruction rates, and males actively removed 'free' decorations provided to them (Madden 2002). This has been described as an apparent act of self-regulation, suggesting a condition-dependent outcome for decoration display (Madden 2002). In contrast, Doerr (2010a)

supplemented the bowers of great bowerbirds and found that the majority of 'free' decorations were accepted by bower owners, who did not subsequently suffer a higher rate of destruction. In separate experiments of three species of bowerbird where decorations were standardised across males, destruction rates were not affected by this standardisation (spotteds: Madden 2002, satins: Wojcieszek et al. 2007, greats: Doerr 2010a). In many cases males restored decorations to their natural levels over the course of the experimental period. Male satin and great bowerbirds that had displayed higher numbers of decorations prior to manipulation suffered lower losses due to theft during the experimental decorations than males that had naturally displayed fewer (Wojcieszek et al. 2007, Doerr 2010a). The results of these manipulations suggest that bower marauding, particularly decoration theft, can act as a method of social control over male display, perhaps ensuring honesty in male signalling through the punishment of males that display above their status within the population. Social interactions may therefore act to maintain variation in signalling ability between males, offering females with a mechanism, via bower inspection, to assess male quality.

In **Chapter Six** I use measures of bower destructions as an indicator of intrasexual competition between spotted bowerbird males in a wild population. If marauding acts as a form of social control, the number of marauds a male receives during the course of the breeding season may relate to the quality of the bower he exhibits. Marauding the structural component of a rival's bower is likely to have a significant impact on his sexual display. I ask whether males vary in the rates of marauding they experience, and whether these are consistent over time in a relatively stable population. I investigate whether marauding is targeted towards particular males in the population, whether these marauds are reciprocated, and what characteristics of the male and his bower may predict the level of marauding he experiences. Finally, I ask what the consequences are of receiving high levels of intrasexual competition, and whether marauding can act as a mediating factor in male mating success, thus maintaining variation in reproductive success between males.

1.11. COLLABORATIVE DISPLAYS

Multi-male sexual displays create an evolutionary challenge, because in many cases certain individuals in the collaboration forego their own reproductive opportunity in order to attend the displays of others (Brown 1987, Koenig and Dickinson 2004). For females assessing male displays, contributions from more than one male may pose problems. In most cases, females are able to assess the individual contributions by each male towards a collaborative display. The simplest example is when male traits are exhibited bodily on the male himself, and can therefore be judged on a male-to-male basis by females (e.g. male body size, mass or plumage traits, Alonso et al. 2010), or where each male performs a courtship behaviour that can be assessed, either sequentially or simultaneously, by comparisons between males performing together (e.g. Gibson et al. 1991). Alternatively, females may be able to judge relative male quality through their position within the display; centrally located males in black grouse leks, for example, are preferentially chosen by females (Hovi et al. 1994), and females can show high fidelity for particular lek territories that only high quality males can hold (e.g. Balmford et al. 1992). In order for sexual signals to elicit consistent female responses they must convey honest and reliable information regarding male quality, and the benefits a female is expected to gain from choosing a particular mate (Searcy and Nowiki 2005). In non-resourced based mating systems signals must accurately convey genetic quality, and sexually selected traits that are corrupted or unreliable will not be able to retain their signalling function (Höglund and Alatalo 1995). For dynamic traits that signal honesty in the long term, such as the displays maintained by male bowerbirds, females may achieve greater accuracy through multiple visits (Luttbeg 1996). When potentially more than one male contributes to a signal, the balance of costs and benefits may help ensure a positive association between the signal and signaller quality is maintained.

In multi-male displays, one male typically gains the greatest proportion of reproductive success, therefore in systems where males only contribute genetic material and the pay-off for display is a single, non-divisible copulation with a female, it can be difficult to understand why secondary males should aggregate. Likewise, it does not always appear obvious why males should tolerate the presence of potentially disruptive, rival males at the sites of their sexual display. Much of the current understanding of the mechanisms

underlying multi-male display come from the extensive studies on lekking species, particularly manakins (family Pipridae) (Prum 1994), although examples of multi-male display have also been described in grouse (Gibson et al. 1991, Hovi et al. 1994), wild turkeys (Krakauer 2005), snipe (Ekblom et al. 2004) and cichlids (Oliveira and Almada 1998). In most lekking species, females visit the lek for the sole purpose of mating, and show strong preferences despite not gaining material benefits (Höglund and Alatalo 1995). Where males aggregate with other related males, their collaboration or cooperation at the display may be explained through the inclusive fitness benefits they acquire (Hamilton 1964, Kokko and Lindstrom 1996). However, when males aggregate with non-kin, the benefits can be less easily attributable. Displaying in collaboration with other males may decrease individual predation risk, attract higher numbers of females or promote female site fidelity (Gibson et al. 1991, Jennions and Petrie 1997, Boyko et al. 2004). Collaboration may also bring benefits to secondary males that are unlikely to achieve high levels of mating success on their own. Secondary males may be able to increase reproductive success through sneaky copulations obtained at the display sites of other males, or through random female choice at the sites of multiple male displays (Friedl and Klump 2005). Secondary males may also receive delayed direct benefits, by increasing their display skills and experience that can increase reproductive success later in life (Cockburn 1998), or securing breeding territory (Beehler and Foster 1988, Trainer et al. 2002, DuVal 2013).

The bowers displayed by male bowerbirds have traditionally been described as being the product of a single male owner, and which reflect the quality of that male through properties of the bower, such as construction and decoration (Marshall 1954, Borgia 1985b, Madden 2003a, Coleman et al. 2004, Frith and Frith 2004). However, anecdotal reports in several species suggest that the presence of other, secondary male bowerbirds at bowers owned by other males is not uncommon. For example, immature satin and golden bowerbirds have been reported attending the displays of mature males (Borgia and Mueller 1992, Borgia 1993), and Lenz (1994) also reported the presence of particular non-bower-owning males at the bowers of established Regent's bowerbird bowers. Other evidence suggests that bower-building is, at least in part, a learned activity, with young males congregating at practice bowers and often making poor decisions regarding material and decoration choice (Vellenga 1970, Lenz 1994, Maxwell et al. 2004). These factors suggest

that non-bower-owning males, especially if they are younger and less experienced, may have much to gain from attending the bowers of more experienced males. However, the nature of the relationship between bower owners and secondary males remains unclear, despite the potential important fitness consequences such collaborations may bring.

In my final data chapter, **Chapter Seven,** I investigate the novel occurrence of collaboration between displaying bowerbird males. I present data that shows that most bowers in my study population have 'auxiliary' males; non-bower-owning individuals that are repeatedly present and apparently tolerated by bower owners at the site of their sexual display. I ask what mechanisms might maintain such collaboration, and test four potential benefits that auxiliary males may gain by attending the displays of another male. I also investigate the collaboration from the point of view of the bower owner, asking what benefits he may receive from the presence of his auxiliary male, including whether auxiliary presence influences or inhibits bower owner mating success. I discuss the implications of bowers not necessarily being the product of a single male owner for female mate assessment and whether such collaborations may add or maintain variation between breeding males.

1.12. CONCLUSION

In this thesis I aim to investigate the different mechanisms that may contribute to the maintenance of variation in male spotted bowerbird displays. Bowerbirds are often one of the classic examples cited in studies of sexual selection, epitomising how elaborate traits evolved through the selection pressures exerted by female choice. However, bower building males are likely to encounter a range of external factors that may be likely to disrupt or alter their ability to produce high quality displays. As extended phenotypic traits, bowers might be expected to be highly susceptible to environmental and social disruption, and such variation poses a potential problem for models of sexual selection. Conversely, such variation may contribute to the maintenance of genetic diversity, thus providing a resolution to the paradox of the lek. By exploring the four mechanisms I have described, I aim to increase our understanding of the underlying causes of variation in the expression of sexually selected male traits. I aim to quantify how measures of each of these mechanisms

vary between individuals, and show whether such variation relates to the mating success of the individual. In doing so, I hope to be able to demonstrate that such mechanisms are important for models of female mate choice, particularly in systems where females gain no direct benefits from their decisions. I also aim to provide techniques for the continuation of study into inter-individual variation in bowerbirds, and other species exhibiting elaborate male traits, and a framework for further investigation.

Chapter Two

General methods

2.1. THE SPOTTED BOWERBIRD

The spotted bowerbird, *Ptilonorhynchus maculatus* (Figure 2.1), is a medium sized passerine (circa 130g) with cryptic brown and beige spotted plumage and a buff-brown breast with dark streaking (Frith and Frith 2004). Unlike many other bowerbird species, the spotted bowerbird is sexually monomorphic. Both males and females exhibit a pink nuchal crest that is flared by males during display (Frith and Frith 2004) although in females, non-bower-owning males and juveniles this nuchal crest is typically smaller (Madden et al. 2004a). Spotted bowerbirds are distributed across inland eastern Australia, and are common throughout central Queensland and New South Wales. They inhabit dry, open woodland and scrubland habitats, typically brigalow, *Acacia harpophylla,* and eucalypt woodland (Miles and Madden 2002, Simpson and Day 2004). Spotted bowerbirds are generally frugivorous, but supplement their diet with insects and other invertebrates (Frith and Frith 1990b, 2004). They are accomplished vocal mimics with a typical mimetic repertoire size of eight heterospecifics (Kelley and Healy 2011), although mimicry is usually produced in response to bower disturbance or alarming situations and, unlike many other bowerbird species, is not used in the context of sexual display (Kelley and Healy 2012).
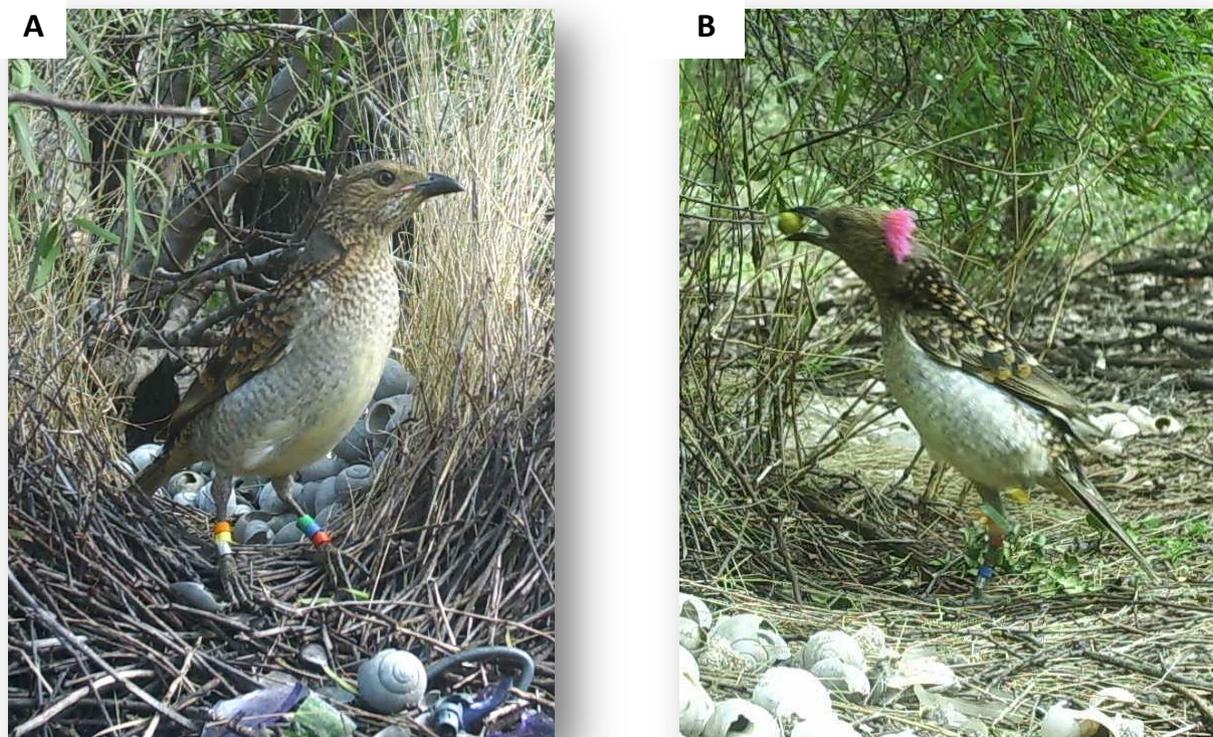
Figure 2.1. a) A banded male spotted bowerbird standing in his bower, and b) a male performing a courtship display with nuchal crest flared and holding a green fruit.

2.2. BOWER DESCRIPTION

Male spotted bowerbirds typically build and maintain their bowers between July and December. They build avenue-type bowers (Frith and Frith 2004, Figure 2.2), usually underneath the canopy of larger bushes and low-hanging trees, showing preference for species which bear edible fruit (Miles and Madden 2002, Frith and Frith 2004). Bowers are widely spaced compared to other species, typically being approximately 1km apart (Borgia and Mueller 1992, Miles and Madden 2002) compared to ~0.1km in satin bowerbirds, *P. violaceus,* (Borgia 1985b), ~0.7km in MacGregor's bowerbirds, *Amblyornis macgregoriae,* (Pruett-Jones and Pruett-Jones 1982) and ~0.4km in great bowerbirds, *P. nuchalis,* (Doerr 2009b). The bower consists of a grass and stick avenue structure with two parallel walls which are fixed in the centre of a wider stick platform (Gillard 1969, Borgia 1995, Frith and Frith 2004). There is no clear consensus on the orientation of spotted bowerbird bowers; whilst Borgia (1995b) reports consistent east-west orientations in one population, in others orientation may be more closely associated with bush canopy architecture (Miles and Madden 2002, Madden 2006). Male satin bowerbirds paint the inside of their avenue walls using masticated plant material to give it a dark red appearance, which may provide chemical signals to females (Diamond 1987, Bravery and Goldizen 2006). Similar red painting has been observed on spotted bowerbird bowers (pers. obs.). Bower structural properties, such as size, neatness and symmetry have been shown to be good predictors of male mating success (Borgia 1985, 1998, Uy and Borgia 2000).

Spotted bowerbird bowers are decorated with discrete, well organised piles of coloured objects, including both natural objects (fruits, leaves, seed pods, stones and shells) and in some cases man-made objects (pieces of glass, plastic and metal) (Borgia and Mueller 1992, Borgia 1995, Madden 2003b; 2006). Males typically place large numbers of white objects at either end of the bower avenue, with shiny objects (glass or metal) at the avenue entrance, and show a preference towards having green objects in the centre of the avenue and red objects on the outer edges of the walls (Borgia 1995, Madden 2003b). They also, less frequently, collect purple, blue, orange, brown, black and metallic objects. Numbers of particular decorations have been shown to predict male mating success, although these predictors may vary across populations and timescales (Borgia 1995, Madden 2003b, Dingle et al. *in prep*).

Figure 2.2. A typical avenue bower of a male spotted bowerbird, showing two walls constructed from sticks and grass upon a wider stick platform. White snail shells and pieces of bone form a distinct pile at the mouth of the avenue. Shiny objects, typically glass or metal pieces are placed at the avenue mouth, with red decorations on the outer edges of the avenue walls, and green decorations placed in the centre of the avenue and across the wider bower platform.

2.3. BOWER OWNERSHIP

Male spotted bowerbirds retain ownership of their bowers across multiple seasons, returning to the same location at the start of each season to commence bower building activities (Frith and Frith 2004). Once a male owner ceases to attend his bower, it is rapidly taken over by another male (Madden, pers. comm.), and this new owner inherits not just the bower location, but also any non-perishable decorations displayed by the previous male (Doerr 2012). Inheriting an established bower site may be advantageous for males over the creation of a new location; established sites may attract higher numbers of visiting females due to site fidelity (Uy et al. 2001), and may benefit from increased access to material

resources (see Madden et al. 2012). During this study, a population of wild spotted bowerbirds were monitored between 2009 and 2011, and data for the same population was also available that drew on previous records dating back to 1998 (see Madden 2001b). Ownership at male spotted bowerbird bowers suggested that an average male tenure of between 3-4 seasons was typical, although one male held tenure for ten years. Ownership changes during data collection for this thesis (between 2009 and 2011) were relatively rare; within seasons, there were no ownership changes in 2009, two in 2010 and three in 2011. Between seasons, there was just one known ownership change between the end of 2009 and the beginning of 2010.

2.4. BOWERS AS EXTENDED PHENOTYPIC TRAITS

Extended phenotypic traits reflect the effect of a gene(s) on the wider environment (Dawkins 1982), and in the context of male sexual display they refer to traits that function in the same way as the sexually selected morphological traits exhibited by many males, but are separated from the body of the male himself (Schaedelin and Taborsky 2009). The bowers constructed by male bowerbirds are considered a classic example of a trait that can impact male fitness whilst remaining external and unattached to the physical body of the male. There are several advantages to studying extended phenotypic traits when considering behavioural and, in particular, sexual signalling evolution. Extended traits can be experimentally manipulated without influencing other, non-sexual aspects of male behaviour or physiology, such as phenotypic alteration or stress (Humphries and Ruxton 1999). Many extended traits function in both natural and sexual selection processes; such as the nest building ability of male barn swallows, *Hirundo rustica,* which relates to female reproductive investment and is also likely to impact chick survival (Soler et al. 1998). Bowers therefore offer an ideal opportunity to manipulate and measure sexual selection processes in isolation from any effects of natural selection (Madden 2002). This is potentially a valuable tool, as strong natural selection processes can preclude the effects of sexual selection and limit our ability to quantify their relative contributions (Schaedelin and Taborsky 2009). Male bowerbird bowers offer an ability to quantify the relative

contributions of selection pressures and to investigate the evolutionary processes supporting them.

2.5. STUDY SITE

Fieldwork was carried out at Taunton National Park (Scientific). Data was collected by the candidate for the specific purpose of this thesis between 2009 and 2011, but research with this same population of spotted bowerbirds first began in 1998 (Madden 2001b). The Park is situated approximately 250km west from Rockhampton, central Queensland (23.54989S and 149.24088E, Figure 2.3a), in an area predominantly used for cattle ranching and coal mining. The National Park was formed from the merger of two cattle properties in 1986, with the aim of protecting a population of bridled-nailtail wallaby, *Onychogalea fraenata,* previously declared extinct and now listed as critically endangered (Department for the Environment n.d.). The Park is currently managed for this purpose by the Queensland Parks and Wildlife Service. An active programme of baiting and capture aims to reduce numbers of introduced feral predators (cats and dogs). As a Scientific Park there is no access to the public and very little human disturbance. Areas surrounding the Park continue to be used for cattle ranching, and as a result are cleared of scrub and trees and are heavily grazed (Figure 2.3b). An introduced grass species used for pasture, buffel grass, *Cenchrus ciliaris*, has spread extensively throughout Taunton, with currently unquantified impacts on native wildlife. Methods used to control this spread include burning regimes, chemical spraying and cattle grazing (Taunton National Park Management Plan 2011).

The Park covers 11,600ha of brigalow and open eucalypt communities, intermixed with combinations of open grassland, ironbark woodland and riverine scrub (Taunton National Park Management Plan 2011). Several artificial dams, legacies from previous use as cattle ranches, continue to provide year round water sources, and the Park has a dense network of seasonal creeks. Bowers were located predominantly in the north and eastern areas of the Park, and despite intensive searching were absent from the south west which is dominated by rosewood and ironbark woodland (Figure 2.3c).
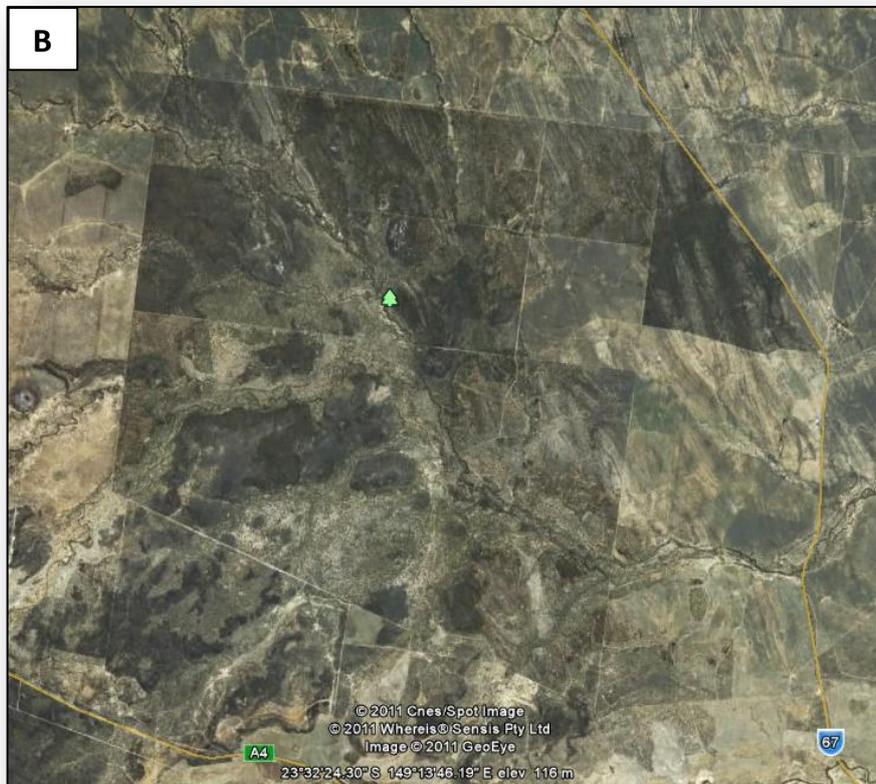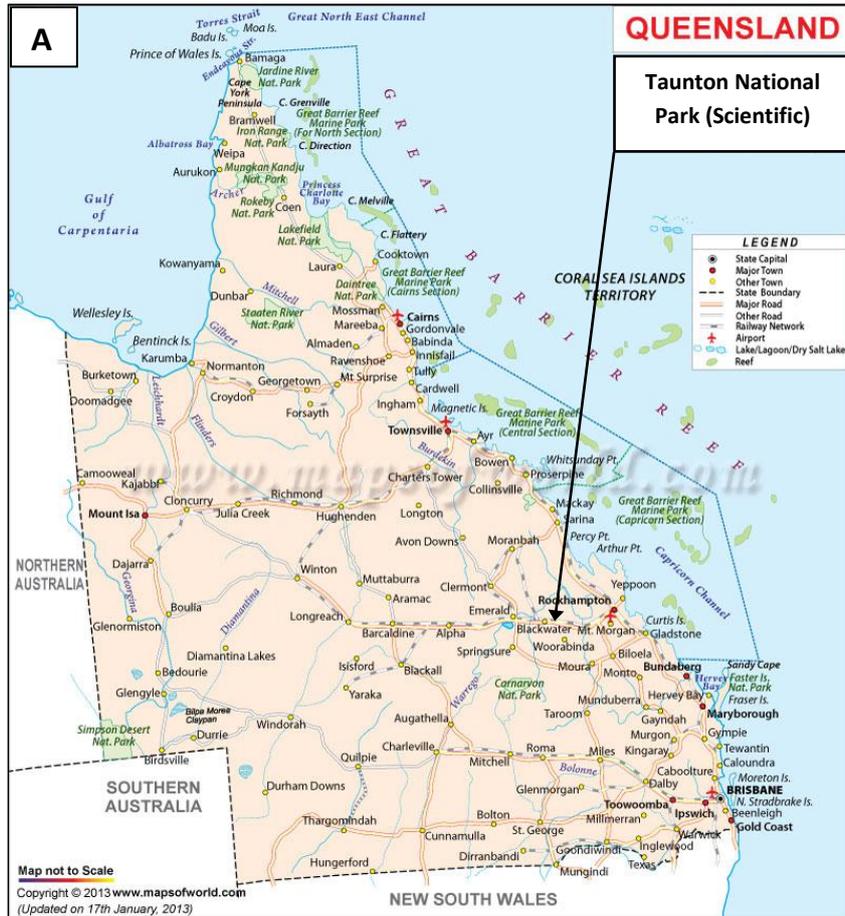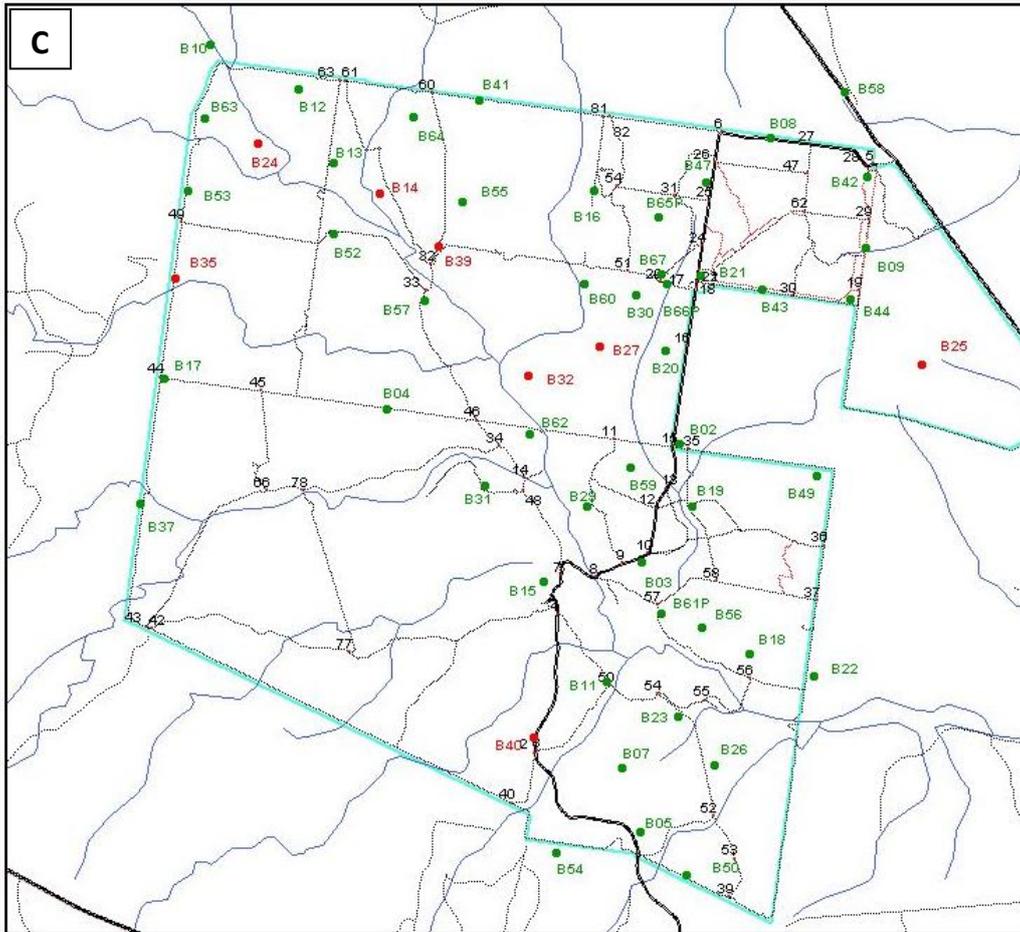
Figure 2.3. Maps of Taunton National Park (Scientific). a) The location of Taunton National Park in Queensland, Australia; b) an outline of the Park seen in a satellite image showing the clearly delineated Park boundary compared to surrounding cleared farmland; c) the location of bowers found during fieldwork; green shows active bowers during the 2009, 2010 and 2011 breeding seasons, red shows bowers previously located but not active/found between 2009-2011 (numbers in black indicate road intersection markers).

2.6. ENVIRONMENTAL CONDITIONS

Taunton National Park sits on the Tropic of Capricorn, and receives highly seasonal rainfall with cool, dry winters (April – July) and hot, wet summers (October – February). Climatic conditions fluctuated widely during the three seasons data were collected (Figure 2.4). In 2009 Queensland experienced a severe drought, with rainfall levels between July

and December being the lowest on record for over 15 years (Bureau of Meteorology 2009). In contrast, 2010 was one of the wettest years on record (Bureau of Meteorology 2010). Rainfall data used in this thesis were obtained from two different sources. Accurate monthly rainfall data were collected at Taunton National Park from 2001, with the only exception being December 2009. Between 1998 and 2012 data was obtained from a weather station at the Dingo Post Office, which is 15km south-east of Taunton, by the Australian Bureau of Meteorology (Bureau of Meteorology 2012). Records from these two sources of data were highly correlated; for the period between 2004-2010 when monthly records were available from both sites we found a strong correlation between the two (R_s = 0.89, N = 59, P < 0.001).
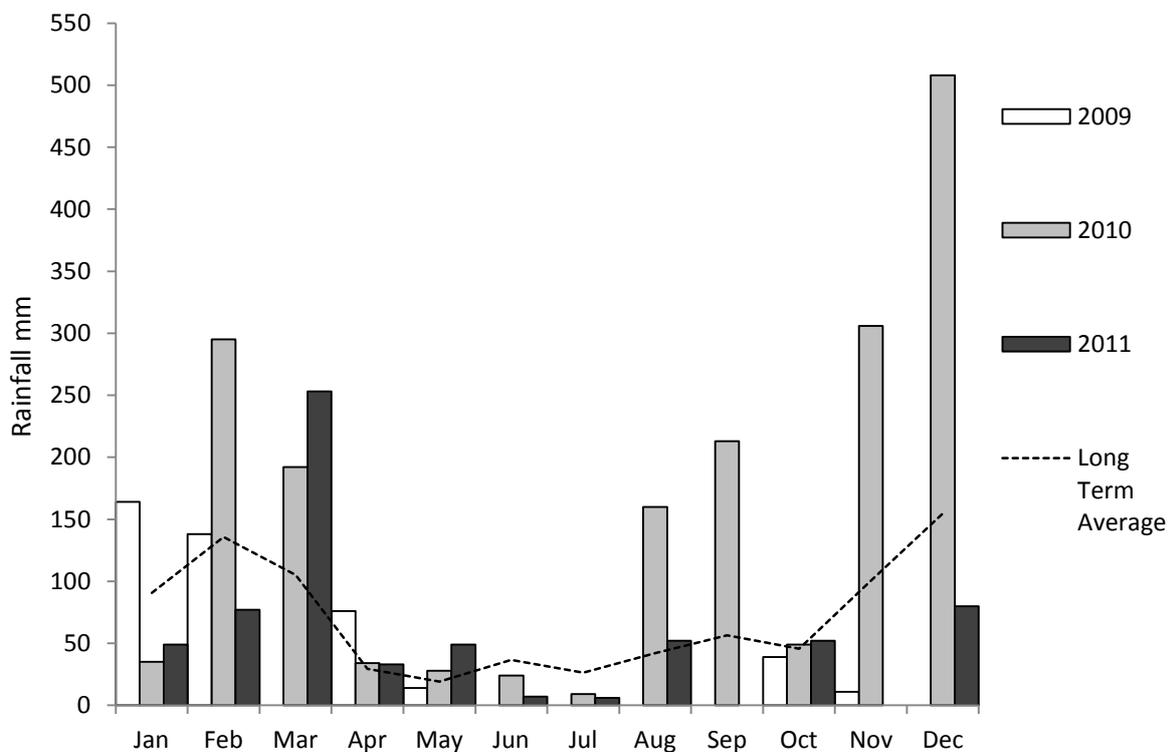
Figure 2.4. Monthly rainfall at Taunton National Park during 2009–2011. The long term monthly average rainfall data was obtained from the Bureau of Meteorology (2012).

2.6.1. Impact of weather conditions on data collection

The impact of the drought conditions during the 2009 breeding season was evident at Taunton National Park and on bowerbird activity. Males initiated bower building in

August, but many abandoned their bowers during November and early December, resulting in a reduction in bower attendance rates (see Chapter 4, Figure 4.1). During 2010 high rainfall at the beginning of the year led to saturated soils and the continued above-average rainfall throughout the season led to widespread flooding across the Park. Flooding created logistical problems for data collection, with areas of the Park becoming inaccessible and equipment at risk of being damaged. During 2011 rainfall levels were more similar to the long term average, however the legacy of the previous year's extensive flooding meant that saturated soils and high ground water levels led to the abundant growth of vegetation.

2.6.2. Impact of bush fires on data collection

Taunton National Park is situated in an area prone to bush fires and during periods of extended dry weather fire hazards were high. Fire is an integral part of the natural and manmade ecology in this region and many native species are adapted to its occurrence (Bradstock et al. 2002). During 2009 no fires directly affected any bowers in the study population. In July 2010, just prior to the start of the breeding season, controlled hazard-reduction burns of small blocks were carried out by the Queensland Parks and Wildlife Service, which covered approximately 25% of the total Park area. These burns damaged the location of five known bower sites, however at all of these sites the males initiated bower-building at the same time as other males in the population. In December 2011 two bowers were destroyed by wildfire and were not rebuilt. A further bower was damaged but recovered by the same owner. Bowers that were affected by fire were excluded from any subsequent analyses.

2.7. GENERAL FIELD METHODS

2.7.1. Bower location

Bowers were located at the beginning of each breeding season between 2009 and 2011. For bowers that had been discovered during previous researcher's data collection, GPS coordinates kindly shared were used to help relocate them. New bowers were found by visiting areas that were approximately 1km from the nearest known bowers (see Section 2.2). Bowers were located by visually searching, and by listening for the distinctive

'advertising' skraa calls given by males at their bowers (Frith and Frith 2004). Bowers typically move <20m between seasons, but can move over 200m. In 2009 the location of 25 active bowers had been recorded, all of which were relocated the next season; 10 bowers moved <10m, with the remaining 15 bowers moving an average 57.6m (min = 0m, max = 242.7m. At the end of 2010, 46 bowers had been located, with 39 being relocated at the beginning of the 2011 breeding season. Of these, 19 moved <10m, with the remainder moving an average of 76.7m (min = 0, max = 196.6m). For bowers located in all three seasons (N = 23) there was no correlation between the distance a bower moved between 2009-2010 and 2010-2011 (R_s = 0.20, P = 0.36).

2.7.2. Capture and banding

All capturing, measuring and banding of bowerbirds was carried out by Dr. Joah Madden and Dr. Caroline Dingle (see 2.9 for details of licences and ethical approvals). Birds were captured using 12mm mist nets surrounding the bower location. Nets were monitored continuously, and birds of other species immediately released. Captured bowerbirds were held in cloth bags and processed immediately. Individuals were banded with size 7 Australian Bird and Bat Banding Scheme (ABBBS) metal bands, and a combination of five coloured plastic wrap-around bands (see Figure 2.1a). Each bird had three bands per leg in a different combination of the same colours to reduce any influence of colour banding on male attractiveness (e.g. Burley 1982). Mortality risks associated with the colour banding in birds have not been found in species that also spend significant periods of time on the ground (e.g. Cresswell et al. 2007), and the longevity of banded owners in our study population (maximum recorded = 10 years) suggests that colour banding also has alow impact in our species.

2.7.3. Bower mapping

For some analyses (Chapters Three, Four, Six and Seven), I used archive data from previous years of study at the site. Between 1998-2000, 2002-2003 and 2007-2008 bowers were mapped at least once during each season, with extra measurements occurring in some seasons. From 2009-2011 bowers were mapped monthly. Mapping was carried out using the same techniques as detailed in Madden (2001b), Coe (2005) and Kelley (2010) to ensure

that data were comparable across seasons. Bower structure was measured using a prescribed set of criteria (Table 2.1.). Bower decorations were counted and their positions on the bower were marked. For shells numbering >100 their numbers were estimated to the nearest ten. For analysing seasonal-scale data, mean values of measures were taken from monthly records to give a single mean measure per bower per season.

Measure	Method
Orientation	A bearing through the centre of the avenue was taken using a Silva compass which was placed parallel to the sides of the avenue wall. When avenues were incomplete or missing the orientation was measured using the direction joining the centre of the two main decoration piles.
Bower platform	The distance between the outer limits of bower decorations and area maintained was measured through the centre of the avenue and perpendicular to the avenue walls.
Bower length	The internal length of each wall was measured at a height of 10cm from the avenue floor.
Avenue width	5 equidistant points along the avenue were selected and the width between the two walls was measured using a metal ruler.
Avenue height	At the same 5 points as above, the height of each wall was measured using a steel tape measure, to the maximum height of the majority of the stems.
Wall thickness	At the same 5 points as above, wall thickness was measured by inserting a metal ruler through the bower walls and recording the thickness of the thatch.
Bower quality	A subjective measure of bower structural quality was made based on a scale 0-4. Subjective measures were made without observer knowledge of the owner's mating success. 0 – No avenue wall present. 1 – Avenue walls present, but comprise only one of a grass or stick component which is incomplete. 2 – Avenue walls are present and contain both grass and stick components, but both of these components are incomplete. 3 – Avenue walls are present and contain both grass and stick components, but one of these components is incomplete. 4 – Avenue walls are present and contain complete grass and stick components.

Table 2.1 Description of methods used for taking bower measurements, based on Borgia 1995 and Madden 2006.

2.7.4. Bower monitoring using cameras

Remote, motion-sensing cameras (StealthCam I590, Grand Prairie, Texas) were installed at a number of active bowers at the beginning of each season (Table 2.2). Cameras were powered by external 12V motorcycle batteries, and recorded data to SD cards. Batteries and SD cards were replaced at regular intervals, approximately every 3-7 days. Cameras took a burst of 9 pictures upon triggering (approximately one picture every 3 seconds). Once triggered, cameras entered a rest period of one minute before re-triggering was possible. Camera positions were standardised as much as possible within the limits of the natural vegetation around the bower. Cameras were positioned a minimum of 1m from the entrance of the bower and were either fixed to existing vegetation or to installed metal posts (Figure 2.5). Most cameras remained *in situ* for the duration of each season, unless males moved the location or orientation of their bowers. Males habituated to the presence of cameras very quickly and with minimal disturbance; in only 2 cases at different bowers (once in 2009 and once in 2011) did males react to the presence of the cameras. These reactions included the repeated attack of cameras, and ceased once cameras were repositioned. Bowers where cameras were not installed for the duration of the season had spare cameras rotated between them to monitor for any changes in ownership; data from these bowers were not included in behavioural analyses. Over the three breeding seasons monitored during this study, over 5.2million camera pictures were collected and analysed. This represented 182,570.4 hours of continuous bower monitoring (2009: 57.717.0 hours, N = 19; 2010: 53,136.5 hours, N = 25; 2011: 71,716.9 hours, N = 19).

Bower	Camera installed for duration of season		
	2009	**2010**	**2011**
B02	✓	✓	✓
B03	✓	✓*	
B04	(shaded)		✓
B05	✓	✓	✓
B07	✓		
B08	✓	✓	✓
B09			✓
B10			
B11	✓	✓	✓
B12		✓	
B13			
B15	(shaded)		(shaded)
B16	✓		
B17			(shaded)
B18	✓	✓*	
B19	✓	✓	✓
B20	✓	✓	✓
B21	✓	✓	✓
B22	(shaded)		
B23	✓		(shaded)
B26	(shaded)		
B29	✓	✓	✓
B30	✓	✓	✓
B31	✓	✓	✓
B37			(shaded)
B41		✓*	
B42	✓	✓ *	✓
B43	✓	✓	✓
B44		✓	✓
B47	✓	✓	✓
B49	✓	✓*	✓
B50	(shaded)	✓	(shaded)
B52	(shaded)	✓	✓
B53	(shaded)		
B54	(shaded)		
B55	(shaded)	✓*	
B56	(shaded)	✓*	✓
B57	(shaded)	✓	
B58	(shaded)		
B59	(shaded)		
B60	(shaded)	✓*	(shaded)
B61	(shaded)		(shaded)
B62	(shaded)		
B63	(shaded)		
B64	(shaded)		

Table 2.2. All known bowers with banded owners identified between 2009 and 2011; ticks indicate a camera was monitoring that bower for the full duration of the breeding season, * indicates bowers that were analysed using the fast data technique (see 2.7.5), shading indicates that bower was inactive or not located during that season.

Figure 2.5. An example of the camera positioning at a bower.

2.7.5. Recording behaviour from camera data

The use of automated cameras to collect behavioural data has been used in previous bowerbird studies (e.g. Borgia 1985, Madden 2003b, Keagy et al. 2009, Kelley and Endler 2012). Behaviours were assigned to seven different categories that could be easily identified from the camera picture data (Table 2.3) (adapted from Lenz 1994, Borgia 1995 and Madden 2001b; 2006). Behaviour duration was recorded using the time stamps recorded on camera pictures. If birds could not be identified due to their bands being obscured from view they were recorded as being 'unknown' individuals. For all behavioural analyses, behaviours were calculated as rates based on the total number of recording hours per bower for each camera. Camera recording hours varied minimally between bowers depending on the date/time of deployment, and due to rare failures of camera equipment. In 2010, two separate types of picture analyses were carried out; full analyses included

extraction of all behaviours listed in Table 2.3. For eight bowers a faster method of data extraction was used, which excluded owner behaviours of 'maintaining bower' and 'at bower' categories (see Table 2.2). Excluding instances of when the male bower owner alone was attending the bower rapidly increased picture analyses whilst still permitting the extraction of other important behaviours and interactions.

Behaviour	Definition
Maintaining bower	Bird is adding, picking up, moving or removing decorations, or is adding, tidying, 'fixing' or painting stems in the avenue.
Displaying	Bird is performing typical display actions orientated towards another bird or the centre of the bower. Typical display behaviours include bower circling, body shudders, wing flaps, forward and backward hops and picking up and tossing decorations.
Solicit	The audience bird exhibits solicitation behaviour whilst being displayed to by another bird. Solicitation poses involve a conspecific bird remaining stationary, usually in the centre of the bower, and in a crouched position with tail raised, and which clearly exposes the cloaca.
Copulation	A displaying bird mounts and copulates with an audience bird, usually in the centre of the avenue. Copulations are extremely quick (circa 3s) and are followed by vigorous wing-shaking by the female bird.
Wingshake	This category was used when copulations themselves were not captured in pictures, but when the audience bird was seen to be taking part in vigorous wing-shaking following a copulation. This behaviour was considered to be a reliable indication that a copulation had taken place.
Maraud	Visiting bird engages is destruction behaviour at a bower owned by another male. Marauding behaviour involves the visiting bird ripping the grass stems out of the avenue walls by grasping stems in feet and violently jumping backwards. Includes incidences of birds stealing decorations.
At bower	Behaviours at bowers which do not fall into any of the above categories, including standing at bowers, drinking or eating. Also used for activities that could not be identified due to bird being obscured from view.

Table 2.3. Definitions of bowerbird activities used in camera data analyses. Adapted from Lenz 2004, Borgia 1995 and Madden 2006.

2.8. MATING SUCCESS

2.8.1. Duration of breeding and measuring mating success

The duration of each breeding season varied between years (Table 2.4). Mating success was calculated for all bowers where cameras were *in situ* for the duration of the breeding season. Copulations occur in the bower avenue, and in the congeneric satin bowerbird, *P. violaceus*, observed copulations accurately predict male paternity (Reynolds et al. 2007). Copulations are very brief (~3s) and are followed by the female vigorously shaking for a number of minutes (Borgia 1995a). Measures of male spotted bowerbird mating success were based on copulation rates. The number of copulations each male received was summed and the dates of the first and last copulation in each season were used to define the copulation season. Female satin bowerbirds engage in two distinct bouts of male sampling, spending much of the initial bout sampling males before resuming a second bout later in the season during which the majority of copulations take place (Uy et al. 2000, 2001). Defining a copulation season within the overall breeding season ensured that copulation rates were not skewed by the varying amounts of time males spent constructing and maintaining their bowers when females were unlikely to mate.

Season	Duration of monitored season	N	Date of first copulation	Date of last copulation	Duration of copulation season (days)
2009	191.95	19	31 Dec	22 Feb	53
2010	146.09	25	11 Sep	08 Dec	88
2011	190.63	19	09 Oct	10 Jan	93

Table 2.4. Differences in season duration, measured in days. Season referred to by the year in which it began. N represents the number of bowers with cameras *in situ* for the duration of each season. The durations of the copulation season were used to calculate copulation rates per male.

2.8.2. Mating success and reproductive skew

A total of 60 copulations were recorded in 2009 (N = 19 bowers), 106 in 2010 (N = 25 bowers) and 41 in 2011 (N = 19 bowers). Thirteen males were monitored across all three seasons, but their copulation rates were not related (repeated-measures ANOVA, $F_{2,11}$ = 2.57, P = 0.10). Considering males that were monitored across any two seasons, there were positive correlations between copulation rates in 2009 and 2010 (r_s = 0.53, N = 14, P = 0.05, Figure 2.6a), and 2011 (r_s = 0.63, N = 15, P = 0.01, Figure 2.6b), but there was no correlation between 2010 and 2011 (r_s = 0.08, N = 16, P = 0.76).
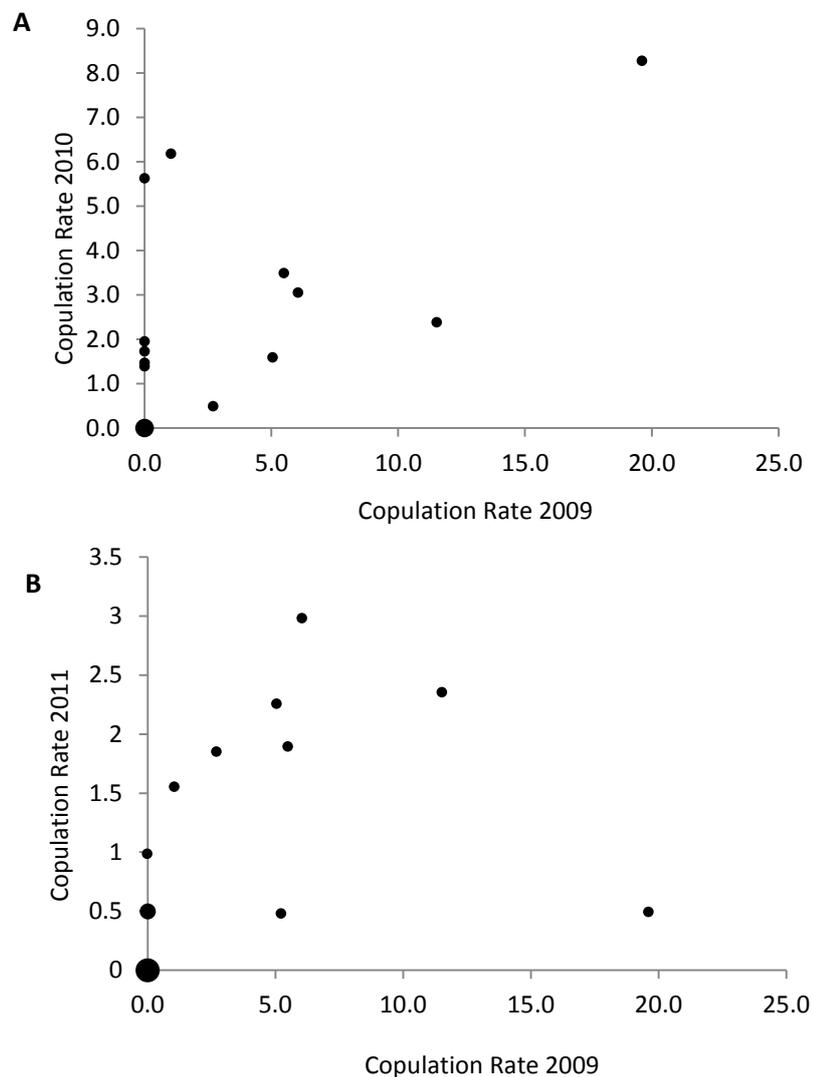
Figure 2.6. Relationship between copulation rates (number of copulations per camera recording time within the copulation season *1000) for bowers that were monitored across seasons A) between 2009 and 2010, and B) between 2009 and 2010. In 2009 two bowers experienced zero copulations in both years, and in 2010 four bowers experienced zero copulations in both years, and two bowers had identical copulation rates in 2011 (0.5) with zero copulations in 2009. These points are represented by enlarged circles on the plot.

Reproductive skew was high in all seasons, as expected in polygamous species with a non-resource based mating system (Table 2.5). Skew was highest in 2009, corresponding to the season with lowest rainfall, and lowest in 2010 when rainfall was high (see Chapter 2.6.). Skew was calculated according to Pamilo (1996) using the equation $S = (N_T - Q_E)/(N_T - 1)$, where N_T = total number of males, Q_E, the effective number of males, = $1/\sum p^2_i$ (p_i = the proportion of matings gained by the ith individual). Measures of skew closer to zero indicate that all males received an equal number of copulations, measures closer to $S = 1$ indicated one male received all copulations in that season.

Season	Reproductive Skew	% males with at least one copulation
2009	0.78	47
2010	0.48	88
2011	0.52	68

Table 2.5. Reproductive skew and the percentage of males that received at least one copulation in each season.

2.8.3. Correlates of male mating success

Previous studies have cited numerous correlates of male mating success across bowerbird species. The number and type of decorations displayed have previously predicted mating success in single breeding seasons (Borgia and Mueller 1992, Borgia 1995, Uy and Borgia 2000, Madden 2003b, Coleman et al. 2004). Between 1998-1999 numbers of *Solanum* fruits, a perishable green fruit, explained a large proportion of variation in male mating success (Madden 2003b). Similarly, female preference for bower structures that are larger and more symmetrical has also been cited (Borgia 1985b, Doucet and Montgomerie 2003a, b, Robson et al. 2005, Endler et al. 2010).

Using data collected between 2009 and 2011, the relationship between male mating success and the numbers of *Solanum* fruits displayed on his bower was not found, when instead pieces of metal foil were the best predictors (Dingle et al. *in prep*). There were no

correlations between measures of total decoration numbers on bowers and mating success nor with measures of bower structural properties (Table 2.6).

Measure	2009			2010			2011		
	r_s	N	P	r_s	N	P	r_s	N	P
Total decorations	0.19	19	0.45	0.08	25	0.66	0.20	19	0.38
Bower quality	0.35	19	0.14	0.10	25	0.63	0.15	19	0.49
Structural symmetry	-0.38	19	0.11	-0.14	25	0.51	-0.17	19	0.45
Bower volume	-0.18	19	0.47	-0.04	25	0.85	0.32	19	0.14

Table 2.6. Spearman's rank correlations between measures of bower decoration and structural properties with male mating success.

2.9. ETHICS AND LICENCING

Permission to work with the population of wild spotted bowerbirds in Taunton National Park (Scientific) was granted by the Queensland Government Environmental Protection Agency, *Permit Number WITK0615290.* Ethics approval was granted by the University of Queensland, *Animal Ethics Approval Certificate SBMS/285/09.* Capture and banding of bowerbirds was carried out by JRM and CD, *ABBBS Authority Number 2323.* Blood and feather samples were brought back to the UK for analysis under export licence *WT2009-6517* and import licence *TARP-2012-61.* For all methodologies and experiments outlined in this thesis, bowerbirds were free-living and could choose whether to interact with equipment. In Chapter 5, we used rewards rather than punishments as motivation. All equipment and experimental materials were removed at the end of the testing periods. No males abandoned bowers as a result of observations or experimental testing.

Chapter Three

The consistency of male spotted bowerbird display

ABSTRACT

Inter-individual variation in male sexual traits may inform female mate choice decisions, but intra-individual variation in sexual signalling has received relatively little attention, despite the importance of such variation in determining the strength of selection and heritability of traits. Traits that are extended phenotypes, such as bowers, nests or decorations, may be particularly susceptible to variation via internal or external factors and stochastic events. We examined consistency in the decorations used by male bowerbirds at their bowers; structures built by males that act as a target of female choice. Male bowerbirds are long-lived, display at the same bower sites over repeated seasons (up to 10 years) and operate a non-resource based mating system providing only genetic benefits to females. Using a long term dataset spanning thirteen years we found that, at the population level, mean numbers of decorations displayed on all bowers across a population of spotted bowerbirds were relatively stable, with only perishable decorations showing a high level of inconsistency. This inconsistency was related to rainfall, a key environmental determinant in semi-arid regions, but only when rainfall was substantially below average; in seasons of average or above average rainfall, perishable decorations showed random fluctuations over time. On an individual level, bower owning males were highly consistent in their decoration use, exhibiting individual preferences over short and long time periods. Males that held the longest tenures did not have higher levels of decoration consistency, indicating that individuals were consistent from the beginning of their bower ownership. However, females did not appear to choose males that were the most consistent displayers, as highly consistent males did not gain greater numbers of copulations at their bowers. Individual consistency in display may be surprising in a long-lived species with apparent indications for a learned basis for display and ample opportunities for flexibility. Consistency may be regulated by limitations in male physical, cognitive or social competence, innate preferences or may function adaptively to minimise female costs and maximise attractiveness given changing female preferences.

3.1. INTRODUCTION

Sexual selection acts on male traits that provide females with information about potential benefits to be gained from choosing a particular mate (Andersson 1994). Inter-individual variation in male trait expression has been widely documented across taxa, and such variation may contribute to differences in male mating success (reviewed in Jennions and Petrie 1997; Johnstone 1995). However, surprisingly few studies have explicitly set out to examine whether individuals vary in sexual trait expression over repeated display events, despite the importance that such consistency may have in determining the strength of selection, the degree of condition dependence and the heritability and genetic basis supporting such traits (Zahavi 1975, Boake 1989, Griffith and Sheldon 2001, Boogert et al. 2011b). Traits providing reliable signals of male quality may be expected to show high individual repeatability, especially in systems where females only gain fixed benefits (e.g. genetic material). Variation within males may cause noise and be costly for females who make repeated visits before choosing the most attractive male to mate with (Janetos 1980). Alternatively, traits which vary predictably over time may reflect attributes related to fluctuations in male quality, such as age, experience or social status (e.g. Griffith & Sheldon 2001, de Kort et al. 2009) and if females can account for factors driving inconsistency (e.g. with age/experience) then variation may enhance their choice. Fluctuations in display may also reveal fine-scale changes in the male, such as parasitic load (Garamszegi et al. 2004), or local environment, such as altered display behaviour depending on predation risk (Warner and Dill 2000). Understanding and quantifying variation in traits within individuals is likely to be crucial to our understanding of the type of information they convey to females and the mechanisms leading to their evolution.

Extended phenotypic traits, signals that are separate from the body (Dawkins 1978), may be particulary susceptible to variation as they can be disrupted by factors external to the male. Consistency in traits independent of the body may provide additional information for females, or signal immediate quality more reliably than displays dependent on morphological and physiological traits (Schaedelin and Taborsky 2009). Currently, the relatively few studies focusing on long term consistency in extended phenotypic traits almost exclusively consider repeatable nest-building behaviour in species with resource-based mating systems. For example, male three-spined sticklebacks, *Gasterosteus aculeatus*,

were found to be repeatable in their construction of three different nest sites within a breeding season (Rushbrook et al. 2008) and male southern masked weavers, *Ploceus cucullastus,* built repeatable nest morphologies (Walsh et al. 2010). However, when it comes to nest building, both natural and sexual selection processes are likely to act, making it problematic to comment on the relative contribution from each, and the trait under selection (the nest) provides both direct and indirect benefits to females. Little is known about extended trait consistency in systems where females gain only indirect, fixed genetic benefits from the male and the trait provides only information rather than any direct benefit. Understanding consistency in trait expression in this context is likely to enhance our understanding of the evolution of female choice.

Male bowerbirds, Ptilonorhynchidae, offer an ideal system in which to tackle questions regarding long term consistency in traits that offer no direct benefits to females and where sexual selection acts without the influence of natural selection. Bowerbirds (with the exception of the catbird species) operate a non-resource based mating system, where males offer only genetic material to females and play no role in the rearing of offspring (Frith and Frith 2004). Males construct and decorate extended display courts (bowers) which act as the target of female choice (Borgia 1985b, Borgia and Mueller 1992, Madden 2003b, Coleman et al. 2004, Frith and Frith 2004), but provide no material benefits to her or her offspring. Bowers are decorated with a wide range of objects, both perishable and non-perishable, and those exhibiting high numbers of particular decorations gain higher mating success (Borgia 1985b, Borgia 1995a, Madden 2003b). Bowers are maintained throughout the breeding season (typically 3-6 months depending on the species), and females repeatedly sample males throughout this time before copulating with a chosen male (Uy et al. 2000, 2001). Males engage in marauding, a unique form of intra-sexual competition, whereby neighbouring bower owners destroy bower structures and steal decorations from each other, a mechanism considered to maintain honesty in male signaling (Borgia 1985a, Wojcieszek et al. 2007, Pruett-Jones and Heifetz 2012). Male bower owners return to the same bower location season after season, and following the loss of an owner another male usually inherits the same bower location (Frith and Frith 2004, Doerr 2009b).

The high level of inter-individual variation in male bowerbird display has received considerable attention in previous literature (Marshall 1954, Borgia and Gore 1986, Diamond 1986a, Hunter and Dwyer 1997, Madden 2002, 2003a, Patricelli et al. 2003, Robson et al. 2005, Madden 2006). However, whether males also exhibit high intra-individual variation, and the consequences of this for female mate choice, is less well understood. As well as external environmental pressures, intra-male variation may be caused by changes in the male during his lifetime. For instance, decoration preferences may alter during maturation (Borgia and Wingfield 1991, Collis and Borgia 1992), or via experience and learning throughout development (Collis and Borgia 1992). Changes in dominance status, which may cause subsequent changes in the frequency/intensity of marauding by rivals, may also lead to inconsistency in display (Borgia and Gore 1986; Doerr 2009b; Pruett-Jones and Pruett-Jones 1994). Male great bowerbirds, *P. nuchalis*, accumulate decorations over time through the inheritance of bower sites and non-perishable decorations from previous owners (Doerr 2009a). As male tenure increases males may gain experience and/or skills which enables them to cope better with environmental, social and stochastic pressures. However, despite these pressures promoting variation, there may be advantages to maintaining a constant display signal, and evidence suggests that males may actively seek to achieve this. Male spotted bowerbirds, *P. maculatus,* actively removed experimentally added decorations, restoring their bowers to pre-manipulated numbers in a process suggested to reduce marauding attacks by rivals (Madden 2002). Similarly, male great bowerbirds that had their decoration numbers standardised engaged in decoration collection activities that positively correlated with pre-standardisation decoration numbers, again suggestive of males maintaining consisent individual differences (Doerr 2010a). Kelley and Endler (2012) found that individual male great bowerbirds maintained a consistent level of forced perspective within and between two breeding seasons, despite experimental enhancement of their displays. Thus, it appears that male bowerbirds may not always display the largest numbers of particular decorations or most extreme decorative patterns, even when these are available at no cost to the male. However, whether males show natural consistency (i.e. without experimental manipulation) over shorter (within season) and longer time periods (>2 seasons) has yet to be addressed, and the potential benefits of their consistent signalling have yet to be explored in detail.

We asked whether male bower owners in a population of spotted bowerbirds were consistent in their natural use of decorations over differing periods of time using a long-term dataset spanning thirteen years. Numbers of particular decorations are good predictors of male mating success in this species (Madden 2003b), and males actively adjust the number, types and position of objects displayed on their bowers over fine-scale time periods of hours or days (Madden 2003a). The combination of a long breeding season (circa 5 months), repeated ownership at bowers between seasons (up to 10 years) and the use of a wide variety of decoration types allowed us to test hypotheses regarding their consistency in decoration usage. First, we explored how mean numbers of decorations across all bowers in our study population varied over time. We focused on common decorations (those occurring on >50% of all bowers), and looked for differences between those that were perishable and more likely to be limited by environmental conditions, and non-perishable decorations that could persist regardless of environmental conditions. We asked whether variation in common decorations were linearly predictable, expecting that decorations at all bowers may accumulate over time as males collect more, inherit them from previous owners or become more proficient at obtaining them. We then investigated the impact of rainfall on population-level decoration consistency to ask whether the display of decorations was influenced byrainfall; a key determinant of metabolic and decoration resources in semi-arid environments.

Next we explored inter-individual variation in bower decoration, and asked whether males showed individual consistency in decoration numbers over short (within-season) and long (between season) timescales. Decorations were analysed by assigning them to non-exclusive categories; we analysed total numbers of decorations, and then categorised these into common, perishable and non-perishable decoration types. We expected perishable decorations to show highest variation in display numbers at individual bowers due to their reliance on rainfall for production and their frequent need for replenishment, whereas non-perishable decorations to persist over longer time periods. To ask whether decoration consistency was a funciton of the bower's location or individual male preferences, we calculated consistency scores for each bower regardless of any changes in ownership at that location. We compared these with consistency scores calculated only from bowers where owners had remained the same between seasons, reducing the impact of the location of the

bower. We used similarity matrices to extract individual consistency scores per male, and examined whether consistency related to a male's length of bower ownership (tenure), and thus provided females with an indicator of male age. Lastly we asked whether consistency was a trait desired by females and predicted male mating success.

3.2. METHODS

3.2.1. General field methods

Data were collected from a population of wild, individually marked spotted bowerbirds in Taunton National Park (Scientific) in central Queensland, Australia (23.54989S, 149.24088E) (see Miles and Madden (2002) for a detailed description of the study site). Male bower owners tend their bowers throughout the breeding season, typically from July to January (we refer to each season by the year in which it began), and return to the same bower location each season, allowing data on bower decorations to be collected both within and between seasons. Bowers were spaced approximately 1km apart (Miles and Madden 2002), with the exact position of the bower sometimes moving between seasons (Chapter 2.7.1). At the beginning of each season bowers were located and their owners identified by their unique combinations of coloured leg bands. Bowers were monitored over ten breeding seasons (1998-2000, 2002-2003, 2007-2011). Not all bowers were active and/or monitored in each season.

3.2.2. Measuring bower decorations

Bowers exhibited a combination of natural and manmade objects and over 100 different decoration types have been found on spotted bowerbird bowers at Taunton National Park, with individual bowers displaying up to 43 different decorations at a single time (unpublished data). Some decoration types are highly perishable (e.g. fruits, berries, leaves and seed pods) while others persist across multiple seasons (e.g. snail shells, bones, stones, plastic and metal). Bowers were either visited once during the middle of the breeding season (2000, 2002, 2003, 2007 and 2008) or multiple times throughout the season (1998, 1999, 2009, 2010 and 2011) and all decorations were recorded. For between-year analyses a single decoration count per bower per season was used; in seasons when

multiple counts were made, we used mean values of decoration counts. For within-season analyses we focused on three consecutive breeding seasons (2009-2011) for which we had the highest number of within-season decoration counts at the highest number of bowers. Exact numbers of each decoration type were counted and summed for each bower, except for white snail shells which often occurred at bowers in large numbers (mean ~350, range = 0-1720); for this decoration type numbers were estimated to the nearest 10. To ensure that analyses were based on consistency measures in relative numbers of decorations, rather than differences in the absolute numbers displayed by individual males, decoration counts were standardised by dividing each value by the maximum value across all bowers in the same category. Analyses were based on total decoration numbers, and three further subcategories; common (those that occurred on 50% or more of all bowers), perishable (those requiring ongoing investment by the male to replenish, including fruits, berries and leaves) and non-perishable (defined as decorations that were resilient to degradation and included natural and manmade objects such as stones, shells, plastic and glass). Decorations in the perishable and non-perishable categories were exclusive; all decorations and those in the common category included both. There was a relatively consistent ratio of perishable:non-perishable decorations across all years studied (Table 3.1).

3.2.3. Variation in common decorations at the population-level

We first asked how mean numbers of decorations displayed on all bowers across the study population varied within a season. Using the three most recent seasons (2009, 2010 and 2011), we restricted our analyses to only those bowers where both the owner and location had remained constant (N = 15, 16 and 19 respectively). This removed any confounds of owner preference or location effects. We also restricted our analyses to common decoration types only, which included perishable (N = 6) and non-perishable (N = 8) objects (we excluded shells from these analysis as estimations of these were unlikely to accurately capture within-season fluctuations). Mean numbers of common decorations were used in repeated measures models; we used within-subject effects to determine whether decoration numbers varied between counts and then asked whether such variations were directional and could be predicted by linear increases or decreases (within-subject contrasts).

We repeated these analyses to ask whether mean numbers of decorations displayed varied between seasons. We analysed data collected from two periods each of three consecutive seasons (1998-2000 and 2009-2011) and again restricted our analyses to only those bowers where the owner and location had remained constant within each period (N = 7 and N = 16 respectively). We analysed all common decoration types (N = 15; this time including average shell numbers as estimates between seasons were likely to be more indicative of between season fluctuations). Where multiple counts were made within a season we used mean values. We carried out repeated measures models using within-subject effects to look for variation between seasons and within-subject contrasts to determine whether variations were linear indicating an accumulation of decorations with tenure.

3.2.4. Rainfall analysis

To ask whether variation in decoration numbers was influenced by rainfall we used rainfall data collected throughout the study period from two sources. For 1998-2000 monthly records of rainfall were obtained from the Australian Bureau of Meteorology data recorded from Dingo Post Office, situated 15km SE of Taunton National Park (Bureau of Meteorology, 2012). From 2001 accurate monthly rainfall data were collected at Taunton National Park, and we therefore used these data for 2001-2011. The only exception to this was during December 2009 when data were not collected at Taunton NP and was obtained from Dingo Post Office instead. These two sources of data were highly correlated; for the period between 2004 and 2010 when monthly records were collected from both Dingo and Taunton we found a strong correlation between the two (R = 0.89, N = 59, P < 0.001).

We looked for within-season (2009-2011) correlations between mean decoration numbers with two measures of rainfall. First, we used rainfall in the same month of decoration counts, and second, rainfall in the month prior to counts, as this may be the more biologically meaningful measure for the growth and development of perishable decorations such as fruits and seeds. We then looked for between year correlations with the mean number of decorations displayed and two measures of rainfall (Table 3.1). We used

the total rainfall during that breeding season (July-January) which we expected would affect short term changes in productivity, and then used the total rainfall experienced in the twelve months prior to the start of that breeding season (June-June) as we expected this to have longer term effects on the availability of perishable decorations.

Season	No. of Bowers Studied	Total Number Decoration Types	% Common	% Perishable	Breeding Season Rainfall (July-Jan)	Year Prior to Breeding Season Rainfall (June-June)
All seasons		109	13.8	52.3	-	-
1998	18	61	4.1	49.2	829	575
1999	18	54	3.6	46.3	273	1157
2000	16	36	2.4	33.3	348	550
2002	15	54	3.6	40.7	138	425
2003	20	56	3.7	41.1	330	487
2007	20	33	2.2	39.4	291	368
2008	15	44	2.9	31.8	669	650
2009	25	64	4.3	45.3	275	897
2010	47	81	5.4	46.9	1290	824
2011	38	60	4.0	45.0	377	1726

Table 3.1. The number of bowers studied in each season with total numbers of decoration types displayed, and percentages of those decoration types which fell into perishable and non-perishable categories. Two measures of rainfall (mm) were used for analysis; rainfall during the breeding season and rainfall in the twelve months prior to the start of each breeding season.

3.2.5. Variation in decorations at the individual-level

Analysing consistency for large numbers of decoration types was challenging for two reasons. First, the trait of interest was multidimensional, with up to 43 different decoration types on any one bower, and we believed that the relative mix of these decorations, as well as absolute numbers, was a measure of interest. Second, our data were not independent, with repeated measures within and across seasons at the same bower. To manage multiple types of decorations we used methods akin to ANOSIM (analysis of similarity, Walsh et al. 2010). We conducted a hierarchical cluster analysis, with a nearest-neighbour cluster method based on Euclidean distances to group bowers with similar proportions of decorations together and obtain a quantitative measure of similarity between any two bowers for a given season. Lower scores obtained through this analysis indicated higher

consistency. Similarity scores were used to construct similarity matrices for within and between season measures.

To overcome problems of independence, we conducted permutation tests in PopTools (Hood 2010) based on 1000 randomised matrices. This allowed us to determine whether bowers of interest were more similar to themselves across time periods than by chance, given the distribution of similarities in the population, and to assign each bower a consistency score. We asked whether the decorations at a bower at one point in time were more similar to themselves when measured on subsequent occasions than expected given the variance in the population. For within-season analyses, we focused on three seasons (2009-2011) and used monthly decorations counts as our points in time to ask whether bowers were consistent within a single season. We expanded these to between-season analyses using mean decoration counts, to ask whether bowers in the same location in one season were more similar to the bower decorated in the same location in subsequent seasons given population similarity distributions. Within season changes in ownership were rare; in 2009 there were no ownership changes, in 2010 two owners were replaced and in 2011 three owners were replaced; two of these were towards the latter end of the season, therefore limiting our scope for comparisons. Ownership changes between seasons were more common (N = 8), therefore limiting our analyses to only those bowers where ownership was constant enabled more meaningful analysis of whether these bowers were more similar than expected given the population as a whole.

3.2.6. Male tenure and consistency

Individual consistency scores may be predicted by male tenure. Male bowerbirds are known to hold bowers for over ten years, and tenure is assumed to be a reliable proxy for age (Borgia 1993; Frith and Frith 2004). We calculated male tenure using a ranking system which adjusted scores according to data on bower ownership collected since 1998. Males were rank ordered based on the known number of seasons in which they were bower owners. Ranks were then adjusted upwards according to whether they were owners at the start and/or finish of the study period (see Borgia 1993). Males that were established owners at the start of the study, or that retained ownership until the end of the breeding

season in 2011 were given a one-rank increase. Males that were owners at both were given a two-rank increase. We used Spearman's correlations to ask whether rank tenure was correlated with individual consistency scores.

3.2.7. Consistency and mating success

Finally, we asked whether bowers that had higher individual consistency scores attracted a higher number of copulations. We measured individual males' mating success during the last three seasons of the study period (2009-2011). In these seasons we deployed remote, motion-sensing cameras (StealthCam I590, Grand Prairie, Texas) at bowers for the duration of the breeding season. Copulations occur in the bower avenue (Borgia et al. 1985; Frith and Frith 2004), and are easily recognisable behaviours captured on camera. Observed male mating success has been shown to be a reliable predictor of reproductive success in the congeneric satin bowerbird, *P. violaceus* (Reynolds et al. 2007). The number of copulations each male obtained was summed for each season, and the dates of the first and last copulations across the study population were used to define the copulation season. Our measure of mating success was defined as the copulation rate per individual, calculated as the number of copulations witnessed at the bower divided by the total number of camera recording hours at the bower during the copulation season. Camera recording hours differed minimally between males depending on the date/time cameras were deployed and due to rare failures of camera in the field.

We used individual consistency scores extracted from within-season similarity matrices for the three seasons in which we had the highest number of decoration counts (2009-2011). We correlated these with individual male mating success scores gained from camera data for each of those seasons using Pearson's correlations. All correlations were two tailed to reflect our predictions that females may prefer either bowers which show consistent levels of decorations or which are inconsistent due to the accumulation of decorations or other factors which may alter a male's display over time. Lastly, we conducted a linear mixed model (LMM) analysis to account for the differences in male mating success and consistency within individuals when measured across the three seasons. We entered mating success scores as a dependent variable for each season as a repeated

measure, with consistency as a fixed effect and season and male identity as random effects. All analyses were carried out in SPSS version 19.

3.3 RESULTS

3.3.1. Variation in common decorations at the population-level

    3.3.1.1. Population consistency in mean numbers of decorations within seasons

Mean numbers of most types of perishable decorations (5/6) varied within season, although this variation was often not linearly significant following correction for multiple comparisons (Table 3.2, Fig 3.1). In contrast, we found almost no variation in mean numbers of the non-perishable decorations, except for clear glass in 2011, suggesting their use was constant across all bowers within a season.

| | | 2009 | | | | 2010 | | | | 2011 | | | |
| | | Within-subject effects | | Within-subject contrasts | | Within-subjects effects | | Within-subject contrasts | | Within-subject effects | | Within-subject contrasts | |
Decoration	Category	$F_{5,70}$	P	$F_{1,14}$	P	$F_{4,60}$	P	$F_{1,15}$	P	$F_{4,72}$	P	$F_{1,18}$	P
Eremophila fruits	C + P	**4.89**	**0.001**	5.60	0.033	**6.10**	**<0.001**	4.78	0.045	2.72	0.04	2.68	0.12
Solanum fruits	C + P	**5.87**	**<0.001**	8.32	0.012	**18.98**	**<0.001**	**20.56**	**<0.001**	2.38	0.06	1.39	0.25
Senna pods	C + P	**3.81**	**0.004**	6.56	0.023	2.70	0.039	5.05	0.04	**10.62**	**<0.001**	5.33	0.03
Green sprigs	C + P	3.05	0.015	0.51	0.49	2.94	0.027	0.93	0.35	1.80	0.14	0.71	0.41
Itchy-grub cases	C + P	**4.91**	**0.001**	1.51	0.24	0.70	0.59	0.11	0.75	4.35	**0.003**	5.25	0.03
Red stems	C + P	1.38	0.24	1.61	0.23	**9.49**	**<0.001**	**17.22**	**<0.001**	**8.43**	**<0.001**	**14.64**	**0.001**
Bones	C + NP	1.81	0.11	1.92	0.19	0.99	0.42	0.40	0.54	3.00	0.02	2.69	0.12
Brown glass	C + NP	0.72	0.61	2.09	0.17	1.23	0.31	0.39	0.54	2.03	0.10	3.91	0.06
Clear glass	C + NP	0.71	0.62	0.24	0.63	1.15	0.34	1.11	0.31	3.72	0.01	**11.87**	**0.003**
Green glass	C + NP	2.05	0.08	1.84	0.20	0.88	0.48	0.45	0.51	2.60	0.04	1.61	0.22
Metal	C + NP	0.59	0.71	1.45	0.25	2.18	0.08	3.42	0.08	2.07	0.09	1.90	0.19
Foil	C + NP	1.03	0.41	0.76	0.40	0.71	0.59	1.03	0.33	2.73	0.04	4.92	0.04
Red plastic	C + NP	0.69	0.63	1.07	0.32	1.03	0.40	1.43	0.25	0.95	0.44	1.37	0.26
Black plastic	C + NP	1.51	0.20	4.74	0.05	1.21	0.32	0.08	0.78	0.48	0.75	0.00	1.00

Table 3.2. Differences in mean numbers of 14 common decoration types at bowers across monthly counts in 2009, 2010 and 2011, during which time the owner remained constant. C = common, P = perishable, NP = non-perishable decoration type. Significant effects after a Bonferoni correction (α = 0.004) are shown in bold.

2009

2010

Mean number of decoration type (left axis, vertical label)

Rainfall mm (right axis, vertical label)
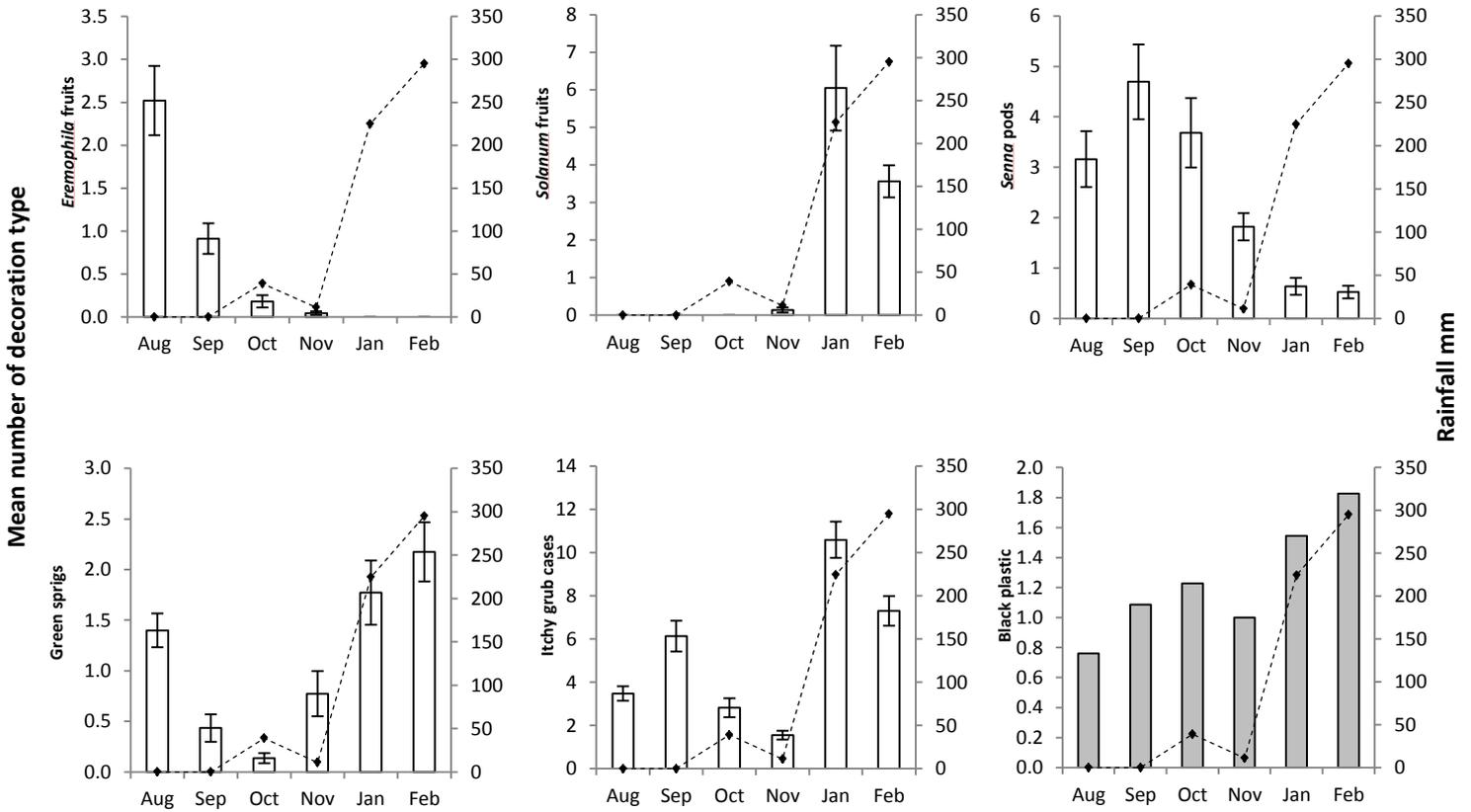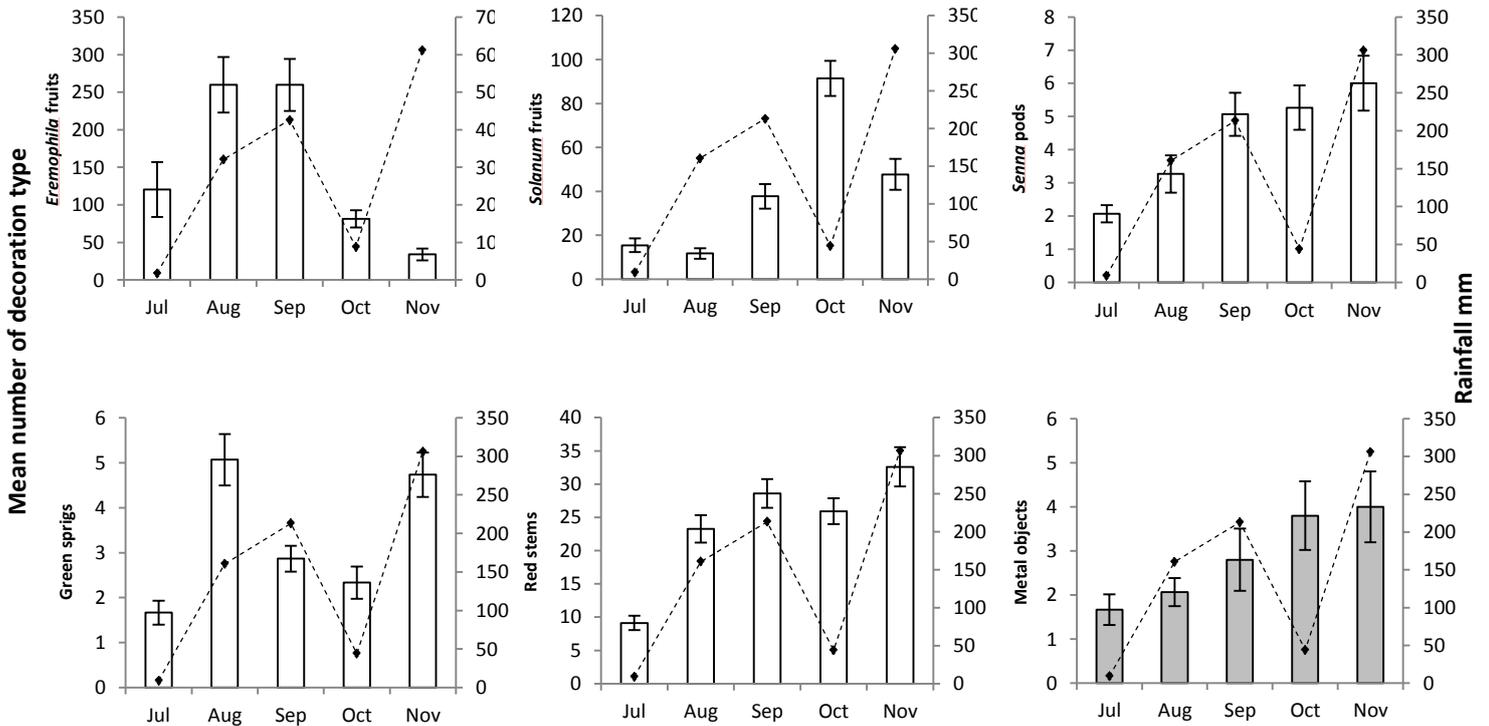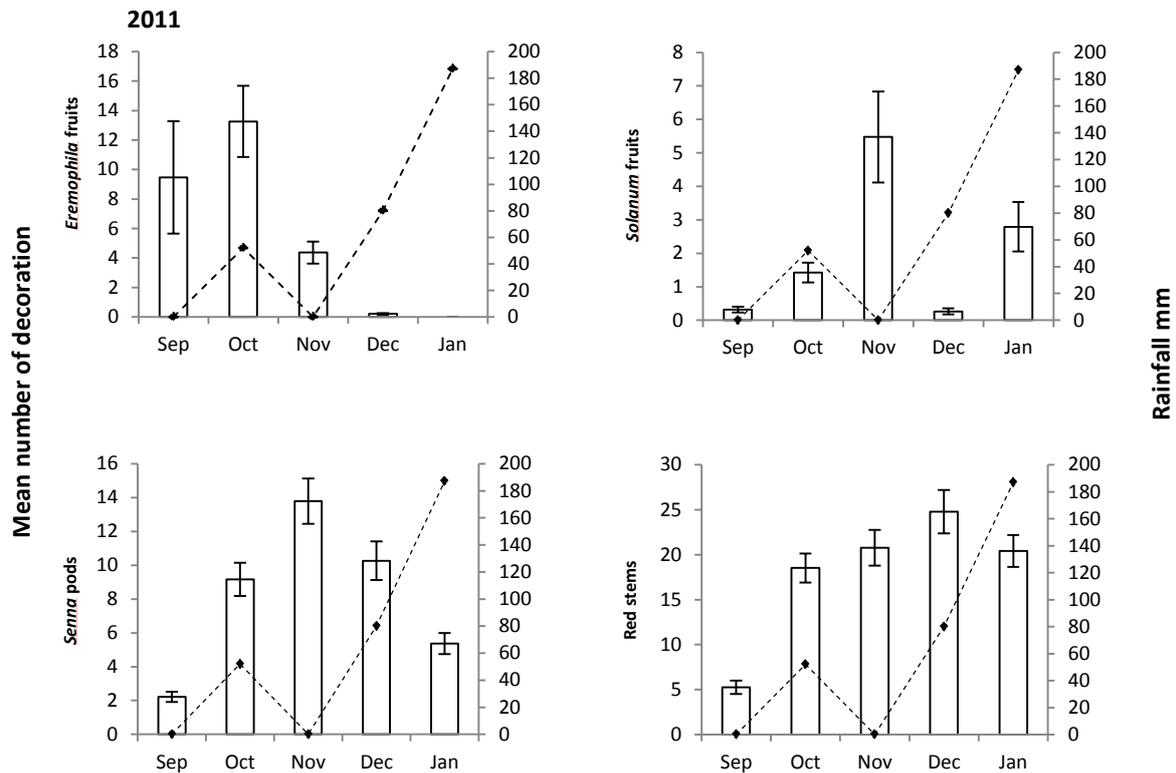
Figure 3.1. Monthly rainfall across three consecutive breeding seasons, with changes in mean numbers of decorations displayed across bowers (error bars show SE) for decoration types which showed a significant variation in number. White bars indicate the decoration is perishable, grey bars indicate a non-perishable decoration type.

3.3.1.2. Population consistency in mean numbers of decorations between seasons

In the first period (1998 – 2000), most common decorations showed no significant changes in numbers between seasons (Table 3.3). However, two categories of glass (green and clear, which are also the most abundant colours of glass found on bowers) did vary, with green glass showing a significant linear decrease in number across seasons. In the second period, from 2009 - 2011, there were significant variations in many of the common perishable decorations, however, many of these showed no consistent linear increase or decrease. In contrast, most non-perishable decorations, with the exception of bones and shells, which both increased in mean number over time, showed little variation between years.

Decoration	Category	1998-2000				2009-2011			
		Within-subject effects		Within-subject contrasts		Within-subject effects		Within-subject contrasts	
		$F_{2,12}$	P	$F_{1,6}$	P	$F_{2,30}$	P	$F_{1,15}$	P
Eremophila fruits	C + P	1.89	0.19	1.26	0.31	**8.88**	**0.001**	3.29	0.09
Solanum fruits	C + P	1.84	0.20	3.62	0.11	**22.77**	**<0.001**	0.44	0.52
Senna pods	C + P	**15.87**	**<0.001**	16.42	0.007	**4.82**	**0.02**	10.54	0.005
Green sprigs	C + P	0.33	0.72	0.53	0.49	**23.98**	**<0.001**	4.40	0.05
Itchy-grub cases	C + P	0.05	0.95	0.03	0.86	3.91	0.03	0.07	0.79
Red stems	C + P	0.72	0.51	0.24	0.64	**18.36**	**<0.001**	**14.03**	**0.002**
Shells	C + NP	2.41	0.13	2.09	0.20	**8.22**	**<0.001**	8.62	0.01
Bones	C + NP	2.30	0.14	3.76	0.10	4.78	0.02	**12.68**	**0.003**
Brown glass	C + NP	2.30	0.14	1.95	0.21	0.86	0.43	0.01	0.92
Clear glass	C + NP	4.64	0.03	2.74	0.15	0.45	0.64	0.60	0.45
Green glass	C + NP	9.20	<0.01	14.78	0.009	0.63	0.54	0.07	0.80
Metal	C + NP	3.48	0.06	3.55	0.11	0.06	0.94	0.07	0.79
Foil	C + NP	2.22	0.15	0.72	0.43	1.05	0.36	0.23	0.64
Red plastic	C + NP	1.07	0.37	2.61	0.16	0.81	0.45	0.03	0.86
Black plastic	C + NP	0.62	0.55	0.60	0.47	0.004	0.99	0.00	0.99

Table 3.3. Differences in 15 common decoration types at bowers over two three season periods during which time the owner remained constant. Categories: C = common, P = perishable, NP = non-perishable. Significant effects after a Bonferoni correction (α = 0.003) are shown in bold.

3.3.1.3. Variation of mean numbers of decorations with rainfall within seasons

In the 2009 season, when rainfall was uncharacteristically low, the mean number of many perishable decorations correlated positively with rainfall during the same month. Surprisingly, many of these did not co-vary with rainfall in the previous month. In seasons when rainfall was either above or at average levels (2010 and 2011 respectively), we found almost no correlations between the mean number of decoration types displayed and measures of rainfall, however, the difference of correlations between years was not significant (Friedman test, χ^2_r = 3.0. d.f.=2, P=0.22, Table 3.4, Fig 3.1).

Decoration	Cat.	2009, N = 6				2010, N = 5				2011, N = 5			
		During month		Previous month		During month		Previous month		During month		Previous month	
		R	P	R	P	R	P	R	P	R	P	R	P
Eremophila fruits	C + P	-0.52	0.29	-0.37	0.47	0.03	0.96	-0.06	0.92	-0.67	0.22	-0.35	0.57
Solanum fruits	C + P	**0.88**	**0.02**	0.37	0.47	-0.08	0.90	0.83	0.08	-0.15	0.81	0.48	0.42
Senna pods	C + P	**-0.83**	**0.04**	-0.62	0.19	0.65	0.23	0.55	0.33	-0.10	0.87	-0.38	0.53
Green sprigs	C + P	**0.81**	**0.05**	0.65	0.16	0.75	0.14	-0.46	0.44	-0.15	0.81	**-0.89**	**0.04**
Itchy-grub cases	C + P	0.75	0.08	0.24	0.65	-0.72	0.17	0.77	0.13	0.46	0.43	0.43	0.47
Red stems	C + P	**0.84**	**0.04**	0.40	0.43	0.81	0.10	0.37	0.54	0.36	0.55	-0.30	0.63
Bones	C + NP	-0.31	0.55	**-0.80**	**0.05**	0.46	0.44	-0.50	0.40	0.16	0.80	-0.02	0.98
Brown glass	C + NP	0.34	0.51	**0.85**	**0.03**	-0.38	0.53	-0.78	0.12	0.21	0.74	0.09	0.89
Clear glass	C + NP	0.17	0.74	0.32	0.54	0.57	0.31	0.56	0.33	0.82	0.09	0.09	0.89
Green glass	C + NP	**0.85**	**0.03**	0.30	0.56	-0.58	0.31	-0.50	0.39	-0.16	0.80	-0.24	0.69
Metal	C + NP	0.62	0.19	0.23	0.66	0.47	0.43	0.54	0.35	-0.05	0.94	-0.38	0.53
Metal foil	C + NP	-0.08	0.89	-0.69	0.13	0.45	0.45	0.57	0.32	0.15	0.81	-0.52	0.37
Red plastic	C + NP	**0.89**	**0.02**	0.37	0.47	0.48	0.42	0.71	0.18	0.72	0.17	-0.25	0.69
Black plastic	C + NP	0.94	0.01	0.73	0.10	0.01	0.99	0.45	0.45	-0.13	0.83	-0.40	0.51

Table 3.4. Correlations between monthly rainfall and mean numbers of decorations displayed at bowers, both during the same month of decoration counts, and for the month prior to counts. Categories: C = common, P = perishable, NP = non-perishable. Due to the small sample sizes (N = 5 or 6) corrections for multiple comparisons were not used, and significant correlations (P < 0.05) are shown in bold.

3.3.1.4. Variation of mean numbers of decorations with rainfall between seasons

Annual rainfall varied substantially (up to 4.5 times) between seasons during the study periods. Despite this variation, we found few relationships between rainfall and the prevalence of common decorations on bowers (Table 3.5). This was the case when we considered both rainfall during the same season as decorations were counted and rainfall in the year prior to decoration counts. Moreover, there was a general lack of correlation between rainfall and measures of variation in the numbers of decorations displayed between different males (coefficients of variation, Table 3.5), suggesting that rainfall may not fully account for differences observed between male usage of decorations across the population.

Decoration	Category	Mean Decoration Number				Coefficient of Variation in Decoration Numbers			
		Rainfall				Rainfall			
		During Season		Previous Year		During Season		Previous Year	
		R	P	R	P	R	P	R	P
Eremophila fruits	C + P	0.36	0.30	-0.26	0.47	0.23	0.95	-0.13	0.72
Solanum fruits	C + P	0.60	0.07	-0.38	0.28	-0.39	0.27	0.16	0.66
Senna pods	C + P	-0.09	0.80	-0.01	0.97	-0.09	0.82	-0.46	0.18
Green sprigs	C + P	0.55	0.10	0.30	0.40	-0.32	0.37	**-0.67**	**0.03**
Itchy-grub cases	C + P	0.22	0.55	0.01	0.98	0.08	0.84	-0.48	0.17
Red stems	C + P	**0.64**	**0.05**	0.41	0.24	-0.07	0.86	-0.35	0.32
Bones	C + NP	**0.69**	**0.03**	0.56	0.09	-0.09	0.81	-0.48	0.17
Brown glass	C + NP	0.24	0.50	-0.37	0.29	0.26	0.46	-0.27	0.46
Clear glass	C + NP	0.29	0.42	-0.17	0.63	0.41	0.24	**0.83**	**<0.01**
Green glass	C + NP	-0.01	0.98	-0.53	0.12	0.62	0.06	-0.11	0.77
Metal	C + NP	-0.24	0.50	-0.56	0.10	0.03	0.93	-0.45	0.19
Foil	C + NP	0.51	0.13	-0.01	0.99	0.35	0.32	-0.05	0.89
Red plastic	C + NP	0.39	0.26	-0.08	0.83	0.37	0.30	**0.71**	**0.02**
Black Plastic	C + NP	0.31	0.38	0.34	0.33	0.31	0.39	0.09	0.80
Shells	C + NP	0.10	0.80	0.22	0.54	0.33	0.35	**0.78**	**<0.01**

Table 3.5. Correlations between numbers of common decorations (N = 15) and measures of rainfall across the study period (ten years, 1998-2000, 2002-2003, 2007-2011). Categories: C = common, P = perishable, NP = non-perishable. Significant correlations (*p<0.05*) prior to correction for multiple corrections are shown in bold. Coefficients of variation indicate variability in decoration numbers between males; positive correlations indicate that higher rainfall leads to a greater difference between decorations on bowers between males, whereas negative correlations indicate that lower rainfall levels leads to a greater disparity in numbers of decorations displayed between males.

3.3.2. Variation in decorations at the individual level

3.3.2.1. Individual bower consistency within seasons

Within seasons, we detected high consistency in the numbers of decorations displayed at individual bowers across all four categories of decorations considered (Table 3.6). It was extremely rare for bower ownership to change within a season, but in the few cases where ownership did change we found no significant changes in their decoration similarities within a season (2010: mean(randomised) similarity = 1.60(1.59), N = 2, *p* = 0.50 2011: mean(randomised) similarity = 1.51(1.49), N = 3, *p* = 0.55).

Decoration Measure	**2009** (N = 25)	**2010** (N = 47)	**2011** (N = 38)
All decorations	1.19 (1.56)	1.34 (1.60)	1.14 (1.49)
Common decorations	1.51 (1.81)	0.49 (0.76)	0.60 (0.87)
Perishable decorations	0.78 (0.83)	0.95 (1.06)	0.79 (0.84)
Non-perishable decorations	0.81 (1.25)	0.82 (1.10)	0.73 (1.16)

Table 3.6. Within season decoration consistency scores for the four different types of decoration measurements. Mean similarity scores were compared with randomised mean similarity scores across all bowers (randomised shown in brackets). All $P < 0.001$.

3.3.2.2. Individual bower consistency between seasons

We detected high individual consistency in the use of common and non-perishable decorations at bowers, regardless of ownership, when measured across seasons (common: mean(randomised) similarity = 0.56(0.64), N = 54, $P < 0.001$, non-perishable: 0.85(0.90), N = 54, $P = 0.032$). However, bowers were not more similar to themselves than expected by chance when we considered all decorations (mean(randomised) similarity = 1.31(1.35), N = 54, $P = 0.08$) or perishable decorations (mean(randomised) similarity = 0.90(0.91), N = 54, $P = 0.45$).

3.3.2.3. Owner consistency between seasons

When considering only bowers where the owner remained the same across consecutive seasons, decorations on the bower were highly consistent in all decorations (mean(randomised) similarity = 1.21(1.36), N =59, $P < 0.001$), common decorations (mean(randomised) similarity = 0.48(0.65), N=59, $P < 0.001$) and non-perishable decorations (mean(randomised) similarity = 0.73(0.90), N = 59, $P < 0.001$). However, bower owners were not consistent in their exhibition of perishable decorations across seasons (mean(randomised) similarity = 0.87(0.91), N =59, $P =0.11$).

3.3.3. Consistency and length of bower tenure

Male consistency scores did not correlate with measures of time a male had held tenure at his bower (r_s = -0.16, N = 46, P = 0.30).

3.3.4. Consistency and male mating success

Mean consistency scores for individual males showed no correlation with mating success scores in the three seasons analysed (**2009:** r_s = 0.10, N = 19, P = 0.68, **2010:** r_s = 0.18, N = 25, P = 0.39, **2011:** r_s = -0.19, N = 20, P = 0.41), nor when scores across these seasons were averaged (r_s = 0.35, N = 14, P = 0.11). When we accounted for differences in male mating success and consistency across seasons we found no relationship between these two factors (LMM: $F_{1,20}$ = 0.14, P = 0.24).

DISCUSSION

The decorations displayed on a male spotted bowerbird's bower showed remarkable consistency across the levels and time-scales measured, considering the ample opportunity that an extended trait such as this has to be disrupted by ecological or social factors, or improved as males get older or become more experienced. At the population level, mean numbers of non-perishable decorations were highly consistent, both within and between seasons. As predicted, perishable decorations were the least consistent category both within and between seasons, although fluctuations in numbers of these were not always linear or related to rainfall. There were positive relationships between rainfall measures and mean numbers of many decorations displayed across all bowers, although these effects were strongest during a drought year and essentially lost in seasons when rainfall was at or above average levels. At the individual level across repeated measures of an individual's display, bowers were highly consistent in all decoration categories within a season, and remained consistent between seasons in their display of common and non-perishable decorations, regardless of bower ownership. This was not just a product of the bower's location and supply of decorations in the local area, but was dependent on preference/choice behaviour by the owner, because a change in ownership between seasons reduced consistency in all except non-perishable decorations. Despite the high

levels of individual consistency exhibited, it appeared unlikely that such consistency provided females with reliable information about a male's bower-owning tenure, and trait consistency did not appear to be a significant factor in determining male mating success.

Sexual signals are often predicted to be condition dependent (Andersson 1986; Cotton et al. 2006), and the size of specific sexual traits can vary with environmental factors such as rainfall (e.g. Cockburn 2008). If the availability and use of perishable decorations fluctuate and correlate with rainfall measures, we may expect the relative abundance of them on bowers to provide females with information regarding relative male quality. In 2009, a particularly dry year, correlations between perishable decorations and rainfall were strongest, perhaps reflecting the limitations all males faced in obtaining these from the environment. However, under circumstances where particular decorations become difficult to obtain, we might expect these to vary the most between males and provide females with the greatest discriminatory power when choosing a mate (Reid and Weatherhead 1990). We found few positive relationships between the coefficient of variation in many perishable decorations and rainfall, suggesting that rainfall levels did not lead to a greater difference in the numbers of these decorations displayed between males. This may explain the observation that male spotted bowerbirds do not select particularly rare or costly decorations, such as perishable objects whose abundance/availability depends on rainfall (Madden and Balmford 2004), and females may not always select for perishable decorations, or decorations which show the greatest variation between males (Dingle et al. *in prep*). Whilst environmental factors such as rainfall impact decoration availability, the wide variation between males in their use of all decoration types indicates that factors other than these environmental limitations may better explain their use on bowers, such as visual appearance, or value as an indicator of social status. Nonetheless, the highest levels of inconsistency were found in perishable decorations, which, in this species, have been good predictors of female choice (Madden 2003b), and may therefore reflect some aspect of the increased costs associated with their acquisition and replenishment.

We therefore asked whether individual males show consistency in their use of decorations, which may indicate individual preferences or limitations rather than population-wide limits. Our results suggest that whilst use of bower decorations varies

widely between males, individual male owners appear to maintain consistent displays even when opportunities to improve or increase them are available. We found little evidence of numbers of decorations increasing linearly over time, suggesting that although males may collect or steal decorations, or inherit them from previous owners, overall numbers of decorations were stable. These results correspond with previous observational and experimental evidence in bowerbirds; male satin bowerbirds showed strong correlations between seasons in numbers of some types of decoration, particularly man-made, non-perishable objects (Borgia 1993). Short term manipulations of bowers of several other species have shown that males return their decorations to pre-manipulation levels and positions (Diamond 1986; Madden 2002; Kelley and Endler 2012). Sexually selected traits have also been shown to be individually consistent in non-bowerbird species; for example, the courtship hisses of Madagascan hissing cockroaches, *Gromphadorhina portentosa,* were shown to be repeatable in character across one day (Clark and Moore 1995), and in two species of *Drosophila* (*D. Montana* and *D. littoralis*) sexually selected pulse characters were highly repeatable across two seasons (Hoikkala and Isoherranen 1997). In another extended phenotypic trait, the stone carrying capacity in black wheatears, *Oenanthe leucura*, showed high repeatability within and between seasons, implying strong and consistent differences between individuals (Moreno et al. 1994).

Intra-individual consistency in use of bower decorations may be a product of the aesthetic preferences of bower owners, which differ from those of other males in the population. Diamond (1986) dismissed claims that bower decoration decisions may be 'automatic' due to observations of male Vogelkop bowerbirds, *Amblyornis inornata*, repeatedly 'trialling' (placing decorations on the bower in several different positions) and moving decorations before settling on a final location; behaviour we also observed in our species (unpublished data). Males appear to be able to respond flexibly to changing situations with regards to bower properties; in response to decorations being experimentally removed from bowers, male satin bowerbirds increased bower construction and avenue painting behaviours, suggesting that males can adjust their preferences and respond to changes in the quality of their display (Bravery and Goldizen 2007). Satin males also engaged in 'templating' behaviours when placing sticks in the walls of their bower avenues, which has been described as a behavioural tool males may use to help ensure

symmetry between walls (Keagy et al. 2012). Such evidence seems to suggest a role for individual preference and attention to aesthetic properties, and may help explain why individual males show consistency in the bowers they create. Kelley and Endler (2012) found that individual male great bowerbirds consistently align their decorations according to a particular individual forced perspective gradient, and favour this consistency over experimental enhancement. They suggested that consistent differences may be due to an individual's ability or tendency for them, although their study makes no attempt to separate these two differing explanations.

Alternatively, consistency may arise from physical, cognitive or social constraints, particular to each male, such that decoration displays function to provide females with an honest indicator of a male's quality. Males may be physically restricted in their ability to display decorations by the trade-off in time and energy required to acquire them against the need to forage. Cognitive constraints may cause variation in an individual's ability to search for, memorise, transport and arrange decorations, or to learn from previous experiences; evidence from another aspect of behaviour, vocal mimicry, appears to support the notion that bower owners are repeatable in this learned behaviour and may not improve over time (Kelley and Healy 2010). Whilst it is feasible that the steepest learning curves occur during maturation, when males are known to build and attend 'practice' bowers (Vellenga 1986, Collis and Borgia 1993, Lenz 1994, Maxwell 2004), it seems unlikely that learning in all aspects of male display halts and competence is fixed at the point of ownership; for example, Loffredo and Borgia (1986) suggest that vocal mimicry in satin bowerbirds is not fixed, but increases in quality over time providing an indicator of male age. Social constraints may also play an important role in determining a male's choice for bower decorations. Males may have differing levels or types of experience prior to bower ownership, for example in differing exposure to objects in the environment, social interactions with other individuals or levels of attendance or observation at other males' bowers (Collis and Borgia 1992), influences that may persist throughout their tenure. Another social influence on bower decorations is the impact of marauding by rival males, which can affect the quality of the bower (Borgia and Mueller 1992, Lenz 1994, Madden et al. 2004). In a previous study using the same population at Taunton, Madden (2002) found that males whose bowers were artificially enhanced with *Solanum* fruits, a good predictor of

mating success, suffered increased levels of marauding by neighbours, and owners actively removed these extra decorations. It seems plausible that consistency in decoration numbers may be regulated by such a trade-off mechanism, which prevents males displaying excessive numbers of decorations. If this is the case, we might expect that as neighbour's change, so too does an individual's relative social ranking and consequently perhaps the level of decorations that they can display. It was not possible to test this prediction formally with our current dataset due to the long tenure and slow turn-over of bower owners in the population.

Finally, consistency in display may simply be due to the local availability of decorations around a bower location. Bowers in well-established locations were surrounded by higher numbers of *Solanum* bushes (Madden et al. 2012), and may therefore enjoy an adequate enough supply of these decorations to maintain a consistent rate of display. In order to fully separate the relative influence of male preference/competence versus bower location we would need to ask whether individual males maintained their decoration selections when the location of the bower changed. Unfortunately, cases of males switching bower locations are not known in our population, making this aspect difficult to analyse. However, decoration consistency was higher when we restricted our analyses to only those bowers were owners remained constant across seasons, in all except perishable decorations. This suggests that individual owner preference for decorations may be more important than simply their availability in the local environment. However, the effect of male preference may be confounded by the occurrence of decoration inheritance, with new owners at bowers encountering collections of non-perishable items that were collected by the previous owner; for example, great bowerbirds are known to retain non-perishable decorations across seasons and to inherit them from previous owners (Doerr 2009b, Doerr 2012). A new owner can incorporate these inherited decorations into his display at low cost, potentially leading to positive relationships in decoration use between consecutive owners at the same site. This may explain why we observed between-season consistency in non-perishable objects at individual bowers regardless of whether ownership had changed or not. Within season ownership changes were rare (N = 5), but we tentatively report that bowers may have remained consistent across these changes due to the rare phenomenon of different males being able to directly inherit another male's trait. Experimental

manipulation of decoration availability would help to disentangle the effects of location versus male, and provide more conclusive evidence regarding this question.

Courtship behaviours are one of the most repeatable behaviours across species, often reflecting fixed aspects of male fitness (Bell et al. 2009). However, mate preference is one of the least repeatable (Bell et al. 2009) and therefore in systems where patterns of female choice are variable, consistency in male display may be detrimental to a males mating success. The decorations that best predict male mating success in our population of spotted bowerbirds appear to change over time (Dingle et al. *in prep*), therefore consistency in display may fail to increase male attractiveness over prolonged periods of time. Consistency in display may also indicate a general inflexibility in behaviour, which may be disadvantageous for male bowerbirds. For example, female satin bowerbirds show preferences towards males that perform intensive courtship displays, but are deterred by displays that are too intense (Patricelli et al. 2006a). Thus males appear to adjust their displays according to specific female behavioural responses, suggesting that sexual selection may favour individuals that are able to rapidly adapt their behaviour.

We found no evidence to suggest that males displaying consistently enjoyed higher mating success. This may not be surprising, as males that constantly display low quality bowers would achieve the same high consistency scores as males that repeatedly produce high quality bowers, yet remain unattractive to females. Nor did we find that decoration consistency provided females with reliable information regarding male bower tenure, a proxy for male age (Borgia 1993, Coleman et al. 2004, Frith and Frith 2004). A more experienced male may be expected to become more proficient at acquiring decorations, thus achieve inconsistency in display as decorations accumulate on the bower or change in relative numbers over time. Other studies have found that sexual signals can develop over time and are not fixed in a consistent pattern; for example, song learning can improve with, and indicate, male age (de Kort et al. 2009). Different elements of bowerbird display have previously been shown to accurately reflect male age, such as plumage (Vellenga 1980) and mimetic ability (Loffrefo and Borgia 1986), therefore decorations may function as signals of other aspects of male display, such as physical condition required for their acquisition or male social status. Condition dependent models of sexual selection predict that traits may

have evolved plasticity in order to honestly signal information about changes in male condition (Hamilton and Zuk 1982, Kodric -Brown and Brown 1984). The consistent display of decorations over multiple timescales despite the many pressures selecting against consistency suggests there should be an adaptive value to males; however, we were not able to find evidence of these benefits in terms of male mating success. From the female's perspective, consistency may reduce costs for females who can gain an accurate, long term representation of a bower's decoration properties from a single visit. This may allow females to restrict re-visits to a small sub sample of preferred males, as has been found in satin bowerbirds (Uy et al. 2001). Females may be paying attention to different aspects of a male's multicomponent display at different stages in her life history (Coleman et al. 2004), or may interact with males away from the bower (e.g. in the canopy above, Lenz 1994), thus consistency in decoration numbers may reduce sampling effort for this component over repeated visits.

Whilst male spotted bowerbirds exhibited a general consistency in their use of decorations, these results highlight the importance of quantifying within-individual variation before assertions can be made about the strength of selection acting on a trait (Griffith and Sheldon 2001). Measures of trait expression taken at a single point in time may not always reflect how that trait is expressed over time, or at points in time when females may be making mate choice decisions (Cockburn et al. 2008). Additionally, our analysis was restricted to decoration counts, and whilst this measure has a strong relationship with female preference in several bowerbird species (e.g. Borgia 1985b, Lenz 1994, Madden 2003b, Frith and Frith 2004), decorations may function in other ways to increase female preference for that male, for example in producing the forced perspective gradients seen in great bowerbird displays (Kelley and Endler 2012), or serving as a conspicuous signal of bower location (Borgia 1995). It is also possible that decorations form one part of a multiple message provided by bower assessment, or interact with other bower or owner components to affect male attractiveness (Möller and Pomiankowski 1993, Patricelli et al. 2003). Whilst we found no evidence for consistency being an attractive quality in itself, it may be that maintaining a consistent suite of decorations is important to males as part of a multi-component display signal.

Bower owning male spotted bowerbirds maintained a relatively consistent sexual display element, despite numerous external factors, particularly rainfall, which could introduce variation. The decorations displayed on male bowers may have been partly influenced by their availability, but only a small number of specific, perishable objects showed population-level fluctuations, suggesting that display is not simply a product of object accessibility but also depends on individual male preferences. This level of consistency is surprising for a long-lived species, which is expected to have a significant learned basis for sexual display and multiple opportunities for disruption and/or flexibility. Our results suggest that bower decoration is fixed in males from early in their bower ownership, which may prove beneficial for female mate searching tactics but also be costly for males by restricting their ability to respond to changing female preferences. Alternatively, consistency in display may be costly for females as it prohibits potential informative variation that may reveal, for example, male age or changes in male condition over time. Finally, our findings for one species of bowerbird may not reflect the behaviour of males in other populations or species, and only extensive monitoring of bower displays over long-term studies can reveal whether other bowerbird species actively maintain a consistent signal. Such information would be important when developing theories for explaining the evolution of these extreme elaborate male traits.

Chapter Four

The physical costs of male attendance at their bowers

ABSTRACT

Elaborate male displays may provide females with honest information regarding male quality due to the handicaps and condition dependence imposed by them. Males vary in their ability to cope with such handicaps, and traits that rely on the acquisition of resources from the environment may be particularly susceptible to fluctuation. Male bowerbirds, Ptilonorhynchidae*,* construct intricate displays which are decorated with numerous objects obtained from the local environment. These displays, known as bowers, are extended from the body of the male and require continuous maintenance throughout the breeding season. We asked whether bowers were costly traits for male bower owners, imposing constraints via the amount of time that males spend attending and maintaining them. Costs of attendance may manifest through a reduction in foraging opportunities, or a loss of time for locating and collecting bower components, such as decorations or structural material, and may therefore be susceptible to environmental fluctuation. Data collected in a wild population of spotted bowerbirds, *P. maculatus*, over three consecutive breeding seasons showed that bower attendance levels were significantly lower in a season of drought compared to two subsequent seasons with average rainfall. During this drought period, experimental provisioning increased both bower attendance rates and the numbers of decorations displayed on bowers, suggesting that these activities were metabolically restricted. However, during seasons of average rainfall attendance rates were increased, but inter-individual variation in bower attendance did not relate to the number of edible plant species near their bower, suggesting that factors other than food availability were producing this variation. Differences in bower attendance rates were not expressed through variation in male display characteristics; higher attendance did not relate to larger or more symmetrical bowers, or bowers with higher numbers of decorations. Furthermore, contrary to some theoretical predictions, spending more time in attendance at the bower did not decrease the rate of marauding suffered at that bower. Finally, males that spent longer attending their bowers did not gain higher mating success. Our results suggest that bowers only impose significant metabolic costs on males during periods of acute environmental stress. Attending the bower for longer periods of time appears to bring no adaptive benefits to males, but may instead be the least costly option for males that are not metabolically limited.

4.1. INTRODUCTION

Elaborate male traits may act as physical handicaps, providing choosy females with honest information regarding male quality, although the exact mechanisms through which this evolves has been subject to debate (e.g. Zahavi 1975, Lande 1981, Kirkpatrick 1991, Grafen 1990a; b). A male's ability to pay the costs associated with an exaggerated display may be condition dependent, and associated with both genetic and environmental components (Grafen 1990a; b, Cotton et al. 2004, Tomkins et al. 2004). Males of higher genetic quality may be better able to cope with fluctuating environmental conditions, and pay less per unit cost than higher quality males (Grose 2011). When the elaborate trait is extended from the physical body of the male, males not only rely on the acquisition of metabolic resources from the environment, but also on acquiring materials essential for constructing their display (Schaedelin and Taborsky 2009). Such traits may show increased sensitivity to environmental fluctuation, and the costs associated with material acquisition may add a further costly dimension to the display (Bussier et al. 2008, Cockburn et al. 2008). Therefore, the ability of a male to cope with the physical cost of display, as reflected in the expression of an extended phenotypic trait, may be particularly useful for female assessment of male quality.

Male bowerbirds, Ptilonorhynchidae, exhibit highly elaborate sexually selected traits, which are extended from the body of the male and expressed through the construction of a bower. Bowers are intricate structures consisting of a display court that is decorated with a wide range of objects obtained from their environment (Marshall 1954, Borgia 1985, Diamond 1987, Frith and Frith 2004). Choosy females select males based on multiple features of the male and his bower, including numbers and type of decorations and the quality of bower construction (e.g. Borgia 1985b, Borgia and Mueller 1992, Uy and Borgia 2000, Madden 2003b, Robson et al. 2005). As extended phenotypic traits, the bower requires ongoing investment during the breeding season to maintain its quality, which includes both bower structural maintenance and decoration replenishment (Borgia 1993, Schaedelin and Taborsky 2009). Species vary in the average proportion of time they spend attending their bowers; male satin, *P. violaceus*, and toothbilled, *Scenopoeetes dentirostris*, bowerbirds spend > 60% of daylight hours in attendance (Donaghey 1981, Frith and Frith 2004), compared to 54% for male MacGregor's bowerbird, *Amblyomis macgregoriae*,

(Pruett -Jones and Pruett-Jones 1982) and just 3.2% for male Regent bowerbirds, *Sericulus chrysocephalus,* (Lenz 1994). Unattended bowers quickly fall into a state of disrepair, and outside of the breeding season bowers are generally not maintained (Frith and Frith 2004, pers. obs.), suggesting that these activities impose certain costs on male owners.

Bowers may act as indicators of a male's ability to cope with the physical demands of bower ownership, providing females with a method of assessing a male's ability to collect materials and cope with fluctuating environmental conditions. High absolute costs of display are often predicted in species exhibiting elaborate traits, which may, for example, increase their conspicuousness, reduce mobility, increase the risk of predation (e.g. the peacock's train, Petrie et al. 1996), or lead to a reduction in male condition (e.g. male red deer losing possession of female harems after one or two seasons due to high energy expenditure associated with the rutting season; Clutton-Brock and Albon 1979). Bowers may be expected to impose high absolute costs, such that ownership ultimately reduces the lifespan or condition of the male over time. However, in a direct test of two models predicting high absolute costs of display (Zahavi's 1975, handicap model and Lande's 1981 quantitative genetic model), Borgia (1993, 1996) suggests that bower ownership does not come at an extremely high cost for males (also see Sheldon 1996), as no increase in mortality or predation, reduction in body condition or deterioration in bower quality over time was found.

One way that other costs of bower ownership accrue to males is via the acquisition and maintenance of decorations or other bower materials that require location and transportation. In some species, decorations types are rare in the environment, for example, the blue feathers and flowers collected by satin bowerbirds, *P. violaceus* (Borgia et al. 1987) and the bird-of-paradise feathers preferred by Archbold's bowerbirds, *Archiboldia papuensis* (Frith and Frith 2004). In contrast, male spotted, *P. maculatus*, and Vogelkop, *Amblyornis inornatus*, bowerbirds do not collect rare or particularly costly decorations (Diamond 1988, Madden and Balmford 2004). Male great bowerbirds, *P. nuchalis,* re-use and inherit decorations across seasons, suggesting direct costs are associated with sourcing them from the environment (Doerr 2009b).

An alternative way in which bowers impose costs on their owners is via the demand for males to attend their bowers for considerable periods of time during daylight hours. Attending a bower may be costly in terms of reduced foraging opportunities or increased predation risk from remaining in a predictable ground location for long periods of time. It has been suggested that the frugivorous nature of the bowerbird diet enables them to rapidly obtain a rich food supply from clustered fruit, and males can therefore afford to devote time to bower maintenance (Diamond 1986b, Frith and Frith 2004). Despite this, some species also appear to mitigate foraging costs; male MacGregor's bowerbirds cache fruit near the bower during the breeding season, a behaviour perhaps allowing them to increase bower attendance time (Pruett-Jones and Pruett-Jones 1985). Spotted bowerbirds may (unintentionally) reduce foraging costs by 'cultivating' fruiting plants near their bowers; this has been shown for a common fruit decoration, *Solanum spp* (Madden et al. 2012), and may be true of edible species too. The demand for males to attend their bowers for high proportions of the day could also be the result of social pressures. Male bowerbirds engage in marauding, a competitive behaviour in which rival bower owners destroy and steal from other males' bowers, thus lowering the quality of rival displays (Borgia 1985b, Borgia and Gore 1986, Lenz 1994, Hunter and Dwyer 1997, Madden 2004a; b, Doerr 2009a). This competitive activity usually only occurs when male owners are away from their bowers, and models of optimal marauding behaviour suggest that leaving the bower unattended is costly as it increases the risk of attack (Pruett-Jones and Pruett-Jones 1994, Morrell and Kokko 2004, Pruett-Jones and Heifetz 2012). Thus, quantifying the physical costs of bower attendance may allow us to better inform models regarding the evolution of this elaborate male trait.

We asked whether bower attendance in the male spotted bowerbird was a costly activity by observing how attendance rates varied across the population with changing environmental conditions. We collected data from a wild population over three consecutive breeding seasons during which there were large fluctuations in rainfall. Spotted bowerbirds are atypical from many other bowerbird species in that they inhabit semi-arid areas with highly inconsistent rainfall and ephemeral fruit supplies (Miles and Madden 2002, Frith and Frith 2004). Males build avenue bowers from sticks, grass and other plant material, and decorate these with perishable and non-perishable objects (Borgia 1985, Loffredo and

Borgia 1996, Diamond 1987, Borgia and Collis 1990, Madden 2003a; b, Frith and Frith 2004). In contrast with many other species, bowers are widely spaced (approximately 1km; Miles and Madden 2002, compared with satins approx. 0.1km, MacGregor's approx. 0.7km, greats 0.4km; Borgia 1985b, Pruett-Jones and Pruett-Jones 1982 and Doerr 2009a respectively). To investigate whether attending the bower imposes physical costs on male owners, we asked whether population-level attendance rates were affected by seasonal differences in rainfall, a key environmental determinant likely to impact availability of food supplies (edible fruit). If bower attendance is costly in terms of reduced foraging opportunities, we expected males to decrease their attendance rates when rainfall was low, as access to metabolic resources would be limited and require higher foraging costs. Of course, this relationship may not be causal, with males not attending bowers when it is dry because females too are less likely to visit, due to metabolic constraints. To exclude this possibility, we artificially provisioned an experimental group of males during a drought season to explore whether reducing foraging costs for males led to an increase in bower attendance rates.

We then investigated inter-individual variation in male bower attendance rates, and asked whether males with greater access to natural food resources near their bowers had higher attendance rates. Male MacGregor's bowerbirds cache food items near (within 13m) of their bowers, suggesting that males with increased resources nearby may be better able to attend their bowers for longer time periods (Pruett-Jones and Pruett-Jones 1985). We conducted vegetation surveys to quantify the number and diversity of edible fruiting plants within 50m of the bower, and expected that both higher numbers and species diversity (representing a spread of fruiting species likely to be ripe throughout the season) would increase the time available for males to attend their bowers. We also explored whether increased food availability correlated with an increased number of decorations on the bower, as males with greater access to metabolic resources may be able to spend more time acquiring decorations. If a male's ability to spend time attending his bower is limited by his physical condition or access to food supplies, we expected that male variation in attendance rates would be evident in features of the bower. We asked whether males with increased attendance rates had (i) bowers with higher numbers of decorations (which can predict female choice, e.g. Borgia 1985b, 1995, Uy and Borgia 2000, Madden 2003), (ii) higher numbers of just perishable decorations (which may better reflect physical costs of

frequent replenishment), and (iii) larger and/or more symmetrical avenue structures (as preferred by females, e.g. Borgia 1985a, Robson et al. 2005, Keagy et al. 2011). Finally, we asked whether increased bower attendance rates would predict lower levels of marauding and/or higher individual male mating success. Models of optimum marauding behaviour suggest that males can minimise the risk of marauding through bower defence (e.g. Pruett-Jones and Heifetz 2012), and we expected that males with higher attendance rates would have lower rates of marauding. Likewise, males that attend the bower for longer may be more likely to intercept visiting females, thus potentially increasing the chance of displaying and gaining copulations.

4.2. METHODS

4.2.1. General methods

Data were collected from a population of free-living, individually marked spotted bowerbirds in Taunton National Park (Scientific) in central Queensland, Australia (see Chapter 2.5 for a detailed site description). Bowers were monitored over three consecutive breeding seasons: July-January 2009, July 2010 - January 2011 and August 2011 – February 2012. We refer to each season by the year in which it began. At the beginning of each season bowers were located and owners identified. Not all bowers were active and/or monitored in each season.

4.2.2. Measuring individual behaviour at bowers

Bowers were monitored using remote, motion-sensing cameras (StealthCam i590), that were *in situ* for the duration of each breeding season. Sixteen bowers were monitored in 2009, 14 in 2010 and 17 in 2011 (Table 2.2). Detailed behavioural data were coded from camera data (Table 2.1) and we used these to construct activity budgets for each male at his bower. We calculated bower attendance rates by summing the total amount of time a male owner spent at his bower, regardless of the specific behaviour he was engaged in. Bower attendance rates therefore include bower maintenance activities and displaying to other individuals. Bower maintenance rates were calculated as the total time a male owner spent engaged in specific activities that contributed to bower improvement, such as structural

enhancement or decoration arrangement (see Chapter 2.7.5). To account for the differences in season length and between camera recording hours, which varied due to the date of deployment and rare camera failures, all behaviours at the bower were calculated as rates per camera recording hours. We used bower attendance rates as our measure of the physical cost of remaining at the bower.

4.2.3. Do mean bower attendance rates relate to rainfall?

To ask how male bower attendance rates were impacted by fluctuating environmental conditions, we compared seasonal and monthly attendance with rainfall measures. Rainfall data were recorded at both Taunton National Park and Dingo Post Office weather stations (see Chapter 2.6). Seasonal rainfall was calculated as the total rainfall recorded from July-January each year. To test the relationship between mean seasonal attendance rates and seasonal rainfall we used ANOVA, with Tukey post hoc tests. Due to the low numbers of months in each breeding season, monthly bower attendance rates were compared with monthly rainfall using Spearman's rank correlations (2009 and 2010: N = 5 months, 2011: N = 6 months).

4.2.4. Does artificially provisioning males increase bower attendance behaviours?

We tested whether male attendance at the bower could be influenced by foraging costs by artificially provisioning an experimental group of males during a season when natural food resources were diminished. During 2009 central Queensland experienced a severe drought (Bureau of Meteorology 2009), which provided us with an opportunity to manipulate food availability. Male attendance during this period was lower than average (Table 4.2). Experimental provisioning was carried out over a ten day period in September/October 2009. Eighteen males were randomly assigned to one of two experimental groups, each of nine males. One group was fed with green grapes (genus *Vitis*), whilst the other group acted as a control and experienced no artificial provisioning. Both groups had small plastic trays fixed to the ground at the edge of their display court the day before feeding began. For each of ten consecutive days the fed group received ten green grapes, halved and presented on the tray. This equates to approximately 20g of food, meaning provisioning provided approximately 14% of average body mass per day (Frith and

Frith 2004). The unfed males received bower visits without provisioning. Provisioning took place between 05:15 and 09:30, and any leftover grapes from the previous day were removed.

We recorded bower attendance and maintenance rates at all eighteen bowers. One male from the fed group failed to attend his bower during the experimental period and was subsequently removed from the analyses. We also recorded the number of visitors each bower received and the amount of time owners spent displaying to them. Visitors were defined as any conspecific that appeared at the bower that was not identified as the owner, and included both banded male and female birds, and unbanded individuals. We compared mean bower attendance time, the number of visitors received and the time males engaged in display towards those visitors between fed and unfed males using Mann Whitney tests. Ideally, this experiment would have been reversed to provide a more powerful analysis of the effect of provisioning treatments. Unfortunately, as the period of drought progressed, many males abandoned their bowers, reducing the opportunity to effectively expose them to extra food resources.

4.2.5. Does artificially provisioning males improve bower quality?

We compared measures of bower decoration and structural properties between males that had been artificially provisioned and the control group to ask whether provisioning allowed males to increase the quality of their bower. Measures were taken the day before and after the ten day provisioning period. Total numbers of decorations were counted. Seven bower avenue structural measures were taken; wall length, height and thickness, avenue width, wall density and symmetry, and visibility through the wall. Wall density was measured by inserting a 5cm wide metal clip through a central section of each wall and counting the number of grass stems contained within it. Wall symmetry scores were obtained by applying the measures of avenue length, height and thickness for both the left (L) and right (R) walls to the equation: symmetry = $(L-R)/(L+R)$. Scores for each measure were averaged to give a single overall score. Scores closer to 1 indicate more symmetrical structures. Visibility through the wall indicated the solidity of thatch, and was measured using a 10x10cm card with 50 dots placed in a grid pattern at 1cm intervals. The card was

held against the inside of the wall whilst an observer counted how many dots were visible from the outside. To compare bower decoration numbers and measures of structural properties before and after the provisioning period we used paired t-tests and repeated measures ANOVAs.

4.2.6. Do increased local food supplies increase individual bower attendance rates?

To ask whether males with greater food supplies near their owners had higher bower attendance rates and/or decoration numbers we conducted 50m radius vegetation transects at 17 bowers during November-December 2011. A list of all known species previously described as providing a food source for spotted bowerbirds was obtained from Frith and Frith (2004, pp439-449, Table 4.1). Not all listed species were present at Taunton National Park, and not all that were present in the Park were recorded within our vegetation transects. All plants that were within a 5m radius from the bower, including if relevant the plant under which the bower was constructed, were counted. Then, eight belt transects were conducted starting from the edge of the 5m bower radius and running for a further 45m along each of the eight compass points away from the bower. Plants rooted within 2m of either side of the transect line were counted. We used the total count of food source plants as our measure of local food supply and considered each species of plant to have an equal value as a food resource across all bowers. We disregarded plants that were <15cm in diameter as these were unlikely to provide a significant food source. To calculate species diversity scores at each bower we used the Simpson's Diversity Index:

$$1\text{-}D = \frac{\sum n(n-1)}{N(N-1)}$$

where n = the number of organisms of a particular species and N = the total number of organisms of all species (Simpson 1949). This gives a measure of the food species richness and evenness with higher diversity scores indicating bowers with a greater diversity of food source species in their vicinity. Due to the low sample sizes Spearman's rank correlations were used to look for relationships between the total number and the diversity of food source plants with bower attendance rates and total bower decoration numbers.

Species name	Common Name	Recorded at Taunton NP	Recorded in vegetation transect
Schinus molle	Peruvian pepper	no	no
Carissa lanceolata	Currant bush	yes	no
Carissa ovata	Currant bush	yes	yes
Capparis lasiantha	Nepine	no	no
Capparis mitchellii	Native orange	no	no
Atriplex sp	Saltbush	yes	no
Enchylaena tomentosa	Ruby saltbush	yes	yes
Spinacia oleracea	Spinach	no	no
Diospyros humilis	Queensland ebony	yes	no
Erythroxylum spp.	Coca species	no	no
Loranthaceae	Mistletoe	no	no
Melia azedarach	Chinaberry tree	no	no
Acacia spp.	Acacia	yes	yes
Acacia salicina	Sally wattle	yes	yes
Acacia trachycarpa	Minni ritchi	unknown	no
Eremophila deserti	Dogwood	yes	yes
Eremophila mitchellii	False sandalwood	yes	yes
Myoporum deserti	Ellangowan poisonbush	yes	yes
Jasminum lineare	Native jasmine	no	no
Citrus aurantifolia	Key lime	yes	yes
Citrus reticulate	Mandarin orange	no	no
Geijera parviflora	Wilga	yes	yes
Santalum sp	Sandalwood	yes	no
Bracychiton acerifolius	Flame tree	no	no

Table 4.1. Species providing a food source for spotted bowerbirds, taken from Frith and Frith (2004, pp439-449). Records for Taunton National Park were obtained from our own surveys, and records held by Queensland Parks and Wildlife Service.

4.2.7. Does increased bower attendance influence bower properties?

To ask whether variation in male attendance rates impacted bower properties, we took monthly measures of decorations and structure during each of the three breeding seasons. Monthly decorations counts were averaged to give a mean decoration count per bower for each season. We calculated both total decoration numbers and just the number of perishable decorations. Perishable decorations were defined as those that would degrade over time and would require frequent replenishment by the owner. Five structural

measures of the bower avenue were taken; wall length, height and thickness, avenue width and symmetry. Avenue measures were averaged to give a mean value per bower per season. Bower decoration counts and structural measures were compared with bower attendance rates using Spearman's rank correlations.

4.2.8. Does increased bower attendance reduce rates of bower marauding?

We explored whether those males that spent longer periods of time attending their bowers experienced lower rates of bower marauding by rival males. Marauding was an easily recognisable behaviour, defined as individuals other than the owner engaged in vigorous destruction activities and/or stealing decorations (Madden 2003a, and see Table 2.3). The number of marauding events suffered at each bower was summed and calculated as a rate per camera recording hours. To test whether bower attendance predicted marauding in each of the three breeding seasons, we used linear regressions with maraud rate as the dependent variable and bower attendance rates as the predicting factor.

4.2.9. Does increased bower attendance increase male mating success?

Finally, we asked whether the variation in individual male bower attendance had any impact on his mating success. We calculated reproductive skew for each of the three seasons (See Chapter 2.8.2) to ask whether differences in environmental conditions affected the number of males gaining reproductive success. Mating success was calculated as the copulation rate per male (see Chapter 2.8.1). We used linear regressions with male mating success as the dependent variable and bower attendance as the predicting factor for each of the three breeding seasons.

4.3. RESULTS

4.3.1. Do mean bower attendance rates relate to rainfall?

Mean bower attendance rates were lower in a season of low rainfall (2009) compared to 2010 and 2011 when rainfall was at or above average levels ($F_{2,46} = 28.70$, $P < 0.001$, Tukey post hoc tests, 2009:2010 and 2009:2011, $P < 0.001$; Table 4.2). There was no

difference in attendance rates between 2010 and 2011 (Tukey, p = 0.60) despite the uncharacteristically high rainfall levels in 2010 compared to 2011. There was a strong positive correlation in all three seasons between bower attendance rates and maintenance rates (2009: R_s = 0.83, 2010: R_s = 0.97, 2011: R_s = 0.98, all P <0.001), although in 2009 this proportion was significantly lower than in the other seasons ($F_{2,46}$ = 4.60, P = 0.02, Tukey post hoc: 2009:2010, P = 0.02; 2009:2011, P = 0.04; 2010:2011, P = 0.90).

Season	Seasonal rainfall	N	Mean rate of bower attendance ± 1SD	Mean proportion of attendance: maintenance ± 1SD
2009	274.5	16	22.34 ± 10.11	0.68 ± 0.16
2010	1289.5	14	63.34 ± 18.59	0.84 ± 0.08
2011	377.0	17	57.60 ± 18.97	0.81 ± 0.20

Table 4.2. Mean rates of bower attendance and the proportion of total time at the bower that was spent engaged in maintenance behaviours, and seasonal rainfall (July-January, mm) at Taunton National Park. Rates are calculated as hours per camera recording hours *1000. The long term (1998-2011) average seasonal rainfall is 425mm.

Average monthly rates of bower attendance were not related to measures of rainfall in the same or the previous month (Figure 4.1). Following a sudden increase in rainfall towards the end of December 2009 male attendance at bowers showed a notable increase in January. In 2010 and 2011 male bower attendance rates reduced as the season progressed. This corresponded with an increase in monthly rainfall, although any causal relationship cannot be inferred from our dataset.
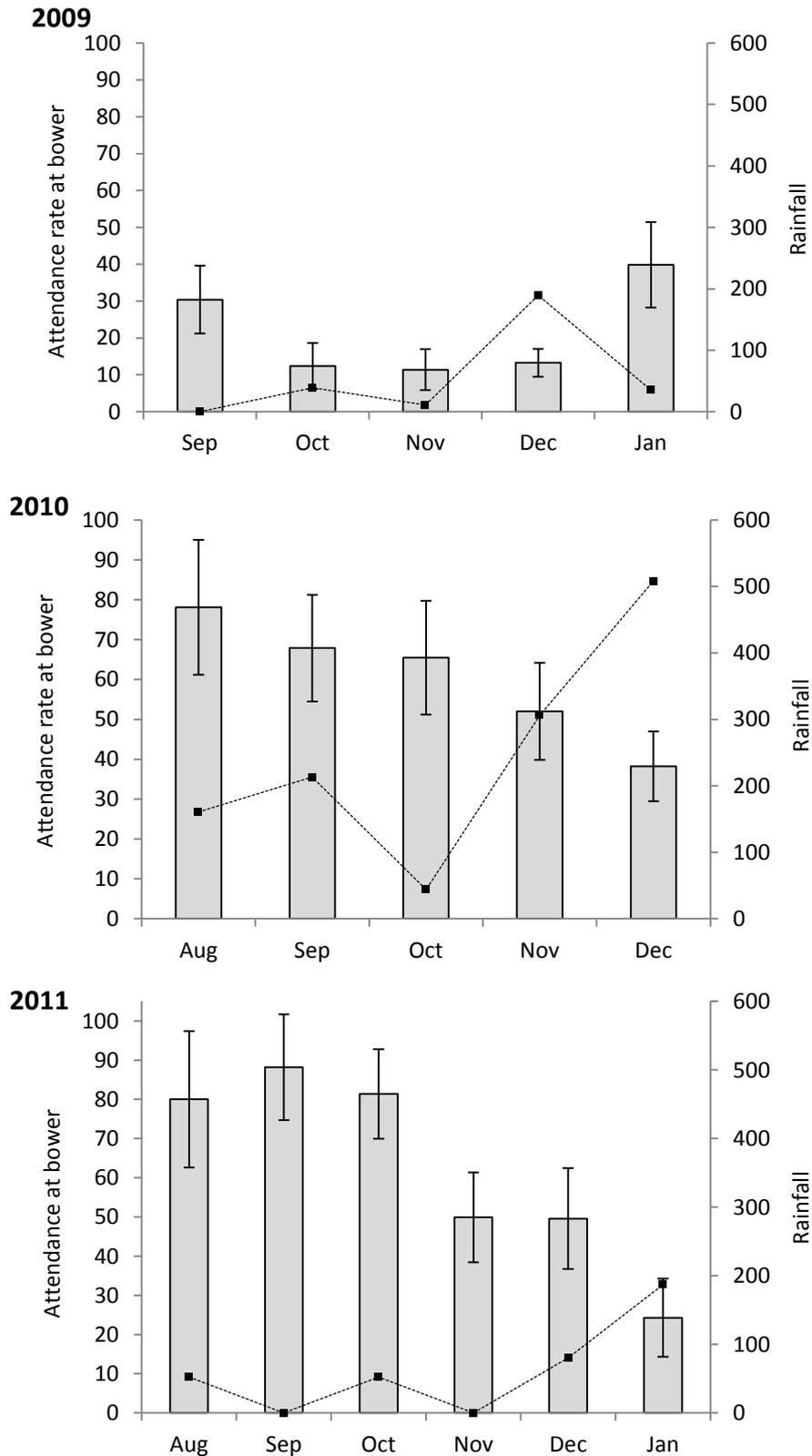
Figure 4.1. Bars show average monthly bower attendance rates with rainfall (mm) indicated by the dashed line. Attendance rates were calculated as hours per camera recording hours *1000. Error bars show one standard deviation.

4.3.2. Does artificially provisioning males increase bower attendance behaviours?

Males provisioned with supplementary food spent more time attending their bowers than the control group (mean attendance rate at bower (SE) fed = 13.64 hours per camera hours *1000(3.00), N = 6, unfed = 1.87(0.97), N = 6; Mann Whitney U = 2.00, P = 0.01). Although fed and unfed groups did not differ significantly in the number of conspecifics visiting their bowers during the provisioning period (Mann Whitney U = 11.00, P = 0.47), fed males spent more time engaged in courtship display behaviour towards their visitors than control males (mean display rate (SE); fed = 11.4 (5.11), unfed = 2.82 (1.45), Mann Whitney U = 2.00, P = 0.02).

4.3.3. Does artificially provisioning males improve bower quality?

Experimental provisioning increased total numbers of decorations at bowers. Prior to the provisioning period, there was no difference in the total numbers of decorations between the two experimental groups (independent samples t-test, t_{13} = -0.276, P = 0.79). Following provisioning, fed males increased the total number of decorations at their bowers (mean; before = 60.50, after = 73.63, N = 8, paired sample t-test, t = -2.60, P = 0.03), whereas unfed males showed no change in decoration number (mean; before = 67.71, after = 64.14, N = 7, t = 0.99, P = 0.36). There was a significant interaction between feeding treatment and time period (repeated measures ANOVA, F = 6.873, P = 0.02, Figure 4.2).
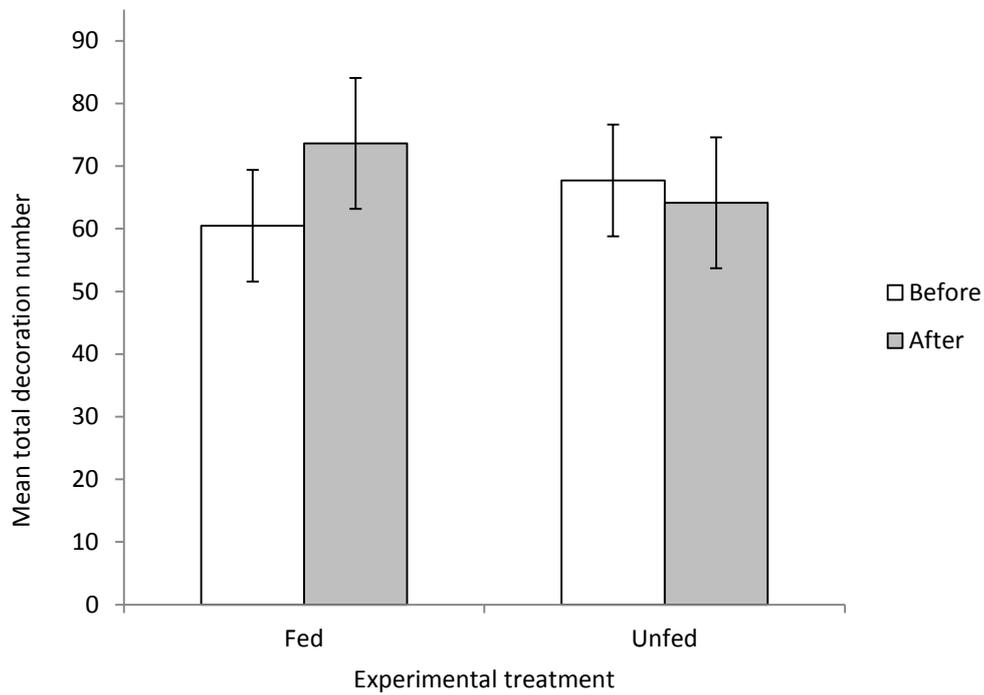
Figure 4.2. Mean total decoration numbers in the two experimental groups before and after the feeding period. Error bars show standard error.

In contrast, provisioning had no impact on bower structural properties. Prior to provisioning, there were no differences in any of the seven structural properties measured between the two experimental groups (Table 4.3). Males in both experimental groups had an increase in the density of wall material after the provisioning period, suggesting that this structural change to bowers was independent of the provisioning treatment.

Structural Property	Prior to provisioning		Fed		Unfed		Interactions	
	t_{13}	P	t_7	P	t_9	P	$F_{1,13}$	P
Avenue length	1.98	0.07	0.76	0.47	0.99	0.36	0.001	0.98
Avenue height	0.12	0.90	-0.75	0.48	-1.16	0.29	0.32	0.58
Avenue width	1.94	0.07	-0.66	0.53	0.20	0.85	0.28	0.61
Wall thickness	1.35	0.20	-0.18	0.86	0.68	0.52	0.52	0.48
Wall density	-0.47	0.65	**-2.72**	**0.03**	**-2.91**	**0.03**	0.31	0.59
Visibility	0.20	0.84	2.18	0.07	-0.18	0.87	2.74	0.12
Symmetry	0.15	0.89	-0.99	0.36	0.81	0.45	1.36	0.27

Table 4.3. Paired t-tests of seven bower structural properties measured before and after provisioning for both fed and unfed groups. Repeated-measures ANOVA indicate interactions between experimental group and each structural property. Statistically significant results prior to correction for multiple tests are shown in bold.

4.3.4. Do increased local food supplies increase individual bower attendance rates?

Males with higher numbers of food plants near their bowers had higher total numbers of decorations on their bowers (r_s = 0.66, N = 17, P = 0.005, Figure 4.3a). The total number of food plants near bowers varied widely between males (mean number of food plants = 156.3, min = 10, max = 561), however, the number of plants near to each bower did not predict male attendance rates ($F_{1,16}$ = 0.00, P = 0.99). Males with a greater diversity of species around their bower spent less time in attendance ($F_{1,16}$ = 9.01, P < 0.01), with species diversity accounting for 37.8% of the variation observed in attendance rates (Figure 4.3b).
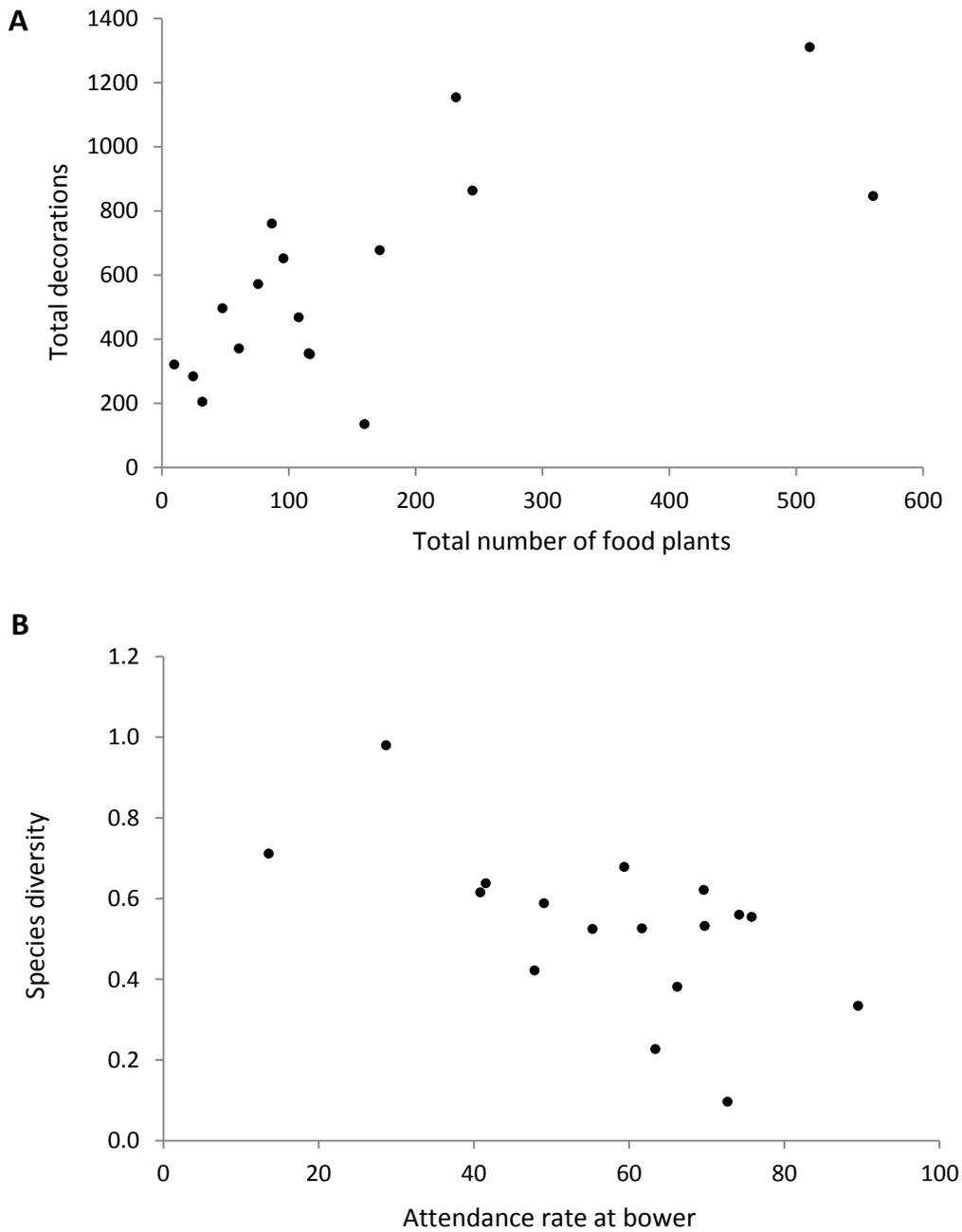
Figure 4.3. For transect counts of food (edible) plants at bowers in 2011, **A**: the relationship between the total number of plants and the total number of decorations at the bower, and **B**: the relationship between male bower attendance rates (calculated as hours per camera recording hours *1000) and edible food plant species diversity.

4.3.5. Does increased bower attendance influence bower properties?

Males that spent less time in attendance at their bowers had higher numbers of perishable decorations, but there was no relationship between attendance time and the total number of decorations displayed on a bower (Table 4.4).

Season	Average total number of decorations					
	All decorations			Perishable decorations		
	R	N	P	R	N	P
2009	-0.38	16	0.14	-0.47	16	0.06
2010	-0.15	14	0.62	-0.48	14	0.08
2011	0.20	17	0.45	-0.15	17	0.57
Fisher's omnibus	**$X^2_4 = 6.49, P < 0.20$**			**$X^2_4 = 11.80, P < 0.03$**		

Table 4.4. Spearman's rank correlations between the rate of bower attendance and (1) the average total number of decorations and (2) the average total number of perishable decorations found at that bower throughout each season. Fisher's omnibus tests were used to combine significance across seasons. Significant results are shown in bold.

Increased attendance rates at bowers had no impact on bowers structural properties; bowers with owners in greater attendance were not larger, wider, taller or thicker, and showed no difference in mean symmetry scores (Table 4.5).

Bower attendance	Avenue length	Avenue width	Avenue height	Wall thickness	Average Symmetry
2009 (N = 16)	R = -0.18, P = 0.51	R = 0.17, P = 0.53	R = -0.30, P = 0.26	R = -0.08, P = 0.76	R = 0.31, P = 0.24
2010 (N = 14)	R = -0.14, P = 0.64	R = -0.10, P = 0.75	R = -0.34, P = 0.23	R = -0.03, P = 0.91	R = 0.49, P = 0.08
2011 (N = 17)	R = -0.15, P = 0.57	R = -0.43, P = 0.09	R = -0.31, P = 0.22	R = -0.13, P = 0.63	R = 0.22, P = 0.40

Table 4.5. Spearman's rank correlations between the rate of bower attendance and multiple structural properties of the bower.

4.3.6. Does increased bower attendance reduce rates of bower marauding?

Contrary to our prediction, in 2009 higher bower attendance rates predicted an increase in marauding rate ($F_{1,15} = 5.15$, P = 0.04, Figure 4.43). In 2010 and 2011 bower attendance rates had no influence on the rate of marauding that bower suffered (2010: $F_{1,12} = 0.47$, P = 0.51, 2011: $F_{1,16} = 1.87$, P = 0.19).
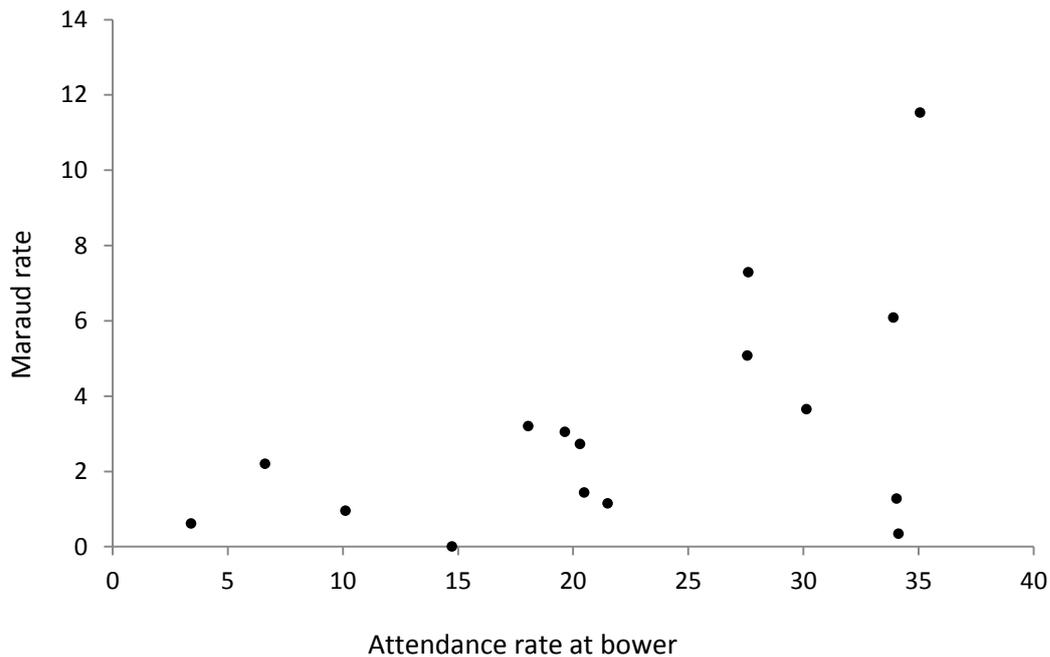
Figure 4.4. The relationship between male bower attendance rates and the rate of marauding in 2009. Attendance rates are calculated as hours per camera recording hours *1000, and marauding rates as events per camera recording hours *1000.

4.3.7. Does increased bower attendance increase male mating success?

Reproductive skew was higher in 2009 compared to 2010 and 2011 (2009: skew = 0.78, 2010 = 0.48 and 2011: 0.52, see Chapter 2.8.2). The variation between males in bower attendance rates did not predict the variation observed in their mating success (2009: $F_{1,14} = 0.15$, P = 0.71; 2010: $F_{1,12} = 0.81$, P = 0.39; 2011: $F_{1,15} = 0.07$, P = 0.79).

4.4. DISCUSSION

Bower building activities impose physical costs on male owners, but bowers do not appear to provide indicators of inter-individual variation in a male's ability to spend time attending his bower. Male bower attendance, the majority of which was spent engaged in maintenance behaviours, was related to significant environmental stress. In a season with low rainfall, unfavourable environmental conditions led to a decrease in average attendance rates compared with seasons when rainfall was at, or above, average levels. Experimentally provisioning males during drought conditions increased bower attendance, the total number of decorations displayed at bowers and the time that bower owners spent engaged in display behaviour towards visitors. These results suggest that in periods of environmental stress males may face trade-offs between bower building activities and foraging opportunities. In subsequent breeding seasons when rainfall was higher average attendance levels increased and bowers that had higher numbers of local, natural food sources exhibited higher numbers of decorations on their bowers. However, natural food supply had no impact on male attendance rates. Males that had lower rates of bower attendance exhibited higher numbers of perishable decorations, suggesting that the need to frequently replenish them required males to spend more time away from the bower. We found no relationship between inter-individual variation in bower attendance rates and other measures of the bower display, and attendance did not predict the rate of marauding that bowers suffered. This suggests that under average conditions males are not limited in their bower-building ability by access to metabolic resources and bowers may not act as indicators of a males' physical condition or ability to dedicate energetic resources to the bower. We found that the ability of a male owner to spend greater time attending his bower appeared to have little adaptive value in terms of increasing the quality of his sexual display, protecting against the social pressure of marauding and did not relate to his level of mating success.

A male's ability to exhibit a highly elaborate sexual trait is thought to be regulated via the handicaps such traits impose (Zahavi 1975, Pomiankowski 1987). Traits that require ongoing investment by males may act as signals of male physical endurance and long-term condition (Kokko et al. 1999), and the level of investment males make may be sensitive to fluctuating environmental conditions (Bussiere et al. 2008). Bowers are considered an

extreme form of an elaborate male trait yet males maintain highly consistent signals despite fluctuations in rainfall (Chapter 3.3), suggesting that males may make considerable physical contributions to maintaining such consistency. During the 2009 drought conditions males appeared to be impeded in their ability to contribute to signal maintenance, and bower attendance rates were low. Low levels of bower attendance were increased by experimental provisioning, suggesting that males were metabolically restricted in their ability to meet the continuous demand for bower maintenance. The impact of food stress during development can have profound effects on a male's quality and subsequent ability to produce a highly attractive signal (Cotton et al. 2004). For example, food stress in male house finches, *Carpodacus mexicanus*, modified the ability of males to produce plumage colouration (Hill 2000) and, conversely, higher food quality increased the ability of male wolf spiders, *Hygrolycosa rubrofasciata,* to perform courtship drumming to females (Kotiaho 2000). However, less is known about individual fluctuation in signalling ability in long-lived species that endure short term environmental change (Cockburn et al. 2008). Bower attendance was not related to monthly rainfall suggesting that short term fluctuations were less influential than the medium term, seasonal variation. During seasons of higher rainfall, male spotted bowerbird attendance at bowers was increased, further suggesting that greater medium-term access to metabolic resources promoted bower activities. The extensive flooding experienced across the region in 2010 led to favourable conditions during the following 2011 season, despite the lower levels of rainfall recorded during this time. This flood legacy may explain why bower attendance was similar in 2010 and 2011 seasons, and suggests that during times of lower environmental pressure males were able to forage more efficiently and return to their bowers for longer periods of time. Our data were collected across three consecutive seasons that showed profound variation in rainfall levels, making it difficult to envisage how our results may have differed if measured over three consecutive seasons of average rainfall levels.

The location of individual bowers in 2011 regarding access to local, natural food sources did not correlate with bower attendance rates. Considering artificial provisioning had increased bower attendance rates in a previous season, we expected males with bowers located in resource rich areas to show higher levels of attendance due to their increased access to metabolic resources. Our results contrast with this, and may also

conflict with the suggestion that caching behaviour in male MacGregor's bowerbirds functions to increase bower attendance (Pruett-Jones and Pruett-Jones 1985). Caching has not been observed in the spotted bowerbird, but, for a species inhabiting semi-arid areas with widely fluctuating resource availability (compared to the rainforest habitats of the MacGregor's bowerbird; Pruett-Jones and Pruett-Jones 1985, Frith and Frith 2004) locating a bower in a resource rich area may have a similar effect as caching resources. There are several potential reasons why we failed to find such a relationship. Males may forage at distances greater than the area reached by our transects, making our measures of food availability inadequate to specify differences between them. Given the relatively close caching distances in MacGregor's bowerbirds (~13m, Pruett-Jones and Pruett-Jones 1985), we expected our limit of 50m to be sufficient as a measure of immediate food supply. An alternative explanation is that all bowers may have been located in areas of sufficient food resources, therefore making measures of food plant variation irrelevant. This suggestion is supported by evidence that bowers are preferentially located in areas of suitable habitat, and that males often position bowers under plants that bear edible fruit (Miles and Madden 2002). Furthermore, bower locations remain constant over many seasons and across males via inheritance, and Madden et al. (2012) found that established bower sites were located in areas with greater numbers of *Solanum* plants, a species that bears fruits commonly used as decorations. These may be unintentionally 'cultivated' by males that discard old fruits in order to replenish the bower with fresh decorations. Whilst *Solanum* fruits have not been identified as providing a food source for this species (Miles and Madden 2002, Frith and Frith 2004), a similar situation with edible fruits may occur, ensuring that established bowers are located in adequately resource rich areas.

A further possible explanation for the lack of relationship between food plant numbers and bower attendance is that those males with increased access to metabolic resources invest in alternative fitness strategies. We found that the number of food plants close to the bower positively correlated with the total number of decorations on the bower. This mirrors a result found in the experimental provisioning experiment, with fed males also increasing numbers of decorations. Having greater access to natural and experimental food resources appears to enable males to allocate more energy to locating and transporting decorations, which may suggest that this activity inflicts greater costs to males than

attending the bower, or has a greater adaptive value. Male great bowerbirds reuse and inherit non-perishable decorations across seasons, indicating that there are inherent costs associated with their acquisition (Doerr 2009a, 2012), and we observed a similar pattern of decoration use in our study population (unpublished data). Male spotted bowerbirds do not use particularly rare or costly decorations (Madden and Balmford 2004), however decorations are displayed in high quantities. Acquisition of high numbers of decorations, including perishable objects that require replenishment, may represent a significant cost for males, especially if they require complex and time-consuming behaviour to obtain (e.g. the acquisition of *Solanum* fruits requires a difficult twisting technique, Madden and Balmford 2004). We also expected to find that a greater diversity of edible species around the bower would enable males to increase overall attendance rates, as diversity might represent a greater likelihood of ripened fruit throughout the season. However, the opposite relationship was found. High diversity in edible plant species may bring higher foraging costs as males need to gather resources from a wider range of species. It may also reflect higher overall plant diversity thus providing males with increased opportunities to gather both metabolic and decoration resources whilst away from the bower. Decorations have shown to be good predictors of male mating success (Borgia 1985b; 1986 , Borgia and Mueller 1992, Lenz 1994, Uy and Borgia 2000, Madden 2003ab, Dingle et al. *in prep*), therefore investing resources into decoration acquisition is likely to be an advantageous strategy for males. Bowers with higher food resources did not enjoy the same increase in structural properties, perhaps suggesting that decorations are a more important priority for male attractiveness.

Variation in male bower attendance rates did not correlate with structural bower properties or the total number of decorations displayed, but importantly, we found a negative correlation between attendance rates and perishable decoration numbers. This confirms the prediction that the requirement to continually replenish decorations requires that males spend time away from the bower, and implies that their display imposes physical costs on the male in terms of decoration acquisition. However, our results also suggest that spending time attending the bower does not yield higher quality bowers. Spending time at the bower may not be particularly costly for males during seasons of favourable conditions when they are able to forage efficiently. Evidence in male satin bowerbirds suggested that

the aerobic capacity of bower owners was not dissimilar to non-bower-owning males, implying that the bower-building component of male mating success was not correlated with performance in this physical capacity (Chappell et al. 2011). Attending the bower may be less costly and offer greater safety for males against predation compared to other activities, such as foraging, marauding rival bowers and/or advertising (Borgia 1993, Nicholls and Goldizen 2006). Bowers are usually built under dense canopy (Miles and Madden 2002), offering increased shelter from intense sunlight, and predation risk at the bower is generally low (Borgia 1993, Miles and Madden 2002, Patricelli et al. 2006). Remaining at the bower may also increase the chance of a male displaying to a visiting female, and offer protection against the bower from being taken over by another male; inheritance of abandoned bowers can be very swift following the loss or removal of an owner (Frith and Frith 2004).

Spending time at the bower has also been hypothesised to reduce the risk of marauding by rival owners, thus offering a further way in which attending the bower can lower potential costs of males. Bower marauding, a form of male-male competition whereby males destroy the displays of rival male bowerbirds, generally only occurs when male owners are absent from their bower, prompting suggestions that spending time away from the bower may be costly for owners (e.g. Pruett-Jones and Pruett-Jones 1994, Morrell and Kokko 2004, Pruett-Jones and Heifetz 2012). We therefore expected to find a negative relationship between rates of bower attendance and bower marauding, perhaps reflecting the fact that lower quality males had an increased need for foraging and/or decoration acquisition and would be away from the bower for longer periods than high quality males. Interestingly, during 2009 we found the opposite trend, with higher bower attendance predicting an increased maraud rate. In 2010 and 2011 no such relationship was found. We make several suggestions as to why this may have occurred. First, no male was able to defend his bower continuously, therefore all bowers were available for marauding at some points in time. Patterns of marauding may be more strongly determined by social factors, such as male dominance status or aggression (Collis and Borgia 1992, Reynolds et al. 2009), and the ability of a male to defend his bower through bower attendance may be weaker than the social determinants of marauding behaviour. Second, the positive relationship in 2009 may reflect the fact that bowers that were marauded stimulated their owners to attend the bower in order to make repairs, whereas owners of non-marauded bowers were

less encouraged to increase bower attendance during a time of environmental stress. This result may indicate that differential costs are paid by high and low quality males, with the requirement for low quality males to invest extra resources into bower repair compared to high quality males that are not required to bear this cost. Similarly, for low quality males remaining at the bower may be the least costly option, and only high quality males can bear the costs of leaving the bower and engage in marauding attacks elsewhere. The differential cost paid by high and low quality individuals is a key prerequisite of the handicap hypothesis as modified by Grafen (1990a; b,). However, again we only found evidence of such a relationship when males were enduring resource shortages, and no such relationship during times of average environmental conditions. Our results raise important questions about the impact of environmental fluctuation on male bower activities, and the implications of this for female mate choice.

The impact of environmental fluctuation on female choice may be complex and difficult to predict, potentially either weakening or strengthening sexual selection pressure (Candolin et al. 2007, Kokko and Heubel 2008). In polygamous species, poor conditions may heighten selection pressure because most females will converge on a lower number of males that can meet thresholds for mating (Cockburn et al. 2008). Female bowerbirds are likely to make multiple visits to males throughout the breeding season (as described in satin bowerbirds, Uy et al. 2001), and may use these repeated visits to make multiple assessments and comparisons of males over time. The impact of environmental stress on male display may therefore heighten or confound her ability to make an informed mate choice decision, especially in a system where females only receive fixed genetic benefits from males. Reproductive skew in our study population was higher in 2009 compared to 2010 and 2011, indicating that a smaller proportion of males successfully gained copulations. Several factors may have accounted for this difference; (i) lower male attendance rates meant that more males missed visiting females and were therefore unavailable for female assessment and/or copulations when females visited, (ii) females were better able to discriminate between males during periods of environmental stress, or (iii) fewer males were able to meet thresholds for mating. Currently little is known about female mate choice strategy in spotted bowerbirds, making it difficult to determine which, if any, of these factors may be most important.

Rates of bower attendance were not related to male mating success in any of the three seasons we measured, nor were properties of the bower enhanced by higher attendance rates. Bowers may not impose high physical costs on males beyond situations of acute environmental stress, which probably precludes elaborate signalling in most systems (Reinhold 2004, Cockburn et al. 2008). Our results concur with previous studies of the costs associated with male bowerbird display, suggesting that bower ownership is not particularly costly for males; male spotted bowerbird decorations do not impose high costs on males through being rare or physically costly (Madden and Balmford 2004) and bower ownership does not increase mortality or decrease male bodily condition over time (Borgia 1993, 1996). One explanation for this may be that only males of a high enough physical condition are able to obtain ownership at bowers (but see Chappell et al. 2011). Alternatively, further selection may be based on other, non-physical factors such as social status and/or the ability to construct a cognitively complex display (e.g. Keagy et al. 2009, Madden et al. 2011). Females do not always chose males with the most attractive physical attributes; female Japanese quail, *Coturnix japonica*, preferentially mate with subdominant males as they are less likely to inflict harm to the female during interactions (Ophir and Galef 2003).

Our study raises important questions for the study of sexual traits in long lived species that signal over long time periods when their ability to signal efficiency changes over time. We found that in a season of environmental stress, bowers appeared to impose higher physical costs on male owners than in seasons of favourable conditions, as reflected in their ability to attend the bower, but these differences may not have been reflected in female mate choice. Our results suggest variation between males in bower building activities may not have evolved to signal male physical condition, and environmental stress determinants of male attendance may not be expressed through properties of the bower. The ability of a male to devote time towards on-bower maintenance may be less important for signalling quality than collecting decorations. Decoration acquisition may impose higher costs than bower attendance, and therefore provide a more efficient signal of variation in male physical ability. However, the degree to which our results are applicable across bowerbird species is uncertain; many bowerbird species inhabit tropical climates that do not experience such high seasonal fluctuation in resource availability as the spotted bowerbird

habitat, and where access to metabolic resources may be more predictable (Frith and Frith 2004). There are, however, several important limitations to our study. Our measure of male bower attendance focused on the time that males spent at the bower, and mainly reflect the contributions he makes towards bower maintenance. However, males may be able to combine several of the activities we assume to be mutually exclusive; for example, if males can forage within a short distance of the bower then they may able to simultaneously defend the bower from rival males and detect visiting females. We were not able to compare male sexual traits with other, non-sexual traits to ask to what extent bower-building had greater condition dependence than other traits – a crucial step in determining selection for handicaps (Cotton et al. 2004). However, the lack of any relationship between male bower attendance and female choice suggests that bower characteristics selected for by females may not provide reliable signals of condition dependent traits, and that spending time at the bower does not burden males with significantly high physical costs.

Chapter Five

Performance in cognitive and problem-solving tasks

ABSTRACT

Individuals exhibiting a high level of cognitive ability may also exhibit more elaborate traits and so gain higher levels of mating success. This suggests that selection may act on cognitive performance through mate choice. Studies investigating this relationship have tended to focus on single cognitive tasks, or tasks that are closely related to existing natural behaviours, and individuals are frequently tested in captive conditions. This can introduce test artefacts and may tell us more about selection on specific display behaviours that we imagine being particularly cognitively complex, rather than a general cognitive ability. We tested free-living male spotted bowerbirds, *Ptilonorhynchus maculatus*, that exhibit elaborate sexual displays which appear to be cognitively demanding. We describe a method for testing individuals in the wild, without the need for constraint or captivity. We looked for evidence of a general cognitive ability in males by assaying their performance in a series of novel tasks reflecting their natural bower building behaviour (bower maintenance) or capturing more abstract measures of cognitive ability (colour and shape discrimination, reversal learning, spatial memory and motor skills). We related performance in these tasks to their mating success. An individual's performance in one task was a relatively poor predictor of performance in any other task. However, an individual's performance across tasks could be summarized by a principal component which explained a level of total variance above which has previously been accepted as evidence of a general cognitive ability. We found no relationships between an individual's overall performance or performance in any single task, and mating success. Our results highlight the need for further investigation of whether selection on cognition in bowerbirds is exerted through mate choice. We offer this as an example of how classic cognitive tasks can be transferred to the wild, thus overcoming some limitations of captive cognitive testing.

5.1 INTRODUCTION

The evolution of enhanced general cognitive abilities poses a challenge to biologists. In order to understand how selective pressures may be acting on cognitive traits, individual cognitive differences must be related to measures of fitness variation (Shumway 2008, Sol 2009, Morand -Ferron et al. 2011, Cole et al. 2012, Cauchard et al. 2013). One promising, yet little explored, context in which cognitive performance may have fitness consequences is via sexual selection (Boogert et al. 2011b). Selection may act through female choice for complex displays which are cognitively costly to produce (Madden et al. 2011). For example, many female songbirds choose mates based on song elements with clear cognitive components, such as repertoire size and song complexity (Reid et al. 2005, Pfaff et al. 2007), and in several manakin species females chose males based on challenging coordinated dance displays (Trainer et al. 2002, DuVal 2007). Females may benefit from such choice because high cognitive ability may come at a metabolic cost of increased neural processing, with only high quality males able to bear such a cost (Miller 2000, Nowicki et al. 2002). Cognitive-based signals, such as bird song, may inform females about the developmental, social and individual learning ability of males (Boogert et al. 2008, Holveck et al. 2008, Riebel et al. 2012). Alternatively, if cognitive abilities are positively correlated across domains then female selection on cognitive traits may confer benefits in other contexts, such as foraging ability or predator avoidance.

Positive co-variance between cognitive abilities has been demonstrated in humans, where this general ability (referred to as *g*) is described as being both heritable and an honest indicator of fitness (Jensen 1998; Miller 2000; Plomin & Spinath 2002; Deary et al. 2010). *g* has also been demonstrated in mice, *Mus musculus,* (Matzel et al. 2003; Galsworthy et al. 2005), rats, *Rattus norvegicus,* (Anderson 1993), cotton-top tamarins, S*aguinus oedipus*, (Banerjee et al. 2009), honeybees, *Apis mellifera,* (Chandra et al. 2000), bumblebees, *Bombus terrestris,* (Muller and Chittka 2012) and pigeons, *Columba livia,* (Bouchard et al. 2007). However, few studies relate measures of *g* to fitness differences and the expression of sexual traits; instead, the focus has been on describing relationships between a trait and a single measure of performance in a specific cogntive task. For example, in male siskins, *Carduelis spinus,* plumage brightness was correlated with performance in a novel foraging task demonstrating insight (Mateos -Gonzalez et al. 2011),

in male guppies, *Poecilia reticulata*, the expression of high orange patch colouration was correlated with algal searching ability (Karino and Shinjo 2007), in male zebra finches, *Taeniopygia guttata,* song complexity correlated with a novel foraging task demonstrating problem solving ability (Boogert et al. 2008) and song bout length in European starlings, *Sturnus vulgaris*, influenced by early rearing conditions, was indicative of spatial learning ability (Farrell et al. 2012). Inferring selection pressure on general cognitive ability by considering only a single measure of performance risks overlooking important elements of such relationships. In those few studies where multiple cognitive measures have been assayed, links between sexual traits and an individual's general cognitive performance are less clear. For example, in male song sparrows, *Melospiza melodia,* song repertoire positively correlated with performance in an inhibitory control task, but not with other cognitive measures (Boogert et al. 2011a). Species which exhibit multiple cognitive elements in their sexual display, perhaps manifested in multi-trait displays, offer improved opportunities for exploring such selection pressures. Females may pay attention to multiple traits because each trait signals a different aspect of male quality, or because using combinations of traits helps to reduce mate-choice error (Møller and Pomiankowski 1993, Candolin 2003)*.

Bowerbirds exhibit multi-trait displays comprising elements likely to depend on a range of different cognitive abilities, presenting females with an opportunity to select for general cognitive performance. Males of seventeen species construct and decorate elaborate display sites, bowers, which serve as targets of female choice (Marshall 1954; Borgia et al. 1985b; Frith and Frith 2004). They construct technically intricate display courts (Borgia 1985b), requiring fine-scale motor skills. They collect and arrange decorations (Diamond 1987; Borgia 1995), categorizing them by colour (Endler and Day 2006) and paying particular attention to those which are good predictors of mating success (Madden 2003b), requiring discriminatory and classification skills. Male great bowerbirds, *Ptilonorhynchus nuchalis,* create a forced perspective to enhance the audience view of their bower display (Endler et al. 2010), suggesting advanced perceptual skills. Display is not limited to bower construction; males perform courtship dances which can be adjusted according to female response (Patricelli et al. 2002; Patricelli et al. 2006), and which can include vocal mimicry (Loffredo & Borgia 1986; Frith & McGuire 1996; Coleman et al. 2007), requiring memory,

learning and further motor skills. Males show flexibility in their display behaviours; they appear to improve their display through learning (Madden 2008), resolve trade-offs between improved signalling to females and increased male marauding (Madden 2002) and are able to compensate for the loss of one signal by enhancing another (Bravery and Goldizen 2007). If multiple traits, such as those exhibited by male bowerbirds, signal individual general cognitive ability we may expect female selection preferences to reflect male performance across a suite of cognitive tasks.

A relationship between cognitive performance and mating success has previously been demonstrated in the con-generic satin bowerbird, *Ptilonorhynchus violaceus.* The speed and degree to which males solved two novel problem-solving tasks was positively correlated with mating success (Keagy et al. 2009). Measures of other traits thought to require high levels of cognitive performance (vocal mimicry and bower restoration behaviour) also predicted mating success individually or in conjunction with one another (Keagy et al. 2011, 2012). However, inter-correlations between performance in tasks were low (Keagy et al. 2009, 2011), and whilst multiple cognitive traits provided a more accurate prediction of overall cognitive ability, the authors suggest that these multiple traits may be used to signal different aspects of male quality rather than a general cognitive ability (Keagy et al. 2012). However, it is not explicit which cognitive processes are being measured, and how the different tests relate to one another in terms of exploring different cognitive domains (e.g. bower building competence reflects motor skills, whilst vocal mimicry reflects aspects of learning and memory), or repeatedly testing the same cognitive domain (e.g. the two novel tasks are assumed to reflect problem-solving). Neither is it clear how discrete selection on cognitive performance in these tasks relates to more conventionally defined selection on the behaviours of bower-building or vocalisations.

We investigated whether individual male spotted bowerbirds, *Ptilonorhynchus maculatus,* differed in their specific or general cognitive abilities across a range of problem-solving and cognitive tasks, and whether their individual or overall performance in tasks correlated with their mating success. We repeated one of the novel problem-solving tasks previously presented to satin bowerbirds (Keagy et al. 2009), to permit comparison across species. In addition, we avoided the confounds of testing cognitive performance in natural

behaviours (such as vocalisations and bower construction) or behaviours closely linked to natural behaviours (bower maintenance and removal of disliked objects) (Keagy et al. 2009, 2011, 2012) which may be subject to strong direct selection without reflecting a broader cognitive ability across contexts. Instead, we implemented a series of classic psychological cognitive tasks, with a proven history of use in the laboratory, to test specific cognitive traits apparently underpinning, but discrete from bower-building behaviour. These included the ability to learn a novel motor task, colour and shape discrimination, colour reversal (as a measure of behavioural flexibility), and spatial memory.

5.2. METHODS

5.2.1. General field methods

Data were collected from a population of wild, individually marked spotted bowerbirds in Taunton National Park (Scientific) in central Queensland, Australia (23.54989S and 149.24088E) (see Miles & Madden 2002 and Chapter 2.5 for a detailed description of the study site). Bowerbirds offer an ideal opportunity for testing cognitive performance in the wild. Male bowerbirds maintain bowers for several months over the breeding season, and spend a significant proportion (up to 70%) of daylight hours tending their bowers (Frith & Frith 2004). Each bower has a single male owner, allowing repeated trials on the same individual, and their regular presence in a specific location is reasonably predictable. Therefore, all tests were carried out on free-living individuals who were not brought into captivity. Males also show relatively low levels of neophobia, interact with novel items willingly and are motivated to gain food rewards.

Fieldwork and cognitive testing was conducted during two breeding seasons, July 2010– January 2011 (subsequently referred to as the 2010 breeding season) and August 2011 – February 2012 (referred to as the 2011 breeding season). At the beginning of each season bowers were located and owners identified with unique combinations of coloured leg bands. Bowers were spaced approximately 1km apart (Miles & Madden 2002). Once located, remote motion-sensing cameras (StealthCam I590, Grand Prairie, Texas) were placed at bowers for the duration of the breeding season. Camera recording hours differed

minimally between males depending on the date/time cameras were deployed, and due to rare camera failures in the field (max. 3 days).

5.2.2. Measuring mating success

We measured an individual's mating success by calculating copulation rates for the two seasons during which testing took place. Females may make multiple visits to bowers during the breeding season (Uy et al. 2000), and copulations occur in the bower avenue (Borgia 1985b; Frith & Frith 2004). Spotted bowerbirds are monomorphic, and we were not able to distinguish females in the field. Therefore, we used the total number of copulations per male captured from camera data as a measure of reproductive success. Copulations were easily recognisable behaviours and observed male mating success has been shown to be a reliable predictor of reproductive success in satin bowerbirds (Reynolds et al. 2007). The number of copulations each male obtained was summed, and the dates of the first and last copulations across the study population were used to define the copulation season. Copulation rates for each individual were calculated as the number of copulations witnessed at the bower divided by the total number of camera recording hours at the bower during the copulation season. Bowers had the same owners in 2010 and 2011 , and reproductive skew, calculated according to Pamilo and Crozier (1996), was similar in both seasons; 0.48 and 0.52 respectively (a score of zero indicates no skew and 1 indicates all copulations are gained by a single male). However, copulation rates were not significantly correlated between seasons (r_s = 0.25, *N* -= 13, P = 0.42).

5.2.3. Measuring cognitive performance

We deployed six different cognitive tasks, designed to capture a measure of individual performance across separate types of cognitive domains (Table 5.1). The first task (i) was the barrier removal task, which replicated and extended the novel problem-solving task previously presented to male satin bowerbirds (Keagy et al. 2009), and represented a task which was based on natural male bower maintenance and restoration behaviour. In the next set of tasks (ii-vi), we presented males with a novel task apparatus, a pokebox, which was used to test five different potential cognitive abilities male bowerbirds may be expected to exhibit, but using an abstract paradigm separated from their natural behaviours.

All tasks were conducted at bowers where male behaviour could be monitored remotely. Not all males were presented with all tasks. The barrier removal tasks were conducted with nineteen males during the 2010 season, however not all these males were available for testing during 2011. The pokebox tasks were carried out in 2011 with fourteen males, of which thirteen had been previously tested in the barrier removal tasks. Of these fourteen, two were lost (presumably predated) during the testing period in 2011. Thus, the total number of males who were presented with all tasks was eleven.

When bowers were located at the start of the season, a Velcro covered board (250x150x3mm plywood) was fixed to the ground on the outer edge of the bower using 75mm nails, to which the test apparatus could be rapidly attached. This prevented males removing the apparatus and ensured it was consistently presented at a specific location. Tasks were presented during two sessions each day: morning (dawn to midday) and afternoon (15:00 to sunset). Tasks were not presented during the middle of the day, when birds are less active at their bowers (Sparfeld 2012). All tasks were filmed using Samsung SMX-C20 camcorders in the absence of an observer to reduce any external influence on male behaviour.

	Task	Equipment	Season	*N*	What the task demonstrated
i)	Barrier removal	Transparent barrier	2010	19	Problem-solving ability
ii)	Novel motor task	Poke box	2010-11	14	Motor skills in a novel task
iii)	Colour discrimination	Poke box	2011	12	Discrimination based on colour
iv)	Colour reversal	Poke box	2011	12	Behavioural flexibility
v)	Shape discrimination	Poke box	2011	11	Discrimination based on shape
vi)	Spatial memory	Poke box	2011	11	Memory for spatial location of rewards

Table 5.1. Summary of the six cognitive tasks. Tasks were presented over two consecutive breeding seasons and were divided by the type of cognitive domain they tested and the equipment used to carry out testing.

5.2.3.1. Barrier removal task

Males were presented with a transparent plastic barrier (10cm diameter x 11cm high clear plastic beaker) underneath which objects could be placed. This barrier was placed 25cm from the entrance to the bower avenue. We presented male spotted bowerbirds with three different trials in a randomised order; an aversive object trial, a desirable object trial and a control trial. The aversive object trial was a replication of the task presented by Keagy et al. (2009) and tested the ability and motivation of males to remove disliked objects (three $1cm^3$ yellow blocks) from their bower by removing them from underneath the barrier. The desirable object trial tested exactly the same mechanism (problem solving via barrier removal) but tested whether motivation differed with desirable objects (two green glass chips and one decoration taken from the bower avenue, typically a *Solanum spp* fruit; see Madden 2003b). The control trial addressed a key limitation of Keagy et al. (2009), where the male's reaction towards the barrier itself was not considered. If males consider the barrier alone to be an object with which they wish to interact (either a disliked object which they want to remove, or a desirable object they want to display) they may be motivated to move it, and this could be seen as a simple bower maintenance task requiring little problem-solving ability, rather than a response to a perceived problem (accessing covered objects) which requires solving. Males were scored on the time taken to gain access to the first object underneath the barrier; males who were faster at solving the trial were deemed to be better problem-solvers. In order to 'solve' the control trial males had to move the barrier one diameter length (10cm) from its original location, which would indicate a motivation towards removing it or adding it to their display.

'Solving' a barrier removal trial may be simply explained by variations in persistence, rather than in cognitive ability. Males who pecked at the barrier at a faster rate may increase their chances of gaining access to the objects in a faster time, yet this may not symbolise any enhanced cognitive ability. Therefore, we counted the number of pecks made to the barrier and used this measure to investigate whether males solving the trial in a shorter amount of time were simply more persistent in their interactions with the task equipment.

Nineteen males were presented with each of the three trials (aversive, desirable and control) once between August and December 2010, in a randomised order and with a minimum of 30 days between trials. Trials were videoed for 3.5hours, after which the barrier and objects were removed. Males were scored on both time attentive to trial (cumulative time male spent interacting with barrier (within 20cm of the barrier and orientated towards it) until solved) and total elapsed time (total time from first attentive until solved).

5.2.3.2. Novel motor task

We explored how fast fourteen males learned to perform the novel motor task of opening a pokebox to access a food reward (see Wills et al. 2009 and Figure 5.1). The pokebox was a M.D.F. 15x15x3cm box with 12 wells (diameter 25mm) drilled around the outside edge. A matching lid (2mm plywood) was fixed to the box. In-between the box and the lid a sheet of paper could be inserted, which prevented direct access to and hid the contents of the wells. Males were trained to peck though a plain white paper lid to gain access to food reward items (fragments of green grapes) using a systematic shaping procedure (Table 2) (Boogert et al. 2008), which guided males through four stages of training, each of which increased in difficulty. Males were required to pass each stage of training before they could progress to the next stage and were scored on the total number of trials taken to pass stages two – four. The first stage of training was considered to be habituation to the novel equipment, and was excluded from the final score given. The minimum number of trials required to pass each stage was two, therefore males required a minimum of six trials in total to complete this task. Males were presented with up to five trials in the morning session and three in the afternoon session. Pokeboxes were reset every 45mins, although the actual retention time between trials was determined by the male's presence at the bower; trials conducted when the male did not attend his bower were discounted. Resetting was quick (2-3mins), caused minimal disturbance to the males, and involved swapping the current pokebox with a pre-set box which had been prepared out of sight from the males.

Figure 5.1. The experimental setup for pokebox cognitive tasks; (a) a male bowerbird completing a colour discrimination task, (b) a male completing a shape discrimination task and (c) showing the general positioning of the poke-box on the outer limit of the bower (the bower avenue can be seen positioned between two white snail shell piles, which usually delimit the outer boundaries of decorations).

Stage	Training:
1	**Habituation to Equipment**: All pokebox wells were open and each contained one fragment of green grape (reward). One fragment of grape and two decorations were placed on top of the pokebox to draw the male's attention to the equipment.
2	**Paper Lid**: Pokebox presented with a reward in every well, and with paper lid added. Six holes fully opened (paper teared open so that reward is easily obtainable) by experimenter and six partially opened (paper teared down centre, so that food can be seen but not obtained without further ripping of the paper by the male).
3	**Closed Holes**: Pokebox presented with a reward in every well, with eight holes fully closed (complete intact paper lid) and four holes partially opened.
4	**Final Test**: Pokebox presented with a reward in every well, with all holes closed.

Table 5.2. The four stages of the systematic shaping procedure used to train males to open a pokebox. Each stage in the procedure was passed when all twelve pieces of grape were taken from all wells on two consecutive trials. Only stages two-four were counted in the novel motor task analysis, as stage one was considered as a habituation stage where males were encouraged to interact with the novel item.

5.2.3.3. Colour discrimination

Fourteen males were presented with a colour discrimination task. Six wells on the pokebox were covered with a paper lid of one colour and contained a food reward (grape fragment). The other six wells were covered with a second colour and contained reward cues (crushed grapes) but access to the reward was blocked by a wooden plug. As bowerbirds show strong colour preferences, we chose two neutral colours with the same grey-scale value to control for preferences towards pecking light/dark. The rewarded colour was randomized between males. We tested how quickly males learned to discriminate the colours, only pecking at rewarded wells. Males passed the colour discrimination task if they pecked at all six rewarded wells before pecking an unrewarded well on two consecutive trials. No males pecked at only rewarded wells on their first trial.

For this and all subsequent pokebox trials, male performance was scored on the cumulative number of trials taken to reach a pass criterion. The maximum number of trials presented was 35; after this males showed a significant reduction in their motivation to engage with the equipment. Some trials were stopped sooner if males decreased in their motivation, for example due to a lack of positive reinforcement. Males who failed to reach the pass criterion were given scores of the maximum number of trials to allow their inclusion in analyses.

5.2.3.4. Colour reversal

Immediately following the colour discrimination task, males were presented with a reversal task, where the previously rewarded colour became the unrewarded, blocked colour. Reversal tasks are considered to provide a measure of behavioural flexibility (Boogert et al. 2010; Tebbich et al. 2010). Males were required to reach the same pass criterion as the colour discrimination tasks. Thirteen males were presented with this task, as one male was lost from the population (presumed predated) before this task commenced.

5.2.3.5. Shape discrimination

Twelve males were presented with a shape discrimination task (a second male was lost before the start of this task). Half of the wells were displayed with blue circles and the

other six were displayed with blue triangles. As with the colour discrimination task, one shape covered rewarded wells whilst the other shape covered blocked wells. The rewarding shape was randomized between males. Males were required to reach the same pass criterion as the colour discrimination tasks.

5.2.3.6. Spatial memory

Twelve males were presented with a spatial memory task. Eight wells were used for testing, with the four corner wells left uncovered and empty. Two adjacent wells on one side of the box were consistently rewarded, with the remaining three pairs of wells unrewarded and blocked. The pokebox was placed in the same location, ensuring that the spatial position of the rewarded holes relative to the bower was constant. All wells were covered with plain white paper lids, and boxes were switched between trials to ensure that males could not use inadvertent cues to aid solving. Males passed this task when they correctly chose the two rewarded wells before pecking any unrewarded wells in two consecutive trials.

5.2.4. Measuring Male Tenure at Bowers

Male bowerbirds are known to hold tenures at bowers for over a decade and tenure is assumed to be a reliable proxy for male age (Borgia 1993; Frith & Frith 2004). Male age data were not available for our study population, however, data on bower ownership collected since 1998 allows us to estimate male tenure at bowers and adjust scores accordingly. Males were ranked ordered based on the known number of years in which they were bower holders. Ranks for males were then adjusted upwards according to whether they were owners at the start and/or end of the study period (see Borgia 1993). Males that were established as owners at the start of the study or males that retained ownership of their bower until the end of the breeding season in 2011 were given a one-rank increase. Males who were owners at both were given a two-rank increase.

5.2.5. Motivation checks

To measure motivation in the barrier removal task, the time taken to move objects more than 20cm from their original position under the barrier once access had been gained was measured (see Keagy et al, 2009). All males immediately (within 1-3s) removed accessed objects >20cm, and thus all showed high motivation in this task.

Motivation in the pokebox trials was checked by presenting males twice with a pokebox with all 12 wells rewarded and covered with plain white lids. This was identical to the final stage in the shaping procedure, and was presented following completion of the colour reversal and spatial memory tasks. These trials served to reinforce the association between opening wells and receiving a reward, and to check whether males had remained motivated to engage with the task. All males passed these trials, indicating that despite being unrewarded in previous cognitive tests, males had not habituated to the presence of the equipment and were still motivated to engage with the pokebox.

5.2.6. Statistical Analysis

5.2.6.1. Individual variation in task performance

For the barrier task we looked for differences in a male's ability to solve each of the three trials presented using a Cochran's Q non-parametric test for dichotomous data, and further investigated these results with pairwise McNemar tests between each of the tasks. When considering the ability of males to solve the tasks, we looked for correlations between the three measures taken; time attentive to task, total time elapsed and number of pecks made to barrier. For the pokebox cognitive tasks we used the number of trials males required to reach the pass criterion as a score of individual performance (Boogert et al. 2008; Boogert et al. 2011a).

5.2.6.2. Relationship between individual performances in different tasks

We explored how a male's performance in one task related to his performance in another task. First, we explored simple relationships between performances in pairs of tasks using Spearman Rank correlations. Second, we explored whether variation in the cognitive performance could be explained by a single underlying factor (analogous to *g*), by

conducting a principal components analysis (PCA) on scores from the 11 birds who had been presented with all tasks (these included solvers and non-solvers). To allow for the inclusion of males who failed to solve tasks, and to normalise the data where possible, we calculated the inverse of our response variables by taking the maximum performance score per trial and dividing this by each male's performance score. In this way, males who failed to solve a task were given a score of zero, with higher scores indicating greater ability. We conducted a PCA with an unrotated factor solution and extracted individual composite scores from the first and second components with eigenvalues > 1.

5.2.6.3. Relationship between cognitive performance and mating success

Spearman's Rank correlations were used to see whether male performances in each task correlated with mating success, both for the year in which the task was carried out, and for his average mating success across both years of testing. We then tested whether individual PCA composite scores were correlated with a male's mating success, both in each year of testing and with average mating success across both years. We also took an alternative measure of cognitive performance by averaging the relative performance of each male on each cognitive task which they were presented with (see Keagy et al. 2011), and related this score to measures of mating success. To control for male tenure, partial correlations on performances between tasks were carried out.

Finally, we implemented a linear mixed model to explore how performance scores and male mating success were related, given the variation within males in their relative mating success across the two seasons measured. Since mating success for each male was not significantly correlated across seasons, we entered both seasons as a repeated measure in the mixed model, with PC1 composite scores as fixed effects, and season and bird identity as random effects.

5.3. RESULTS

5.3.1. Individual variation in task performance

5.3.1.1. Barrier removal task

Males did not solve the three barrier trials equally well (Cochran's Q, χ^2 = 14.53, N = 19, P < 0.001). Fourteen of the nineteen (74%) males solved the aversion trial, and males were more likely to solve this trial than the control trial (Pairwise McNemar tests: control-aversion, N = 19, P < 0.01). Nine males (47%) solved the desirable objects trial, and males were more likely to solve this trial compared to the control trial (Pairwise McNemar tests: control-desirable, N = 19, P = 0.04). Only two of the nineteen (11%) males solved the control trial.

When considering the aversion trial only (for which we had the largest sample size of problem-solvers), the time that males which solved the task spent attentive was strongly related to the total elapsed time (r_s = 0.80, N = 14, P < 0.001). Males varied widely in the time they took to solve this trial (mean time attentive to trial ± SD = 92.7s ± 76.7s, range 19-305s). The number of pecks that males (solvers and non-solvers) made to the barrier was positively correlated to the time spent attentive to trial (R^2 = 0.88, N = 19, P < 0.001, Figure 5.2). This relationship held when only solvers were included in the analysis (R^2 = 0.85, N = 14, P < 0.001).
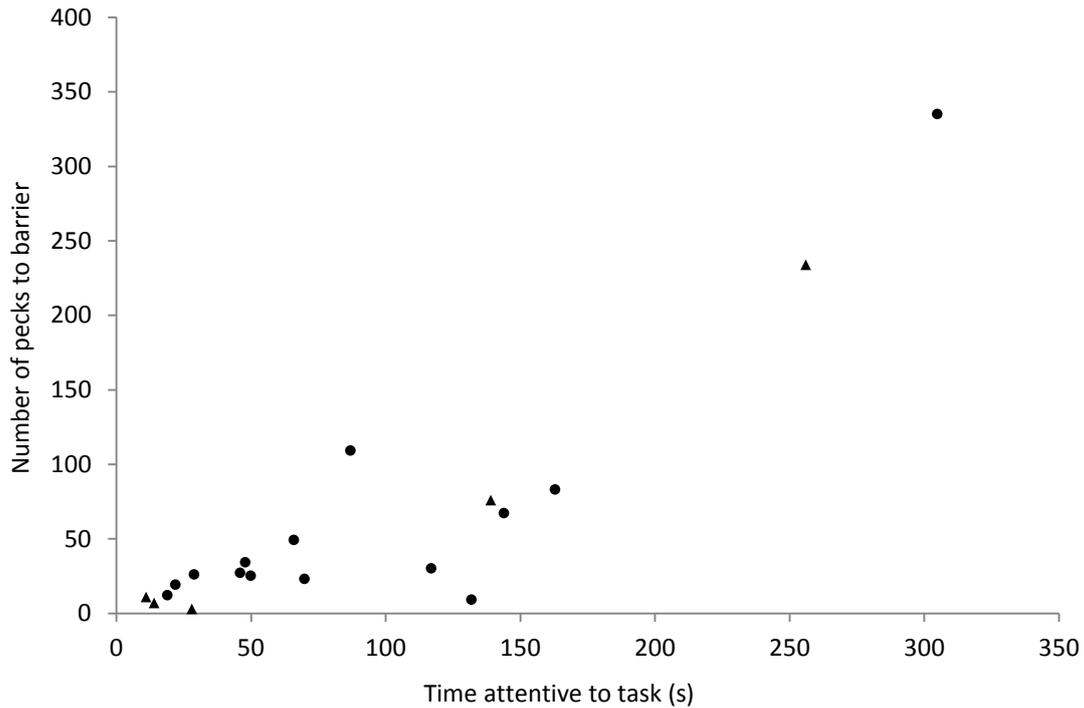
Figure 5.2. Relationship between time attentive to task and number of pecks made to the barrier in the aversion trials for all males. Solvers are indicated by circles, males who failed to solve are indicated by triangles.

5.3.1.2. Pokebox tasks

Males varied in their ability to learn the novel motor task of opening paper-covered wells (N=14, mean ± SD to pass = 8.35 ± 2.82, range 6-15). Five males passed the motor task with the minimum number of trials required. All males passed the colour discrimination task (N=14, mean ± SD = 5.93 ± 2.56, range 4-13) but only half solved the reversal task (N=13, solved = 7: mean ± SD = 20.86 ± 4.78, range 14-35, 35 being the maximum number of trials given). Twelve males were presented with a shape discrimination task; three failed to solve this task and those who passed took, on average, a higher number of trials than in the colour discrimination task (N=12, mean ± SD = 9.78 ± 4.21, range 5-35). The spatial memory task was also presented to twelve males and had the lowest completion rate and the largest variance between solvers (N=12, mean ± SD = 12.75 ± 9.67, range 4-35). Males who were unable to solve this task tended to peck repeatedly at non-rewarded holes, leading to a lack of positive reinforcement.

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5.3.2. Relationships between individual performance in different tasks

Bivariate relationships

Performances across pairs of tasks were generally positively correlated; the spatial memory task showed negative correlations with some tasks (Table 5.3A). No correlations were significant after a Bonferroni correction for multiple comparisons was applied. When controlling for male tenure at bowers, there was no significant qualitative change in these results (Table 5.3B), however, correlations tended to have higher coefficients.

	Barrier Task	**Motor Task**	**Colour Discrim.**	**Colour Reverse**	**Shape Discrim.**
Motor Task	$r_s = 0.00$ $P = 0.99$ $N = 13$				
Colour Discrim.	$r_s = 0.13$ $P = 0.67$ $N = 13$	$r_s = 0.43$ $P = 0.12$ $N = 14$			
Colour Reverse	$r_s = 0.25$ $P = 0.44$ $N = 12$	$r_s = 0.06$ $P = 0.84$ $N = 13$	$r_s = 0.44$ $P = 0.13$ $N = 13$		
Shape Discrim.	$r_s = 0.33$ $P = 0.32$ $N = 11$	$r_s = 0.41$ $P = 0.19$ $N = 12$	**$r_s = 0.60$** **$P = 0.04$** **$N = 12$**	**$r_s = 0.60$** **$P = 0.04$** **$N = 12$**	
Spatial Memory	$r_s = -0.07$ $P = 0.83$ $N = 11$	$r_s = 0.18$ $P = 0.47$ $N = 12$	$r_s = 0.41$ $P = 0.19$ $N = 12$	$r_s = -0.22$ $P = 0.50$ $N = 12$	$r_s = 0.36$ $P = 0.24$ $N = 12$

Table 5.3A. Spearman rank correlations between performances in cognitive tasks. Bonferroni correction: α level of significance = 0.003. Tasks showing a trend towards positive correlations are shown in bold. *N* reduces in some trials due to the loss of male owners during the breeding season.

	Barrier Task	Motor Task	Colour Discrim.	Colour Reverse	Shape Discrim.
Motor Task	r_s = 0.41				
	P = 0.36				
Colour Discrim.	r_s = 0.59	r_s = 0.50			
	P = 0.16	P = 0.25			
Colour Reverse	r_s = 0.53	r_s = 0.29	r_s = -0.11		
	P = 0.22	P = 0.53	P = 0.82		
Shape Discrim.	r_s = 0.27	r_s = 0.54	r_s = 0.47	r_s = -0.22	
	P = 0.56	P = 0.21	P = 0.90	P = 0.64	
Spatial Memory	r_s = 0.14	r_s = 0.47	r_s = 0.69	r_s = -0.45	r_s = -0.75
	P = 0.76	P = 0.29	P = 0.09	P = 0.28	P = 0.05

Table 5.3B. Spearman's partial correlations between rank performances in cognitive tasks (df = 5 for all correlations). Partial correlations controlling for male tenure at bowers (as a proxy for age). Bonferroni correction for multiple correlations: α level of significance = 0.003.

Principal Components Analysis

Two components were extracted with eigenvalues > 1 (Table 5.4). Male performances in all tasks loaded positively onto the first component, which captured over 44% of the total variance. Performance in the barrier and colour reversal tasks loaded on the second component, which explained a further 23% of the variance. The spatial memory task loaded strongly on the negative pole of the second component, with the motor task and colour discrimination showing weaker negative associations with this PC.

Task	Component 1	Component 2
Barrier Task	0.16	0.57
Motor Task	0.67	-0.26
Colour Discrimination	0.80	-0.09
Colour Reverse	0.58	0.66
Shape Discrimination	0.89	0.25
Spatial Memory	0.63	-0.72
Eigenvalue	**2.65**	**1.42**
% variance explained	**44.12**	**23.62**

Table 5.4. Results from the unrotated principle components analysis. Results are based on inversely transformed performance scores in the barrier and pokebox tasks, showing the two components extracted with eigenvalues >1 and percentage of total variance in performance explained.

5.3.3. Relationships between cognitive performance and mating success

We found no relationships between an individual's performance in any of the cognitive and problem solving tasks, and their mating success. There were no significant relationships between each of the individual trials and measures of mating success (Table 5.5). We also found no relationship between mating success and composite scores on the first and second principal components of the PCA (Pearson's correlations between task composite scores and average mating success: PC1: R^2 = -0.04, N = 11, P = 0.91, Figure 5.3, PC2: R^2 = -0.01, N = 11, P = 0.78). Additionally, there was no relationship between an alternative measure of cognitive ability, the average of each male's rank performance on each cognitive task completed, and mating success in the year of testing (r_s = 0.13, N = 13, P = 0.68). Finally, we found no overall relationship between PC1 scores and mating success scores when adjusting for season and male identity (LMM, $F_{1,\ 10}$ = 0.01, P = 0.91). We repeated the linear mixed model with tenure included as a fixed effect, and again found no significant relationship with mating success and cognitive performance ($F_{2,\ 9}$ = 0.01, P = 0.92).

Trial	Year	Mating Success in same year			Average mating success across years		
		Correlation coefficient, r^s	N	P-value	Correlation coefficient, r^s	N	P-value
Barrier – time attentive	2010	0.20	17	0.47	-0.05	18	0.83
Barrier –time elapsed		0.19	17	0.48	-0.11	18	0.65
Motor Task	2011	0.24	13	0.42	0.42	14	0.14
Colour Discrim.	2011	-0.26	13	0.40	-0.25	14	0.39
Colour Reverse	2011	0.15	13	0.63	0.27	13	0.38
Shape Discrim.	2011	0.17	12	0.59	0.07	12	0.84
Spatial Memory	2011	0.34	12	0.27	-0.19	12	0.56

Table 5.5. Spearman's rank correlations between individual task performances and mating success. Correlations are shown for both the individual year in which males were tested, and for mean mating success over both years.
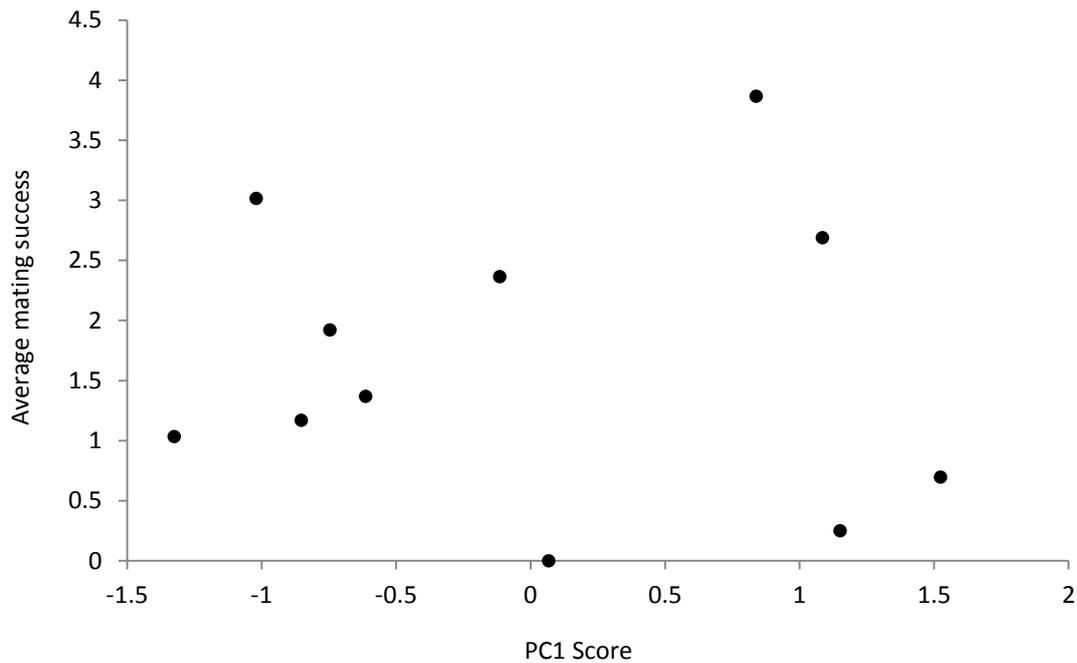
Figure 5.3. Relationship between individual composite scores on the first principle component and average mating success across both years of testing.

5.4 DISCUSSION

In this study we describe a method which enables the cognitive testing of wild individuals over extended trials, without the need for constraint or captivity. We presented a series of novel tasks which tested a range of cognitive domains, including problem-solving, novel motor skills, colour and shape discrimination, behavioural flexibility and simple, local spatial abilities. Male spotted bowerbirds differed in their ability to solve these tasks, and performance in any one of these tasks was a relatively poor predictor of performance in any of the other tasks. We found weak, non-significant positive correlations between individual performances, which, in part, mirrors results gained from the con-generic satin bowerbird (Keagy et al. 2011). Few species have been subject to an in-depth battery of cognitive testing with an emphasis on quantifying within-species individual variation (Thornton & Lukas 2012), but in those species which have, this positive co-variation has been summarised by a single factor and has been described as analogous to human *g* (Chandra et al. 2000; Plomin & Spinath 2002; Matzel et al. 2003; Banerjee et al. 2009). Although the PCA extracted more than one principal component with an eigenvalue >1, all tasks loaded positively onto this component which captured over 44% of the total variance in

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performance. This is above levels which have previously been accepted as evidence for *g* in humans (circa 40%) (Plomin & Spinath 2002), and in mice (circa 30%) (Matzel et al. 2003), and is also higher than has been found in satin bowerbirds (28-33%) (Keagy et al. 2011). Thus, it could be concluded that male spotted bowerbirds exhibit individual differences in cognitive performance which operate within a general cognitive structure across domains; a general intelligence. Such domain-general intelligence may be important for tackling nonrecurrent problems, which are evolutionarily novel in nature (Chiappe & MacDonald 2005, Sol 2009).

The first set of tasks (barrier removal) tested naturalistic behaviours with assumed cognitive domains. Males were more motivated to interact with the barrier when there were objects (aversive or desirable) underneath, suggesting that the presence of the barrier did not pose a problem in itself. Therefore, we can be confident that this task reflected a male's capacity to remove a barrier to access novel objects, with the highest motivation being to remove unwanted aversive objects. A similar proportion of males solved the aversive object tasks as had been found in satin bowerbirds (Keagy et al. 2009). Males who pecked the barrier more times were not faster solvers, indicating that solving this task was not simply a product of persistence and vigour.

As with many problem-solving tasks, it can be difficult to identify the specific cognitive ability being tested, or to rule out alternative, non-cognitive explanations for success (Thornton & Lukas 2012). Males may have been able to solve such tasks through luck, for example, by inadvertently tipping the barrier against debris. The fact that this problem-solving task loaded positively, albeit weakly, onto the first component suggests that it may align with general cognitive performance across domains. We suggest further evidence is required which investigates this potentially important, yet so far unverified, relationship between problem-solving tasks based on maximising ecological validity and more abstract, domain-specific cognitive tasks with clear psychological definitions. Such evidence would help confirm the tentative relationship we present here.

Our subsequent five tasks aimed to provide a measure of cognitive ability based on paradigms generally accepted within cognitive psychology. Males varied widely in their

success in solving these tasks in the wild. The majority of males were able to solve the colour and shape discrimination tasks, however, surprisingly, many failed to pass the spatial memory and reversal tasks. Male song sparrows required 40+ exposures of a similar reversal task (Boogert et al. 2011a), suggesting that the lack of performance seen in spotted bowerbirds may be due to the limited number of trials presented. Alternatively, the failure of males to pass this and other tasks may be an unintended consequence of our presenting them to free-living animals. Reversal tasks are considered to measure behavioural flexibility (Bond et al. 2007; Tebbich et al. 2010; Boogert et al. 2011a; Leal & Powell 2012) and we expected male bowerbirds to exhibit a high level of behavioural flexibility based on the complex nature of their display behaviours and their inhabiting fluctuating environments. However, we detected no such ability. One reason may be because wild male bowerbirds were more easily able to switch to an alternative choice strategy, for example, by searching for reward resources elsewhere in their environment. Under constrained laboratory conditions individuals presented with cognitive experimental equipment are often presented with the task in isolation, preventing the opportunity to switch to an alternative. Arguably, switching in itself is a demonstration of behavioural flexibility, but our tasks were not designed so as to detect it in this context.

One further explanation why males failed to solve some of the tasks may have been due to our inability to control motivation in the wild. Male bowerbirds continually engaged with task equipment and showed high levels of motivation throughout the study period but we could not control their individual motivation level for each task on any given day. However, motivation is rarely standardised in laboratory conditions either; starvation periods may increase, but are unlikely to equalise, motivation and may also increase stress which can impact on performance (Kolss & Kawecki 2008; Lupien et al. 2009). Increasing motivation artificially through starvation and restricting behavioural responses to a single task may not accurately reflect inter-individual variation, and as Thornton and Lukas (2012) point out, it may be difficult to envisage how abilities which are only manifested under artificial conditions are selected for in nature. This highlights a potential important limitation of relying solely on captive studies to draw evolutionary explanations, and calls for the further development of cognitive tests to be transferred to the wild to complement conclusions drawn from captivity.

We found no relationships between a male's performance on any single problem-solving or cognitive task and his mating success, nor between composite measures of performance (the principal components and individual average rank score across tasks) and mating success. We are reticent about drawing strong conclusions from our dataset considering the relatively limited number of tasks (six) that we set the males and, due to the nature of conducting such tests in the wild, our sample sizes for all tasks were limited, and as such suffer from low statistical power. We had the largest sample size in our barrier tasks, with the number of individuals tested being similar to the number of male satin bowerbirds tested in the previous study (Keagy et al. 2009). However, our lack of relationship with mating success contrasts with the satins, which is surprising, as the complex nature of the spotted bowerbird display when compared to the satin's, coupled with the associated relative difference in brain size (Madden 2001a), suggest a stronger dependence on cognitive performance for the construction of the spotted display. Similarly, the results from composite measures of performance differ in part from those found with satin bowerbirds, where low inter-correlations between tasks initially suggested independence between cognitive domains, yet an integrated measure of performance across cognitive tasks predicted mating success (Keagy et al. 2011, 2012). We repeated our analyses controlling for male bower tenure, and found no significant impact of this on our results, supporting previous results on problem-solving in satin bowerbirds. We used male bower tenure as a proxy for male age; male tenure is arguably a more reliable indicator of male experience, as males may differ in the age at which they gain bower ownership and thus the amount of experience gained within similar age brackets. However, although male age has been shown to influence certain aspects of male display and mating success in bowerbirds, performance in novel cognitive tasks may not be intrinsically linked to age and/or experience in species which already delays display until maturity (Collis & Borgia 1992; Keagy et al. 2009, 2012). In both the satin and spotted bowerbird studies results rely on relatively small sample sizes and thus are susceptible to noise, but the lack of consistency between performance in two very similar tasks may indicate meaningful differences between con-generic species.

There are several explanations for why a lack of a positive relationship between cognitive performance and mating success may be a true reflection of mate choice decisions

in spotted bowerbirds. In contrast to satin bowerbirds, we found no correlation between mating success measured in the two consecutive years of our study, suggesting there is variation in intra-male display quality and/or female mate preferences over time. Such variation in mating success may be better explained by non-cognitive factors, such as a male's social status and/or opportunities for learning and experience (Collis & Borgia 1992) or with changes in male physical attributes, such as parasite load (Borgia & Collis 1989). Alternatively, this lack of relationship may reflect variable female preferences for males; females may differ in their choices of mates in ways that are not directionally aligned with male quality (Cotton et al. 2006). Low quality females may actively choose lower quality males (Riebel et al. 2010), or have weaker mate preferences compared to high quality females (Cotton et al. 2006), and preferences may change as females age (Coleman et al. 2004). Variable or assortative female choice may confound any directional selection for cognitive traits. Relationships between sexually selected traits and cognitive performance may not always be direct; in male guppies, females showed a preference for males with an enhanced rate of learning, but this was not related to well described sexually selected traits in this species (body size and orange patch saturation), and the mechanism by which females are gaining such information remains unknown (Shohet & Watt 2009). Similarly, cognitive ability may be indirectly reflected in display traits via its influence on other behavioural mechanisms, such as foraging ability (Boogert et al. 2011b).

An additional explanation for a lack of relationship may be because the construction of a high quality bower, known to be an important target in female choice, (Borgia 1985; Borgia & Mueller 1992; Lenz 1994), relies on singular cognitive skills which are not transferable across even quite conceptually similar tasks. Specific traits may be independently selected without a requirement for overall intelligence (for example, face perception ability in humans may be determined by specific cognitive specialist genes which are not necessarily related to any general cognitive measure (Zhu et al. 2010). Alternatively, the complex and multi-faceted nature of bowers could suggest that successful bower-building can be achieved through numerous combinations of skills; for example, little is known about the degree to which bower-building is socially learned (Madden 2008). Evidence in satin bowerbirds suggests that multiple display traits may indicate one

integrative measure of overall cognitive ability to females and/or different aspects of male quality (Keagy et al. 2012) although the exact nature of these associations remains unclear.

Finally, inferior individuals may be more likely to adopt innovative behaviour; Cole and Quinn (2012) found that in great tits, *Parus major*, competitive ability was negatively correlated with novel problem-solving ability, and Thornton and Lukas (2012) raise the interesting notion that perhaps individuals who are low achievers are the ones who employ an elevated expression of innovation in order to compete with superior competitors, thus confounding any effects of selection for such traits.

We employed a range of cognitive tasks with which male bower owners were repeatedly motivated to engage with in the wild. We based our tasks on natural behaviours that males appear to exhibit, but de-coupled the specific tasks from the natural expression of these behaviours in the wild, allowing for a more rigorous exploration of defined cognitive traits. We found little support for the suggestion that enhanced cognition is selected for through mate choice, but accept there are limitations to the conclusions we can draw from this limited dataset, and encourage further exploration of these concepts. We hope that the methods described here will inspire others to develop opportunities for exploring the link between cognitive performance across domains in a range of contexts. We expect the increasing number of studies testing the relationship between cognitive performance and fitness outcomes will create more opportunities to refine the methods used and generate a deeper understanding in both males and females of the evolution of cognitive differences within species and the selective forces operating on them.

Chapter Six

Competitive social interactions

ABSTRACT

Intrasexual competition can act to maintain honest signalling in elaborate male traits, via the costs involved in negative social interactions. Male bowerbirds, Ptilonorhynchidae, participate in an unusual form of intrasexual competition that involves the destruction of structural components and theft of decorations at another male's bower; the site of male courtship display. We asked whether the rates of marauding received by male bower owners varied in a population of wild spotted bowerbirds, whether these marauds were targeted towards particular males and what factors may predict the rate of marauding a male received. Rates of marauding varied between males, and were positively correlated across two of the three seasons we monitored, suggesting that individuals experience a moderately consistent level of attack from their rivals. Marauding occurred predominantly between nearest neighbours, but was rarely reciprocated between males. Pairs of males within short geographical distances were not more likely to maraud each other based on differences in mating success rates, owner attendance rates, tenure, the total number of decorations on a bower, bower structural symmetry, volume or quality scores. Bower maraud rate was negatively correlated with bower quality scores and reduced bower structural consistency, but we found no relationship with other male or bower characteristics. Marauding rates did not predict male mating success. Marauding by rival males may act to limit the overall quality of a male's sexual display, and therefore socially control a male's ability to exhibit a display above his status. However, our results show that whilst marauding is often targeted towards particular individuals in the population, we found no indication of what factors predicted such directed attacks.

6.1. INTRODUCTION

The impact of intrasexual competition can result in variation in the ability of males to exhibit sexually selected traits and, combined with directional selection pressure exerted by female choice, can determine differences in mating outcomes and reproductive skew (Maynard Smith and Harper 1988, Andersson 1994, Berglund et al. 1996, Kokko and Johnstone 1999, Wong and Candolin 2005). Elaborate traits may therefore act as signals of male social status and quality and convey information regarding his dominance, strength or condition. For example, the width of the black breast strip in great tits, *Parus major,* can signal male dominance to naïve individuals (Lemel and Wallin 1993) and achromatic plumage colouration in male black-capped chickadees, *Poecile atricapilla*, indicates social rank and age (Mennill et al. 2003). Often, elaborate traits function simultaneously as competitive male status symbols (directed towards rivals) and as sexually selected traits (subject to female assessment) (Berglund et al. 1996); the plumage badges of collared flycatchers, *Ficedula albicollis*, for example, reflects male social position and predicts female choice (Pärt and Qvarnström 1997).

Competitive interactions between males may be costly, and these costs may help maintain honesty in trait expression. Males may be punished for signalling above their social status (Candolin 2000a, b). Male house sparrows, *Passer domesticus*, whose sexually selected throat patches were experimentally enhanced engaged in higher numbers of aggressive encounters with other males compared to control birds, suggesting that cheaters were socially controlled through targeted attacks (Möller 1987). As signalling is expected to be condition dependent, the maintenance of honest signalling may therefore offer an explanation for individual variation in male trait expression (Grafen 1990a; b). Due to the potential costs involved in engaging in competitive exchanges, interactions between individual males are likely to be non-random and targeted to maximise fitness benefits (Krause et al. 2007, Pruett-Jones and Heifetz 2012). The non-random assortment and impact of intrasexual competition may be dynamic as the social environment changes over time, and therefore provide a mechanism for the maintenance of variation between males. Understanding the nature of intrasexual competition may play an important role in, and further our understanding of, the evolution of elaborate traits and intrasexual behavioural strategies.

Male bowerbirds offer a unique system in which to test the assumptions and impacts of male-male competition on inter-individual variation in the expression of male display. Unusually, an important sexually selected trait in male bowerbirds is extended from the body of the male and instead it is represented via the intricate and complex construction of bowers (Borgia 1985b, Borgia and Mueller 1992, Borgia 1995, Madden 2003b, Frith and Frith 2004). These bowers consist of decorated display courts with stick and grass constructions, which act as the site of sexual display and copulation (see Frith and Frith 2004) and function to increase male attractiveness whilst being physically separated from the male. Thus, they may be described as extended phenotypic traits (Schaedelin and Taborsky 2009). Properties of the bower, such as construction quality and the number of decorations, predict female mate choice (Borgia 1985b, Borgia and Mueller 1992, Lenz 1994, Madden 2003).

The bower is a target of competitive interactions between males, who attempt to disrupt the displays of rivals by destroying the bower structure and stealing decorations (Borgia 1985b; 1995, Pruett-Jones and Pruett-Jones 1994, Madden et al. 2004a; Madden 2006, Wojcieszek 2007, Doerr 2009; 2011). Unlike many other forms of intrasexual competition, bower destruction behaviour (marauding) acts directly on the sexual trait without affecting the physical or bodily condition of the male (Humphries and Ruxton 1999), and impacts can be detached from any resultant changes in natural selection pressures (Madden 2002). Furthermore, engaging in decoration theft can simultaneously decrease a competitor's attractiveness and increase the bower quality of the marauder (Borgia 1985a; b, Morrell and Kokko 2004). The impact of marauding on a victim's display can persist long after the initial interaction has taken place, and the balance of time taken to rebuild/redecorate may influence the optimum maraud versus guard strategy for individual males (Pruett-Jones and Heifetz 2012).

Marauding may be a costly activity for males to participate in. Marauders are required to leave their own bowers in order to visit another, potentially leaving them unattended and vulnerable to attack. There may be energetic costs associated with marauding behaviour, as males must travel to other bower locations and vigorously rip up bower structures, or transport decorations stolen to their own bowers (Pruett-Jones and

Pruett-Jones 1994, Frith and Frith 2004). Due to such costs, the pattern of marauding within bowerbird populations may be expected to be non-random and instead targeted to maximise impact with minimum cost to the marauder. Males may minimise such costs by targeting bowers within a short distance, and many studies report that males most frequently maraud their nearest neighbours (Borgia 1985a, Borgia and Gore 1986, Lenz 1994, Madden 2004b). Marauding neighbours may be of greater profitability to males through reduced travelling costs and also increase the relative attractiveness of their own bower within a local population (Pruett-Jones and Pruett-Jones 1994, Hunter and Dwyer 1997). Males may maximise benefits by selectively targeting other males within their suite of neighbours. These may be direct benefits, accrued by targeting neighbours most similar to them in attractiveness or, alternatively, those with the most elaborate bowers thus raising the relative quality of the focal male's bower in comparison to those of his neighbours. Benefits may also be indirect, with focal males avoiding targeting close relatives (Reynolds et al. 2009). Rates of marauding can vary widely between populations; records of bower destruction rates at one population of spotted bowerbirds was almost 20 times lower than at another, despite inter-bower distances being half as much (Madden 2006). This suggests that, at a population level, factors other than simply inter-bower distances determine the level of intrasexual competition. We revisited a population of spotted bowerbirds at Taunton National Park (see Madden 2006), and asked whether particular features of the bower, or differences in features between males, determined the rates of marauding male bower owners endured, and which factors may have predicted the inter-individual variation in marauding rates observed.

We asked whether male bowerbird variation in the expression of a sexually selected trait was mediated by their social environment. If marauding acts to socially control the signalling status of males, then we may expect males to vary in their ability to produce a high quality signal due to differences in their social position. First, we asked how marauding rates at bowers varied over the course of a season, and between seasons for males that retained their bower ownership. Within a season, males construct and maintain their bowers over a period of months, during which females may make repeated visits to bowers before choosing a male (Uy et al. 2000, 2001). We expected that bower marauding may be more frequent during the time when males were constructing and maintaining their

bowers, and decrease later in the season once females begin copulating. Ownership changes were relatively rare (between 2009-2011, N = 6), and we expected that if marauding was determined by male status within the social environment, then the rate of marauding an individual male experienced would be stable across seasons. We then asked what factors may influence the rate of destruction a male experienced. We asked whether marauding was predominantly targeted at males within a locally geographic area as the marauder, or dependent on the number of other bower owners within a short radius. Additionally, if males target bowers within their local area we may expect there to be a high rate of reciprocated attacks between pairs of individuals that are closer together.

Second, we asked how each of eight factors correlated with the rate of marauds experienced by an individual, in order to help characterise bowers at which marauding was a greater occurrence; an individual's mating success, his relatedness to the marauder, the total number of decorations on the bower, the symmetry of the bower structure, bower volume (as a measure of structural size), the attendance rate of the bower owner at his bower, bower owner tenure (as a proxy for age) and bower quality. We looked at the impact of marauding on (i) a male's ability to retain a consistent display over the season, looking at changes in both structural properties and decoration number. We expected marauding; a competitive activity occurring between males, to decrease the attractiveness and overall quality of a male's bower. Consequently, if the rate of marauding experienced by an individual is a reflection of his social position within the population and/or his ability to maintain a high quality bower then we might expect that males experiencing the highest rate of marauding to gain the lowest number of copulations.

6.2. METHODS

6.2.1. General field methods

A population of wild spotted bowerbirds were monitored for three consecutive breeding seasons between 2009-2011 in Taunton National Park (Scientific) in central Queensland, Australia (see Miles and Madden 2002 and Chapter 2.5 for a detailed description of the study site). Males construct and decorate their bowers between July-

January, and return to the same bower location each season. We refer to each season by the year in which it began. Males are long-lived and can hold tenures at their bowers for >10 years, and during our study period we observed only six changes in bower ownership (Chapter 2.3). Males were individually identifiable by coloured leg bands. Bowers where owners changed within the season (N = 5) were excluded from analysis.

6.2.2. Collecting behavioural and marauding data

Bowers were monitored using remote, motion-sensing cameras which were *in situ* for the duration of the breeding season. Not all bowers were active and/or monitored in each season. All behaviours were scored and calculated as rates based on the number of camera recording hours at each bower. Camera hours differed minimally between bowers based on the date of deployment and due to rare camera failures in the field. Attendance rates by male owners at their bowers were calculated based on the total amount of time a male was present in the immediate vicinity of his bower, regardless of the activity he was engaged in (Chapter 4.2). Attendance rates were not available for all bowers, due to differences in picture analysis techniques (see Chapter 2.7.4).

Marauding was defined as the physical destruction of the bower through the violent ripping apart of its structural components by an individual identified as not being the bower owner (see Table 2.3). We recorded a total of 684 individual marauding events at bowers across three seasons (2009-2011), the majority of which were carried out by males that could be individually identified (Table 6.1). The percentage of identified individuals that were known bower owners was lower in 2009 when fewer birds were banded, and increased each subsequent season as more bowers were located and owners identified. Marauding rates were calculated as the number of marauds experienced at the bower per camera recording hours at that bower *1000.

Season	Bowers monitored with cameras	Total number of marauds observed	% by identifiable marauders	% by known bower owners
2009	18 (16)	188	67.74	37.63
2010	24 (14)	261	70.88	54.02
2011	19 (17)	235	81.28	74.89

Table 6.1. The number of bowers monitored in each season, with the number of individual maraud events observed and the percentages of which were carried out by identifiable individuals. Numbers in brackets indicate the number of bowers for which full attendance rates records were available; for bowers without attendance rates, marauding rates were obtained from camera data in an identical manner as bowers for which attendance rate data were available.

6.2.3. How do males vary in their rates of marauding?

We asked whether marauding was targeted at bower owners during two particular periods in each season. Each season was divided into pre- and post-copulation periods based on the date of the first observed copulation in the population. Paired t-tests were used to ask whether marauding rates varied between these two periods in each of the three seasons (the differences in which bowers were monitored across each season precluded the use of repeated measures across seasons). We then compared rates of marauding experienced by males that were present as owners for more than one season across seasons using Spearman's rank correlations; positive correlations may indicate that a male's tendency to be attacked by his rivals was consistent over time.

6.2.4. What factors determine marauding rates at bowers?

Bower locations were recorded using a Garmin GPS in each season in which they were found, and these coordinates were used to calculate inter-bower distances for each season using the Geographic Distance Matrix (Ersts n.d.). Mantel correlations, computed using PopTools (Hood et al. 2010) and based on 1000 randomisations, were used to compare matrices of inter-bower distance with a matrix of the number of marauding events recorded for each pair of males that were monitored with cameras. Goodness-of-fit tests

were used to ask whether males whose bowers were within 2500m of each other were more likely to maraud each other than any other random pair of males from the population.

To ask whether marauding interactions were reciprocated between males, we constructed directional marauding matrices based on interactions between each pair of males in the study population. We compared the top and bottom halves of these matrices using Mantel correlations, based on 1000 randomisations, to test whether marauds performed by one male towards another were mirrored by a reciprocated maraud in the opposite direction. A positive correlation would indicate that marauds received by one male from a rival male were similar to the marauds that victim inflicted on his marauder.

6.2.5. What characteristics of the male and his bower correlate with the maraud rate it experiences?

Spearman's rank correlations were conducted between the measures of seven different characteristics of the male and his bower and the rate of marauding that he experienced. We looked for correlations with marauding rate between (i) a male's mating success (Chapter 2.8), (ii) the attendance rate of the bower owner at his bower (see Chapter 4.2), (iii) owner tenure (as a proxy for male age, see Borgia 1993 and Chapter 5.2.4), (iv) the total number of decorations on a bower, (v) bower volume (as a measure of structural size), (vi) bower symmetry (see Chapter 4.2.5) and (vii) bower quality scores (see Table 2.1).

6.2.6. What factors predict whether male pairs interact?

To determine why some male pairs interacted whilst others did not, we asked whether male pairs within a short geographical distance of each other were more likely to maraud each other based on differences in the seven male and bower characteristics listed above, and also with relatedness scores for the same pairs of bower owners. Each possible male pair with bowers within 2500m of each other was assigned a single value for each characteristic. This value was the difference between measures determined for each individual in that pair. We calculated relatedness scores between pairs of individuals using DNA genotyping from blood and feather samples collected in the field (see Griffiths et al. *in prep)*. Relatedness scores, *r*, between pairs of individuals were obtained and compared

between the pairs of males within short distances of each other. To account for directionality in marauding (i.e. that marauding by male 1 directed towards male 2 could be considered to be independent of male 2 marauding male 1), each pair was listed twice, once with each individual assigned as the marauder and once as the victim. We considered these pairs to be independent due to the lack of reciprocation of marauding between individuals in a pair (see 6.3.2.), suggesting that different factors may be governing each male's motivation to maraud the other. Generalised linear models with binary response terms were used to ask which characteristics may determine whether a pair interact (binary responses were coded as "yes" for when the assigned marauder attacked the assigned victim, and "no" when there was no interaction between the marauder towards the victim).

6.2.7. What impact does marauding have on bower consistency?

Bower consistency was a measure of how constant an individual male's bower structure and decorations were across seasons. Consistency was calculated by generating similarity matrices which grouped bowers with similar proportions of decorations or structural properties together to gain a quantitative measure of similarity between two bowers for a given season, which were compared using permutation tests (see Chapter 3.2 for full description of the methods). We extracted individual consistency scores for each male and used linear regression to ask whether the rate of marauding experienced by a male predicted how consistent he exhibited his sexual display.

6.2.8. What impact does marauding have on a male owner's mating success?

Finally, we asked whether higher rates of marauding experienced at a male's bower decreased his attractiveness to females, and thus reduced his mating success. Mating success was measured as the rate of copulations gained by a male during each season. Copulations were easily recognisable behaviours from camera data, occurring in the bower avenue (Borgia et al. 1985, Frith and Frith 2004). We summed the number of copulations each male gained, and calculated his mating success (see Chapter 2.8). We used linear regression to ask whether maraud rate predicted mating success in each of the three seasons, and then conducted a linear mixed model (LMM) analysis to account for the differences in mating success and maraud rate within individuals that were present across

all three seasons; mating success were entered as the dependent variable, with maraud rate as a fixed effect, and season and male identity as random effects.

6.3. RESULTS

6.3.1. How do males vary in their rates of marauding?

Male bower owners were marauded throughout each breeding season, with no difference in marauding rates before and after the first copulation (paired t-tests, 2009: t_{17} = 1.30, P = 0.21, 2010: t_{23} = -1.51, P = 0.14, 2011: t_{18} = -0.62, P = 0.54, Figure 6.1). Mean rates of bower marauds across the population did not differ between the three seasons (mean 2009(±SD) = 2.94(2.95), 2010(±SD) = 4.78(3.27) and 2011(±SD) = 2.96(3.61), $F_{2,60}$ = 1.86, P = 0.16). Individual rates of marauding across seasons were positively correlated between 2010 and 2011 (r_s = 0.66, N = 17, P = 0.004), however neither marauding rates in 2010 or 2011 were correlated with rates in 2009 (2009-2010: r_s = 0.25, N = 15, P = 0.38; -2011: r_s = 0.40, N = 15, P = 0.14).
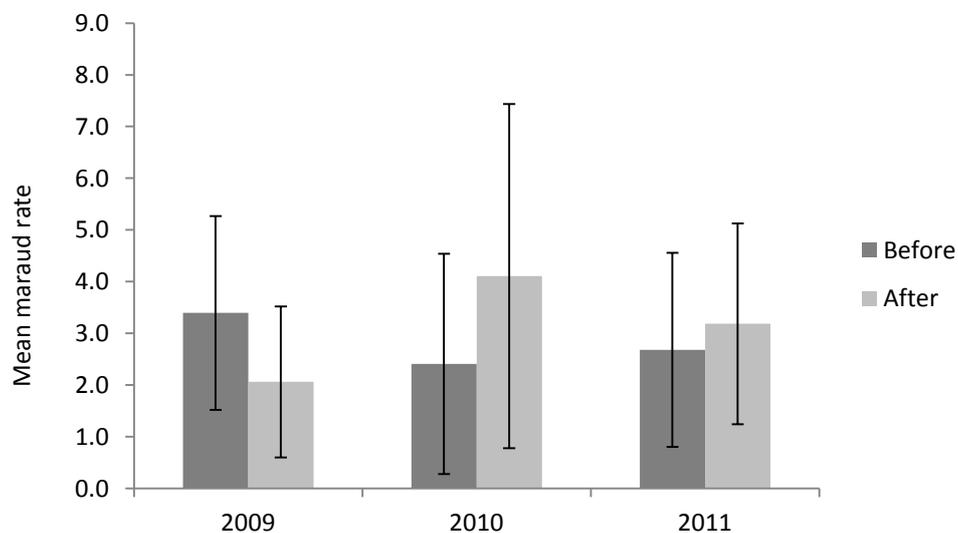
Figure 6.1. Mean rates of marauding (calculated as the number of events per camera recording hours *1000) in each season before and after the first copulation in the study population was recorded.

6.3.2. What factors determine marauding rates at bowers?

Males marauded bowers that were geographically nearby (Mantel correlations; 2009: r = -0.28, 2010: r = -0.20, 2011: r = -0.21, all P < 0.001, Table 6.2). Males whose bowers were within 2500m were more likely to maraud each other than random pair of males in the population (goodness of fit test: G = 32.7, P < 0.001).

Season	Average distance between pairs	Min	Max	Mantel correlation
2009	1406	913	2799	-0.28
2010	1415	788	2524	-0.20
2011	1377	945	2878	-0.21

Table 6.2. The distances (metres) travelled by male bower owners from their own bower location to maraud another male's bower. Mantel correlation coefficients reported are all P < 0.001.

Marauding was not reciprocated between males more than would be expected by chance (Table 6.3), and the majority of marauds were carried out in a uni-directional manner and with a high level of skew towards certain individuals (Figure 6.2).

Season	No. of interacting pairs	No. reciprocated	r	P
2009	13	3	0.29	0.84
2010	11	4	0.03	0.95
2011	10	2	0.18	0.98

Table 6.3. The number of camera-monitored pairs of bowers in each season that were known to interact, and the number of pairs in which marauding activities were reciprocated. Mantel correlations were used to determine whether reciprocity was significant.
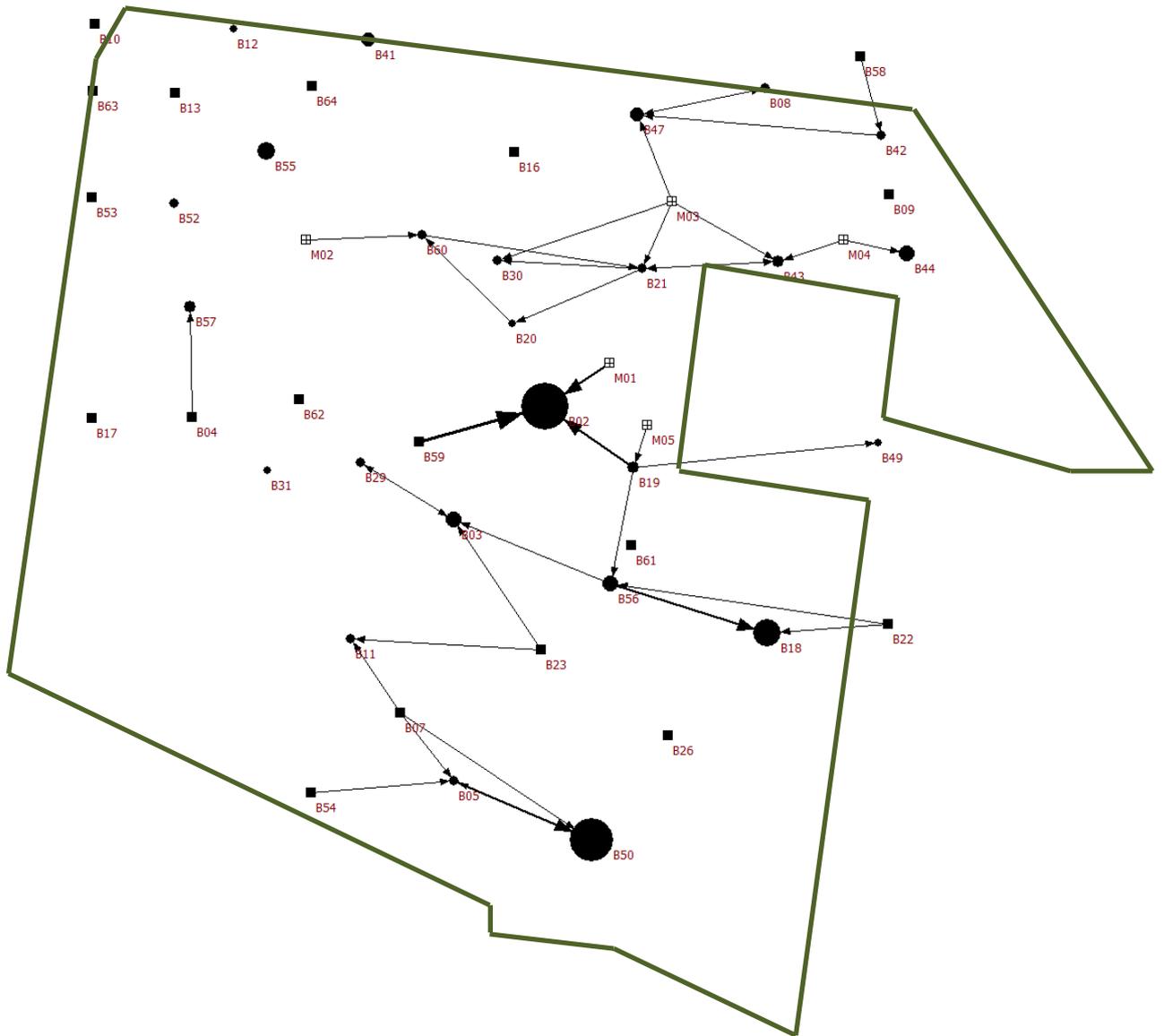
Figure 6.2. The marauding network for bowers in 2009 at Taunton National Park (outlined). Circles indicate bowers monitored with cameras, squares indicate bowers without. Size of the nodes represents rate of marauding suffered by that individual. Arrows are directed from marauder towards victim, with double-ended arrows representing reciprocated marauds between pairs. Arrows are weighted according to the number of marauds experienced between that pair. Unfilled squares with individuals denoted by the prefix M refer to identifiable males whose bower locations have not been found; their spatial position on the map is inferred.

6.3.3. What characteristics of the male and his bower correlate with the maraud rate it experiences?

Males that were marauded at higher rates had lower quality bowers (Table 6.4). There were no correlations between a high rate of marauding and any of the other variables we measured.

Characteristic	2009			2010			2011			Fisher's omnibus	
	r_s	N	P	r_s	N	P	r_s	N	P	X^2_6	P
Mating success	-0.21	19	0.38	-0.36	24	0.08	-0.2	19	0.41	8.77	<0.20
Attendance rate	0.44	16	0.09	0.43	14	0.13	0.24	17	0.35	11.00	<0.10
Tenure	-0.14	19	0.56	-0.35	24	0.10	-0.02	19	0.94	5.89	<0.25
Total decorations	-0.26	19	0.29	-0.22	24	0.31	-0.16	19	0.51	6.16	<0.25
Symmetry	0.05	19	0.83	0.12	24	0.59	0.37	19	0.12	5.66	<0.25
Bower Volume	-0.04	19	0.88	-0.14	24	0.51	-0.02	19	0.94	1.73	<0.25
Quality	**-0.54**	**19**	**0.02**	-0.40	24	0.06	**-0.51**	**19**	**0.03**	**20.46**	**<0.003**

Table 6.4. Spearman's rank correlations between characteristics of the male and his bower characteristics and the maraud rate experienced at that bower. Fisher's omnibus tests were used to combine significance across seasons. Significant results are in bold. N is reduced in some attendance rate analyses due to the availability of camera data.

6.3.4. What factors predict whether male pairs interact?

We found that marauding interactions between pairs of male bower owners were not predicted in any season by differences in their mating success rates, bower attendance rates, tenure, total decoration number, relatedness, bower volume or symmetry and measures of bower quality (all P > 0.05). None of these factors predicted interactions in any of the three seasons studied.

6.3.5. What impact does marauding have on bower consistency?

Bowers that experienced higher rates of marauding had lower structural consistency in 2009 and 2010 (2009: linear regression, adjusted $R^2 = 0.34$, P < 0.01, 2010: $R^2 = 0.16$, P = 0.03, Figure 6.3). In 2011 marauding had no impact on structural consistency ($R^2 = 0.002$, P = 0.32). Marauding rate did not explain the variation observed in decoration consistency in any year (2009: $R^2 = 0.01$, P = 0.29, 2010: $R^2 = 0.03$, P = 0.20, 2011: $R^2 = -0.06$, P = 0.98).
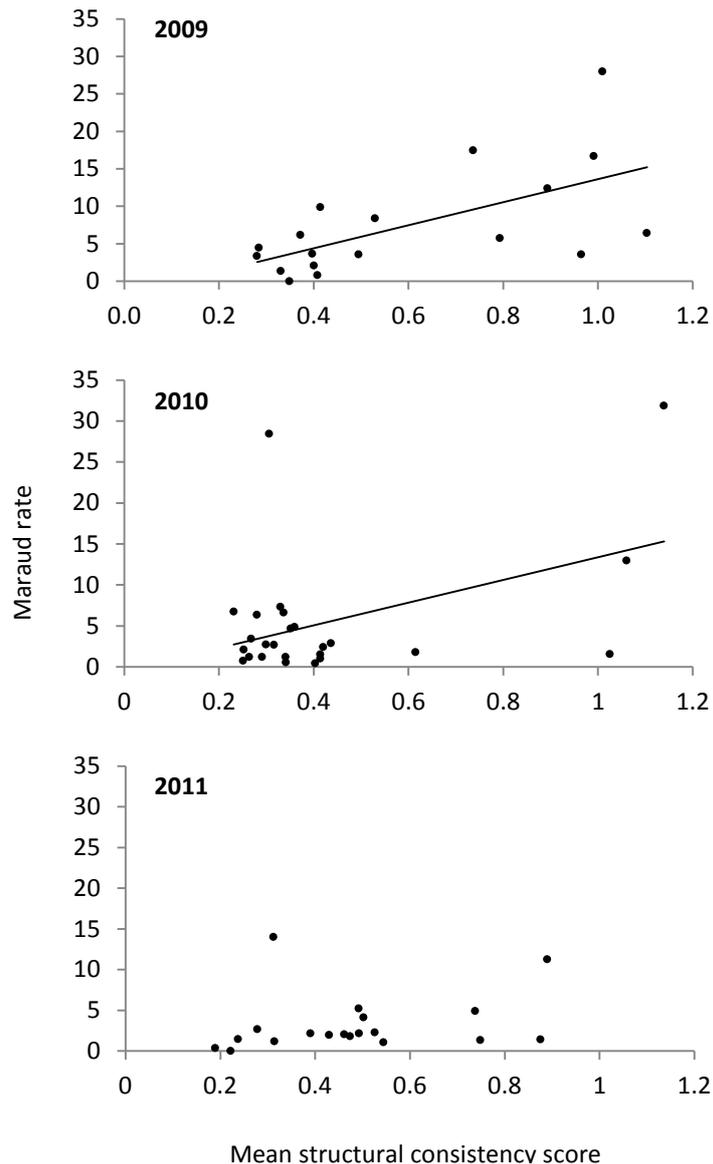
Figure 6.3. Mean structural consistency scores with maraud rates across three years of study. Marauding rates were calculated as the number of marauds experienced per camera recording hours *1000. Lower consistency scores indicate bowers are more consistent, high scores indicate inconsistency across measuring periods. In 2009 and 2010 a significant proportion of the variation in structural consistency was explained by marauding rates, however in 2011 marauding had no significant impact on structural consistency.

6.3.6. What impact does marauding have on a male owner's mating success?

The rate of marauding experienced at a bower did not predict the bower owner's mating success (2009: $F_{1,18} = 0.95$, P = 0.34, 2010: $F_{1,24} = 2.54$, P = 0.12, 2011: $F_{1,18} = 1.67$, P = 0.21). When we accounted for differences in marauding rates and mating success across seasons there was no relationship between the two factors (LMM: $F_{1,40} = 2.78$, P = 0.10).

6.4. DISCUSSION

Male spotted bowerbirds experienced varying levels of intrasexual competitive interactions, which appeared to be highly targeted towards particular individuals in the population. Mean rates of marauding did not differ between seasons, and were correlated for individuals across two of the three seasons we monitored. Our results suggest that particular individuals are commonly the target of competitive attacks carried out by other individuals in the population, and that such victims can be consistently targeted over multiple seasons. Marauding rates across the population did not change as seasons progressed, with no differences in periods pre- and post- the onset of copulations. This suggests that marauding is effective at all times when bowers are being attended by their owners, and the lack of fluctuation in marauding rates indicates that marauding behaviour is not dependent on, or determined by, changes in local environmental conditions or factors such as the availability of decorations. Models of marauding strategies suggest that males that guard their bowers and do not maraud always do better (Pruett-Jones and Pruett-Jones 1994) and that males that are able to repair bowers quickly should also maraud most (Pruett-Jones and Heifetz 2012). Such models indicate that marauding should reflect condition dependence and/or vary with changing ecological conditions, however, we found no evidence to suggest that males respond dynamically to changes in the social or ecological environment, and remained fixed in their role as perpetrator or victim across seasons.

Marauding predominantly occurred between neighbouring individuals, with the majority of males attacking rival bower owners within 2500m of their own bower (approximately 2.5 times the average inter-bower distance). This result corresponds with many previous studies, across different bowerbird species, which all report marauding occurring between geographically nearby individuals (e.g. Borgia and Gore 1986, Lenz 1994, Borgia 1995b, Madden et al. 2004, Wojcieszek et al. 2007, Doerr 2009; 2010b). In satin bowerbirds, Reynolds et al. (2009) reported that males aggregate to display near kin, as is also observed in many lekking species. Displaying near kin may bring direct and indirect inclusive fitness benefits, but where the cost of competition between individuals within a limited area exceeds those benefits related males may avoid displaying near each other (Pruett-Jones and Pruett-Jones 1994). Male spotted bowerbirds do not cluster with relatives, which may be due to the high level of hindrance and interference such

aggregations could bring (Madden et al. 2004). Furthermore, marauders have also been found to not discriminate between relatives and nonrelatives (Madden et al. 2004), suggesting that there may be a lack of kin recognition mechanisms underpinning this lack of population genetic structuring. The pattern of marauding only your nearest neighbours potentially produces an interesting social environment, where each male only competes directly with others within a short geographic distance of his own bower. This may lead to localised populations of males of higher or lower quality, thus maintaining variation between individuals at the population level.

Marauding rates in spotted bowerbirds are considerably lower than recorded in other species, and this corresponds with significantly higher inter-bower distance (Borgia and Mueller 1992, Borgia 1995a, b). Optimum models of marauding strategy suggest that a requirement to travel long distances may impede marauding as being the best individual strategy (Pruett-Jones and Pruett-Jones 1994). There may be energetic costs associated with travelling, or costs associated with being away from the bower, such as missing an opportunity to display to a female or risking the bower being subject to marauds itself. The low rate of marauding might suggest that in this species, bower marauding does not play a major role in affecting the quality of a male's display (Borgia and Mueller 1992). Alternatively, the comparatively low rates of marauding may reflect a relatively high cost of cheating paid by a male owner in this species; in contrast to spotteds, male Regent's bowerbirds frequently maraud and abandon their own bowers following an attack by a rival, rapidly rebuilding elsewhere (Lenz 1994). In an honest system, the variation in male spotted bowerbird bowers may honestly reflect differences in male quality. This 'self-regulation' of display signal in response to a perceived threat of attack by a rival may be sufficient to ensure that maraud rates remain low whilst still effectively acting to regulate honest signalling (Madden 2002). Despite this propensity to maraud bowers within a short geographic range, the majority of marauds occurred in a single direction between pairs and were rarely reciprocated. This is in contrast to the bower destructions recorded in satin bowerbirds (Borgia 1985b), and also with records of the theft of decorations in two independent satin bowerbird populations, where the majority of interactions were reciprocal in nature (Borgia and Gore 1986, Wojcieszek et al. 2007). The directional targeting of particular individuals within the population, often with more than one

neighbour targeting a specific victim, suggests that characteristics of certain males make them more vulnerable to attack.

However, increased rates of marauding showed no correlation with measurements of other male characteristics, or with decoration consistency, suggesting that these factors were neither a causal factor in determining maraud likelihood nor an effect of experiencing increased marauds. Thus, we were unable to identify any particular characteristic that commonly described heavily marauded or untargeted males. Moreover, we found no evidence to suggest that marauding between geographically nearby individuals was governed by differences in their mating success, bower attendance rates or tenure, nor by differences in the physical traits of the bower – the number of decorations, symmetry and volume. As none of these variables emerged as a predictive factors in our binary model, it remains unclear which absolute or relative factors describing a male bower owner make him vulnerable to attack. Wojcieszek et al. (2007) found a similar lack of predictive factors (other than geographic distance) when investigating the likelihood of interaction between pairs of satin bowerbird males. These results also contradict what has been suggested in models of optimal marauding behaviour; Pruett-Jones and Heifetz (2012) suggest that males most likely to mate should maraud the least, whereas rival, unsuccessful males should maraud at maximum levels. It may be that our objective measures of the male's behaviour and properties of his bower fail to capture more subjective aspects of this complex, multi-component display.

Experiencing increased marauding rates was associated with lower bower quality scores and a decrease in structural consistency, but did not predict male mating success. It is difficult to disentangle this result, as higher quality bowers may be targeted, hence causing a decrease in their mating success but the overall effect is lost when measured using our techniques. Costly social interactions, such as marauding, may provide a competitive constraint on a male's ability to display at a high level (Candolin 2000). Our results support this hypothesis in part, as male bowerbirds experiencing higher rates of marauding exhibited lower quality bowers. These results confirm previous findings in spotted bowerbirds; Borgia and Gore (1986) and Madden (2002) both report that males with lower quality bowers endured higher rates of marauding. This could suggest that male bowerbirds

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engage in marauding as a form of social control, punishing males that may be displaying above their status and thereby reducing the quality of their sexual display (Candolin 2000). Marauding may function to maintain trait honesty. In an experimental manipulation of bower decorations in spotted bowerbirds, low quality males rejected artificially provisioned decorations, potentially to avoid negative reprisals from rival males (Madden 2002). The ability to maintain a high quality bower may be determined by a male's social or physical dominance over others. Such condition dependence may maintain variation between males, particularly in a social context where dominance hierarchies may change over time.

Alternatively, marauders may actively target low quality males because the relative impact of marauding is greater than the potential impact on a higher quality bower (Pruett-Jones and Pruett-Jones 1994). For example, in satin bowerbirds, it was suggested that the theft of a decoration from a male with naturally low numbers of decorations had a greater impact relative to the theft of a decoration from a bower exhibiting high numbers (Hunter and Dwyer 1997). Our results do not allow us to tease apart the cause and effect of the relationship between marauding and bower quality. However, we might expect that if males were maximising the impact of their marauding on their rival through decoration theft then they might target low quality rivals, whereas to maximise the impact of bower destructions they might target high quality bowers. This is because the theft of one decoration from a male exhibiting lower numbers may have a greater relative impact than a male with numerous decorations. In contrast, the destruction of the bower structure is likely to have a greater impact on males with the highest quality bowers. We did not consider the movement of decorations between bowers in this study, partly due to the difficulty in marking and keeping track of the hundreds of decorations which could be moved. However, we found no impact of marauding on decoration consistency scores, suggesting that higher rates of marauding were not accompanied by a high rate of decoration theft.

However, the cost of bower attacks on the bower structure, rather than decoration numbers, is likely to be greater for high quality males than low quality males and may disproportionately increase a rival's attractiveness to a greater degree than would be expected from decoration theft. Marauds were characterised by the violent ripping up of the bower structure, often destroying the bower avenue structure (Borgia 1985b; 1995b,

Madden 2002). Following a marauding event, males reused structural material to rebuild their bowers, but may not have been able to reconstruct their bowers to the same quality as before, thus disrupting consistency. This indicates that the act of marauding may have a long term impact on a male's display long after the initial interaction, and, in contrast to decoration theft, may have a higher relative impact on higher quality structures.

To what extent the male interactions in spotted bowerbird populations mediate the expression of their sexually selected trait remains unknown. Individual males experienced consistent levels of marauding across two out of three seasons monitored, which corresponded to minimal levels of disruption in the composition of the social environment (only six males changed ownership). The comparatively low rates of marauding in the spotted bowerbird has led to previous suggestions that it is unlikely that negative social interactions influence female assessment (Borgia and Mueller 1992). To a certain extent, our results agree with this suggestion, as we found no relationship between marauding rates and male mating success. However, this lack of relationship does not imply that social control plays no role in determining the quality of the bower exhibited, thereby indirectly influencing female choice. Males may be able to respond to fine-scale changes in their social environment by adjusting the expression of their sexual signal in order to avoid provoking attacks by neighbouring individuals (Madden 2002). A male's ability to respond to social conditions was observed in three-spined sticklebacks, *Gasterosteus aculeatus*, where males reduced their sexual signalling in the presence of superior competitors (Candolin 2000). For bowerbirds, extended phenotypic traits may offer flexible opportunities for signals to rapidly respond and vary according to changes in male social position with the incoming and outgoing of other males. Flexibility in traits that are able to vary temporally may be useful for females, as they can gain an accurate assessment of male quality at any point in time, thus reducing sampling costs.

Chapter Seven

The role of auxiliary males in collaborative display

ABSTRACT

There are growing numbers of examples of sexual displays in which multiple males participate but opportunities for copulations are limited to a single alpha individual. Alpha males gain benefits from the presence of these secondary males, but the reasons why other males collaborate can be less obvious. Here we report a novel occurrence of collaborative display in male bowerbirds, Ptilonorhynchidae, where male bower owners appear to accept the repeated presence of particular non-bower-owning males (referred to as auxiliaries) at their bowers. Auxiliary males were identified at almost every bower in our study population and, as well as being frequent passive observers, also took part in bower maintenance and performed courtship displays. We examined this novel system and quantified the costs and benefits that each party incurred or accrued as a result of this collaboration. We found that auxiliaries did not appear to gain either direct or indirect benefits; they receive no copulations at bowers and are not related to the owners of whose bowers they attend. However, auxiliaries did have a higher than expected chance of inheriting their bower, or a nearest neighbouring bower, once owners departed. Bower inheritance is potentially an important benefit in a system where display sites may be limited, and there are known advantages of displaying at an established location. Owners that accepted higher rates of auxiliary attendance did not gain obvious benefits; there were no associated reductions in workload, and bower structural and decoration properties were not altered. Nor did owners enjoy a reduced rate of marauding at their bowers. Auxiliary attendance rates at bowers did not relate to owner mating success, further limiting our ability to suggest adaptive benefits from the presence of their auxiliaries. However, our results were confounded by the lack of bowers without an auxiliary, and we are therefore limited to making judgements based on the relative, not absolute, contributions an auxiliary may make to male display. We suggest that auxiliary presence may have been an overlooked form of male collaboration in bowerbird displays, potentially adding an important source of variation to male display.

7.1. INTRODUCTION

In male sexual displays there can often appear to be no obvious role for collaboration between males, especially when they are only providing genetic material to females, and thus the pay-off is typically a single, non-divisible copulation. Yet we find examples of multi-male display across taxa, and particularly in a wide variety of avian species; for example, in manakins (e.g. McDonald and Potts 1994, DuVal 2013), grouse (Kokko et al. 1999), wild turkeys (Krakauer 2005), boat-tailed grackles (Poston 1997) and screaming pihas (Fitzsimmons et al. 2008). Males displaying in coalitions may be able to hold higher quality territories (Oliveira and Almada 1998), inherit breeding positions (Kokko and Johnstone 1999) or increase overall fitness by associating with related males (Shorey et al. 2000). In many collective male display systems there is a skew in copulation success, with a single alpha male in the partnership dominating the majority of reproductive effort at the expense of secondary males (Brown 1987, Poston 1997, Koenig & Dickinson 2004). Alpha males may gain multiple benefits from the presence of secondary males during their display. For example, displaying with others in close proximity may reduce individual predation risk (Boyko et al. 2004) or increase the overall numbers of females visiting and/or the fidelity of females at particular display sites (Gibson et al. 1991, Jennions and Petrie 1997).

Fitness benefits to secondary males may be more difficult to envisage, as the costs of foregoing their own breeding opportunities in order to collaborate with others appears high. Three mechanisms that may lead to selection for collaboration by secondary males have previously been described; (i) direct benefits through an increase in their own reproductive success relative to what may have achieved singularly (Höglund et al. 1993), (ii) indirect benefits through helping closely related individuals breed, thus passing on genetic material indirectly (Hamilton 1964) and (iii) delayed direct benefits where secondary males gain an advantage later in life, for example, through an increased chance of survival, gaining a breeding territory or position, or in gaining skills and experience which later increases productivity (Skutch 1935, Brown 1987, Trainer et al. 2002). In some cases, benefits to secondary males may impose a direct cost on the alpha male, for example, if secondary males secure sneaky or forced copulations with visiting females (Nonacs and Hager 2011), or harass, disrupt or attempt to take over display territories (Kokko and Johnstone 1999). Alternatively, alpha males may simultaneously gain benefits through the presence of a

helper, actively conceding to their presence in order to encourage a cooperative relationship (Kokko & Johnstone 1999).

In many examples of multi-male displays, males collect or cooperate with related individuals in a behavioural display trait which involves participation by all males. Some of the most widely studied and modelled examples of avian multi-male displays are found in lekking species, where males display together in closely clumped distributions (e.g. Oakes 1992, Kokko and Johnstone 1999, Fiske et al. 1998). The exact cost and benefit mechanisms leading to collaboration, and thus the nature of relationships between males can vary widely across species, and numerous pathways to selection for collaboration have been described. For example, the skills and experience gained through cooperation in Seychelles warblers, *Acrocephalus sechellensis*, appears to improve later reproductive success (Korndeur 1996), although cooperation in male lance-tailed manakins, *Chiroxiphia lanceolata*, did not increase subsequent breeding success, but may have offered an alternative route to securing a territory (DuVal 2013). Often it is not possible to separate the effects of immediate from delayed benefits, making the balance of costs and benefits difficult to establish (Koenig and Walters 2011).

The costs and benefits of collective display may differ in cases where the traits targeted by female choice are external to the body of the male. Extended phenotypic traits may be susceptible to different forms of modification and disruption compared to other behavioural traits (Schaedelin and Taborsky 2009). Here, we describe one novel system in which there appears to be collective sexual display in an extremely elaborate and extended phenotypic trait. Male bowerbirds, Ptilonorhynchidae, construct, decorate and maintain complex structures, bowers, which act as a target of female choice (Borgia 1985b, Borgia and Mueller 1992, Madden 2003b, Coleman 2004, Frith and Frith 2004). Each bower has typically been viewed as the product of a single male, who is considered to own, maintain and defend his site over multiple breeding seasons. He secures copulations at these sites, and mating success observed at a bower often relates to physical and aesthetic properties of the bower (Marshall 1954, Borgia 1985, Frith and Frith 2004, Uy & Borgia 2000, Madden 2003b, Endler et al. 2010). However, using long term data from a population of wild spotted bowerbirds, *P. maculatus,* we observed that bowers were frequently maintained by several

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different males. These secondary males were present at particular bowers repeatedly within and across seasons, and, unlike other visiting birds from neighbouring bowers who were attacked if they were detected at the bower, their presence did not usually lead to aggression with other regular males. At each bower, one particular male appeared to perform the majority of bower maintenance and display behaviour, habitually frequenting a bower site from one year to the next, and we term these males as the bower 'owners'. We refer to other males that repeatedly attend the bower as 'auxiliaries'. The aggregation of males at bowers appears to have been reported anecdotally for several species, but has yet to be fully investigated, and the regular occurrence of particular non-owner males has yet to be fully described. Immature satin, *P. violaceus,* and golden, *Prionodura newtonia*, bowerbirds are known to visit bowers owned by mature males (Borgia and Mueller 1992, Borgia 1993), and two Regent bowerbird males, *Sericulus chrysocephalus,* were recorded to have attended and engaged in maintenance behaviour at bowers owned by others (Lenz 1994). Immature males also often gather to form practice bowers at which they construct poor quality bowers and display singularly or to other males (Vellenga 1986, Lenz 1994, Maxwell et al. 2004). However, the repeated presence of auxiliaries at the bowers of other males is likely to have important fitness consequences for both the bower owner and auxiliary, and may challenge the previously accepted notion that male bowerbirds produce an individual sexual signal in their decorated bower.

We explored this novel occurrence of multi-male display using data collected from a long-term study of a population of wild spotted bowerbirds, *P. maculatus*. We provided a detailed description of auxiliary behaviour at bowers, asking how they were distributed across bowers and what activities they engaged in whilst at the bower. We also looked for patterns in auxiliary presence, asking whether auxiliary males showed even patterns of bower attendance throughout the breeding season. We divided each season into two distinct periods; the pre- and post-copulation period. The pre-copulation period was characterised by male bower owners constructing and maintaining bowers, and displaying to visiting birds, but before any observed copulations in the study population had taken place. In satin bowerbirds, it has been suggested that the pre-copulation period allows females to sample multiple male displays, and possibly begin nest-building, before making a final mate choice decision (Uy et al. 2001). The post-copulation period referred to the

remainder of the season after the first copulation in the population had been observed.. We then explored three forms of benefits auxiliaries may gain from attending the bowers of other males. First, we asked whether auxiliaries gain direct benefits by securing copulations at the bower. Non-bower owning males may have a greater chance of encountering females at the bowers of higher ranking males, thus increasing their chance of gaining a sneaky or forced copulation. Second, we explored the possibility that auxiliaries attended the bowers of related owners, thus gaining indirect benefits through kin selection. Third, we asked whether auxiliaries gained delayed direct benefits by having an increased chance of inheriting bowers at which they attend when owners depart. Inheriting bowers could be an important delayed benefit in a system where females show increased fidelity to existing bower locations (Uy et al. 2000; 2001) and males inherit decorations (Borgia 1985a, Doerr 2012).

We assessed the impact of auxiliary attendance on bower owners' behaviour and their bower's properties to ask whether owners benefited or paid costs because of auxiliary attendance. Auxiliary males that contribute towards bower maintenance activities may reduce the maintenance workload required of owners. We asked whether the variation in auxiliary maintenance contributions was reflected by a reduction in owner maintenance workload, predicting that greater contributions by auxiliaries would lead to a lower contribution by owners. Crucially, we asked whether increased auxiliary maintenance affected any bower structural or decoration properties, specifically whether they had more decorations, larger avenue structures or were more symmetrical. Bowers with structures that are symmetrical and densely packed with sticks are favoured by females (Robson et al. 2005, Keagy et al. 2012), and numbers of decorations have also been shown to predict female choice (Borgia 1985, 1995, Uy and Borgia 2000, Madden 2003). A second key benefit that auxiliaries may confer to owners is by offering protection to the bower from marauding conspecifics. Male bower owners engage in a unique form of intra-sexual competition, destroying and stealing from the bowers of other males (Borgia 1985b; 1995b, Doerr 2009a, Pruett-Jones and Pruett-Jones 1994, Madden 2001a, Wojcieszek et al. 2007). Leaving a bower unattended may increase the risk of such attack (Pruett-Jones and Heifetz 2012), thus we asked whether auxiliary males bring benefits to owners through an increased level of protection against marauders. Finally, we asked whether increased auxiliary presence at a

bower conferred tangible fitness benefits on owners, facilitating an increase in mating success.

7.2 METHODS

7.2.1. General field methods

Data were collected from a population of wild spotted bowers in Taunton National Park (Scientific) in central Queensland, Australia (23.54989S, 149.24088E, see Miles and Madden, 2002, for a detailed description of the study site). Spotted bowerbirds are long-lived, and owners return to the same bower location each season, sometimes holding tenures for >10 years (Frith and Frith 2004). Bowers are spaced approximately 1km apart (Miles and Madden 2002), and males begin constructing their bowers in August/September, maintaining them throughout the breeding season until December/January. We refer to each season by the year in which it began.

7.2.2. Identifying owners and auxiliaries

Individual recognition of bower owners was possible from 1998 when banding in this population began. Capture and banding was carried out at bowers using mist nets (see Chapter 2.7.2). Each male was given a unique combination of coloured leg bands and a numbered metal Australian Bird and Bat Banding Scheme band which ensured accurate identification over many years. Blood or feather samples were taken for genetic analysis, allowing genetic and sexing analysis (see Madden et al. 2004a for details of methods). Banding at bowers and subsequent detailed monitoring of behaviour at them revealed the presence of auxiliaries, and their presence at bowers was recorded from 1999 onwards. During three seasons between 2009 and 2011 we used remote, motion-sensing cameras (StealthCam I590, Texas) at bowers to intensively study behavioural patterns at bowers, allowing us to be more precise in our identification of auxiliaries due to higher levels of capture and banding. Auxiliary males engaged in bower maintenance activities and display, but were not observed marauding the bowers at which they attended.

7.2.3. Measuring individual behaviour at bowers

The use of motion-sensing cameras allowed us to intensify our behavioural data collection across three consecutive breeding seasons (2009-2011). Cameras were deployed at bowers at the beginning of each season and remained *in situ* until the end. Not all bowers were active or monitored, and not all auxiliaries were banded and identified in each season. Bowers where owners and/or auxiliaries were not banded were excluded from our analyses, meaning that 11 bowers were assessed in 2009, 13 in 2010 and 15 in 2011. Camera recording hours differed marginally between bowers depending on the date/time cameras were deployed and due to rare camera failures in the field. Behaviours were therefore calculated as rates per camera recording hours. Behaviours at bowers were coded from camera data (see Table 2.3), and we used these to construct detailed time budgets for owners and auxiliaries at their bowers. Total attendance rates included all instances of when an individual was present at a bower, regardless of the behaviour he was engaged in. Bower maintenance rates only included the time an individual spent contributing to improving aspects of the bower, such as maintaining the avenue structure or placing decorations. Both owners and auxiliaries engaged in displaying behaviour at bower, although only bower owners tended to engage in marauding behaviour at other bowers. We recorded one instance of an auxiliary male engaging in marauding, and this auxiliary later became an owner in the same season and at the same bower he had attended.

Individuals attending the bower for a total of less than one hour during a season were excluded, as such contributions were considered to be minimal. Where more than one auxiliary male was present at a bower we summed individual attendance rates to gain overall auxiliary contributions. To look for patterns in auxiliary attendance rates, we compared mean rates across the three seasons using ANOVA, and used Spearman's rank correlations to ask whether auxiliary attendance rates corresponded to rates of attendance by owners. To compare whether patterns of auxiliary attendance were equal across the season, we divided each season into pre- and post-copulation periods based on the date of the first observed copulation. We used paired t-tests to ask whether rates of attendance varied between these two periods.

7.2.4. Benefits to auxiliaries

7.2.4.1. Do auxiliaries gain mating success at bowers they attend?

Copulations occur in the bower avenue (Borgia 1985, Frith and Frith 2004), and were easily recognisable behaviours from our camera data, often preceded by a male engaged in display behaviour. We made observations across 163,877 hours of camera observation data in three seasons between 2009 and 2011, and recorded the identity of all individuals that obtained copulations at bowers to ask whether auxiliary males gained a proportion of these copulations.

7.2.4.2. Are owners and auxiliaries related?

We tested whether auxiliaries gained indirect benefits by attending the bowers owned by individuals related to them. We calculated relatedness scores between pairs of 166 individuals for which blood and/or feather samples had been obtained during capturing between 1998 and 2011. DNA was genotyped using a panel of 16 loci that were originally isolated in satin bowerbird, *P. violaceus,* or wood warbler, *Limmothlupis swainsonii* (Bardeleben et al. 2005, Reynolds et al. 2007, Winker et al. 1999). Relatedness scores, *r*, between pairs of individuals were obtained using methods outlined in (Griffiths et al. *in prep*). We compared mean relatedness scores between known owner-auxiliary pairs (N = 43, consisting of 21 bower owners, some of which were paired with more than one auxiliary) with background levels of relatedness generated by randomising scores between all owners and auxiliaries (N = 455). Randomisations were carried out in PopTools (Hood 2010) using 1000 iterations, and generated a value for relatedness expected by chance given the natural range of relatedness scores between individuals observed in this subpopulation.

7.2.4.3. Do auxiliaries obtain breeding positions via bower inheritance?

We used records of bower ownership and auxiliary identity dating back since 1998 to ask whether known auxiliaries had a greater chance of inheriting the bowers they attended compared with inheritance at chance level. Testing this hypothesis required careful consideration of a relevant null model against which we could compare real rates of inheritance. We faced several complications in developing this model. First we could not be confident that in every season all active bowers were located, therefore there were likely to

be opportunities for auxiliary attendance and inheritance of bowers unknown to us. Second, not all auxiliaries were likely to have been identified prior to their becoming owners. Our null model was therefore constructed using the most conservative estimates of owner-auxiliary inheritance patterns. In each monitored season since 1998 (N = 10 seasons) a minimum of 20 active bowers were recorded in the study population. We assumed that each active bower had one auxiliary male, and that each of these auxiliary males had an equal chance of inheriting any bower in the population. Our model, based on these conservative assumptions, suggests that each auxiliary had a 5% chance of inheriting any specific bower following the loss of an owner. In reality, this estimated percentage is likely to be considerably lower, as in some years >40 active bowers were recorded, and many bowers were known to have >1 auxiliary. Whilst acknowledging the limitations of our model, we suggest it provides a useful starting point to ask whether known auxiliaries at bowers were more likely to inherit the bowers they had attended compared to chance. If auxiliaries only inherit their own bowers ≤5% of the time then we can assume that they have no greater chance than any other auxiliary in the population. Inheritance levels markedly over 5% may suggest that auxiliaries were more likely to inherit the bowers they attended than expected purely by chance.

7.2.5 Benefits to owners

7.2.5.1. Does auxiliary presence reduce owner workload?

We used bower maintenance rates, as opposed to total attendance rates, to ask whether the relative contribution by auxiliaries to bower maintenance corresponded to a reduction in owner maintenance rates. To explore this possibility further, we also asked whether increased auxiliary maintenance allowed bower owners to reduce the proportion of total time at the bower that they dedicated to maintenance, and instead were able to engage in other behaviour such as display. We used Spearman's rank correlations to look for relationships between auxiliary maintenance and owner behaviour rates.

7.2.5.2. Do auxiliaries contribute to improving bower quality?

Structural measurements and decoration counts were conducted monthly at bowers in each season 2009-2011. Mean structural measures were calculated per season from

monthly counts, and comprised of the length, width and height and thickness of bower avenue walls, and a score of avenue symmetry. Symmetry was calculated applying measures of length, height and thickness from the left (L) and right (R) walls of the avenue to the formula: symmetry = (L-R)/(L+R). An average score was used as an overall measure of symmetry, with scores closer to 0 indicating high symmetry and 1 indicating asymmetrical bowers. The total number of decorations from each monthly count at individual bowers was summed, and the mean across the season was used as our measure of each bower's decoration number. We again used maintenance rates as our measure of auxiliary contribution, and used Spearman's rank correlations to ask whether auxiliary maintenance related to increases in the structural and decoration properties of the bower.

7.2.5.3. Does auxiliary attendance at bowers decrease the rate of marauding?

Marauding was an easily identifiable behaviour captured on cameras. A single marauding event was defined by the presence of any individual other than the bower owner, who engaged in bower destruction; ripping up of avenue wall structures and the theft of decorations (Borgia 1985b, Pruett-Jones and Pruett-Jones 1994, Madden 2002, Wojcieszek et al. 2007). The total number of marauds a bower received was converted to a rate per camera recording hours. We used linear regressions to ask whether (i) auxiliary attendance rates and (ii) combined owner and auxiliary attendance rates at bowers could predict marauding rates.

7.2.5.4. Does auxiliary attendance increase mating success for bower owners?

Male mating success was calculated as the rate of copulations gained per male. Observed male mating success has been shown to be a reliable predictor of male reproductive success in the congeneric satin bowerbird (Reynolds et al. 2007). The number of copulations each male obtained was summed, and the dates of the first and last copulations across the study population were used to define the copulation season. Copulation rates per individual were calculated as the number of copulations gained divided by the total number of camera recording hours at that bower during the copulation season. We hypothesised that male owners may gain increased mating success through three potential mechanisms; (i) auxiliary attendance rates as a factor alone, (ii) combined owner

and auxiliary attendance rates and (iii) the improvement of owner display through time spent 'practicing' to auxiliary audiences. As copulation rates differed for males across seasons we entered each male's copulation rate as a dependent variable in a linear mixed model, with season and individual male identity as random effects. We ran the model three times, with auxiliary attendance rate, combined owner and auxiliary attendance rates and owner display to auxiliary rates respectively as separate fixed effects.

7.3 RESULTS

7.3.1. Auxiliary behaviour at bowers

7.3.1.1 How were auxiliaries distributed across bowers?

Auxiliary males were identifiable through their repeated presence at bowers across the season. All except one of the bowers monitored between 2009-2011 had at least one auxiliary (2009 N = 11, 2010 N = 13, 2011 N = 15; total auxiliary presence at 97.4% of bowers over three seasons). This single non-auxiliary bower was not exceptional from other bowers in any of our observations; owner mating success was within the 95% confidence interval of the population average, as were measures of its structural properties and decorations. Almost half (46.7%) of bowers had more than one auxiliary in each season. Of the 33 identified auxiliaries across three seasons, twelve (36.4%) were recorded as auxiliaries at more than one bower within a season. These auxiliaries divided their time disproportionately between these bowers, spending a mean of 68.5% of their time at their primary bower and the remaining 31.5% spent at geographically neighbouring bowers. Thirteen individuals were recorded as auxiliaries over multiple seasons, with ten of these remaining faithful to the same bower and three moving to become primary auxiliaries at different bowers to the previous season.

7.3.1.2. What did auxiliaries do at bowers?

Bower owners spent an average of 78.5% of their total time at bowers engaged in maintenance behaviours, compared to an average auxiliary spending 48.7% of time at bowers engaged in maintenance (Table 7.1). Both owners and auxiliaries spent a lower proportion of their time engaged in maintenance during 2009 compared with 2010 and

2011. For the remaining times that auxiliaries were in attendance at bowers they were not engaged in any specific activity, and commonly appeared to behave as passive attendees at the bower. On average, owners spent approximately 13.2% of their time at bowers engaged in display behaviour, of which almost half (46.2%) was directed primarily towards their auxiliary males (Table 7.1). Owners spent the remaining time displaying towards females, unidentified individuals or to no other observed individual.

Season	Mean rate of auxiliary attendance at bowers	Mean % of owner time at bower spent engaged in maintenance	Mean % of auxiliary time at bower spent engaged in maintenance	Mean % of time owners spent displaying to auxiliaries
2009 (N = 11)	7.66 (± 6.74)	68.04 (± 16.94)	35.06 (± 26.81)	6.96 (± 8.06)
2010 (N = 13)	20.67 (± 14.60)	83.51 (± 8.30)	49.97 (± 34.96)	5.75 (± 3.45)
2011 (N = 15)	43.69 (± 24.11)	85.13 (± 2.03)	61.20 (± 29.00)	6.75 (± 2.76)

Table 7.1. Average auxiliary attendance and time owners and auxiliaries engaged in maintenance behaviours as a proportion of the total time they were present at the bower (± 1 standard deviation). Rates are calculated as hours per camera recording hours *1000. When more than one auxiliary was present at a bower, total times for all auxiliaries were summed.

7.3.1.3. When were auxiliaries present at bowers?

Mean auxiliary attendance rates differed between the three seasons, with lower rates of auxiliary attendance in 2009 compared with 2010 and 2011 ($F_{2,38}$ = 10.98, P < 0.001, Tukey post hoc tests; 2009:2010, P = 0.02; 2009:2011, P < 0.001; 2010:2011, P = 0.16, Figure 7.1A). Auxiliary attendance rates tended to positively correlate with owner attendance rates, although this relationship was only significant in 2011 (2009: r_s = 0.46, N = 11, P = 0.16; 2010: r_s = 0.49, N = 13, P = 0.09; 2011: r_s = 0.53, N = 15, P = 0.04). In 2010 and 2011 auxiliaries dramatically reduced the time that they spent at bowers after copulations were first observed, but not in 2009 when rates of attendance were low in both the pre- and post-copulation periods (paired t-tests, 2009: t_{10} = 0.87, P = 0.41; 2010: t_{12} = 3.55, P = 0.004; 2011: t_{14} = 4.96, P < 0.001, Figure 7.1B).
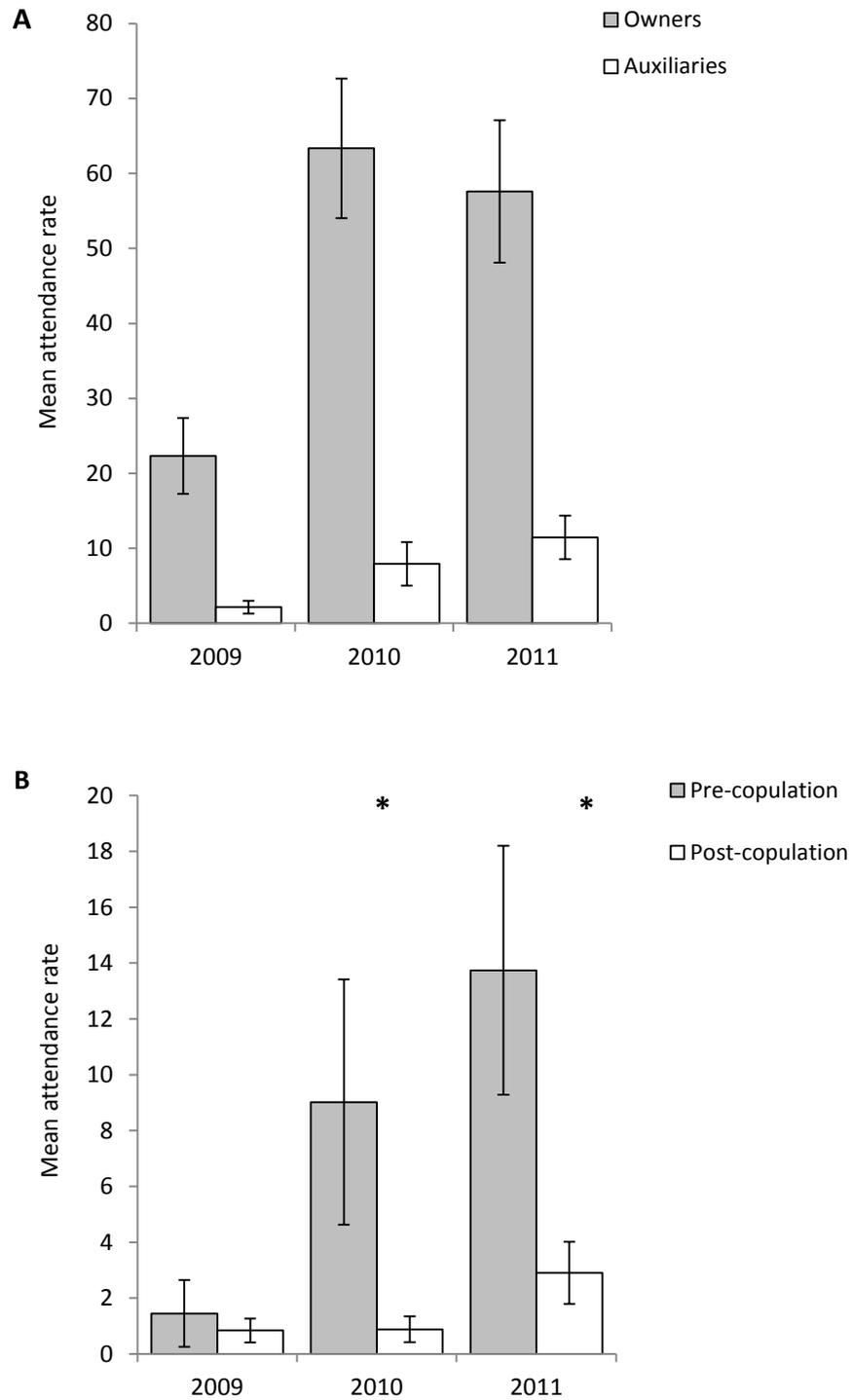
Figure 7.1. Mean attendance rates (calculated as hours per camera recording hours *1000) at bowers across three seasons monitored; **A**: showing how mean owner and auxiliary attendance rates co-vary in each season, **B**: mean auxiliary attendance rates in the pre- and post-copulation periods of each season. Error bars show standard deviation.

7.3.2. Benefits to auxiliaries

7.3.2.1. Do auxiliaries gain mating success at the bowers they attend?

Auxiliaries did not gain direct benefits in the form of mating success. No auxiliary gained copulations at any of the monitored bowers in our study population. The only males observed to copulate at bowers were the bower owners, although in some cases auxiliary males were present during the preceding courtship display to the female by that owner.

7.3.2.2. Are owners and auxiliaries related?

Auxiliaries could not gain kin-selected fitness benefits by attending bowers, as they were not especially closely related to their bower owners. Mean relatedness scores, *r*, for owner-auxiliary pairs (N = 43) did not differ significantly from mean *r* expected by chance given values of background relatedness (*r* = 0.07:0.05 respectively, P = 0.87). In both cases relatedness scores fell predominantly on zero or near-zero relatedness values, and owner-auxiliary pairs appeared to be representative subsamples of the randomly generated population distributions (Figure 7.2).
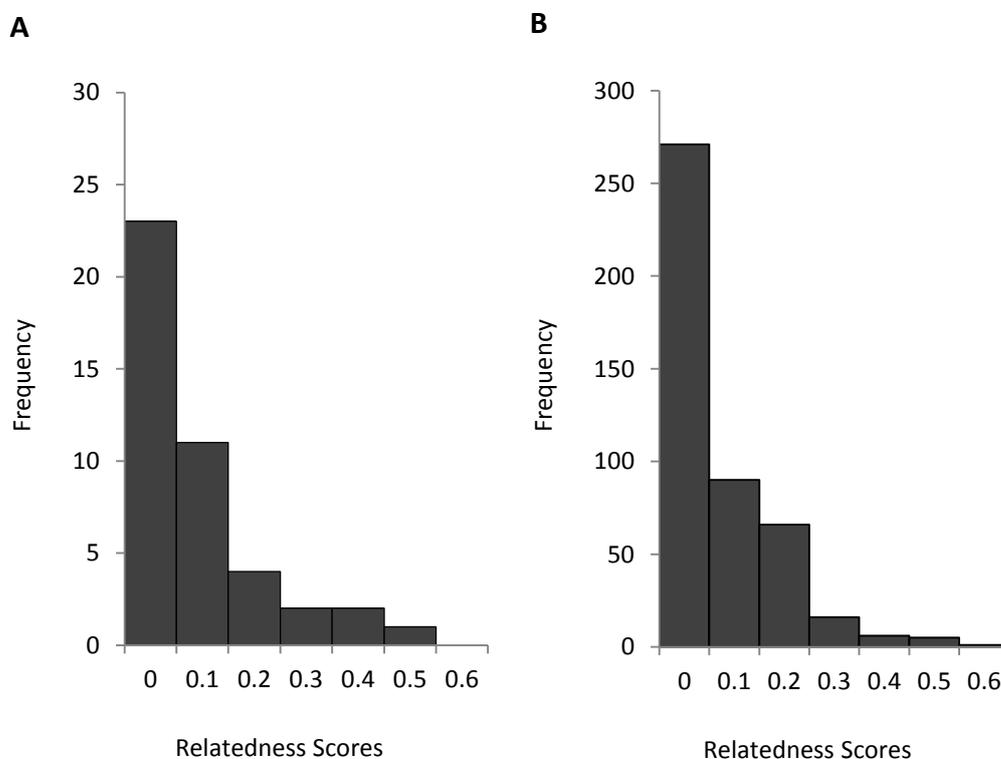
Figure 7.2. Frequency histograms of pair-wise-relatedness values for **A**: owner-auxiliary pairs (N = 43), and **B**: background relatedness scores drawn randomly from the population (N = 455).

7.3.3.3. Do auxiliaries obtain breeding positions via bower inheritance?

Auxiliaries could gain delayed direct benefits through a disproportionate chance of inheriting the bower site at which they had previously been an auxiliary. Known auxiliaries (N=19) inherited the bowers at which they had attended in 24% of cases, with a further 18% inheriting a nearest neighbouring bower. Compared to a conservative model estimate of chance inheritance of 5%, auxiliaries were considerably (almost five times) more likely to inherit their own bowers than any other bower in the population.

7.3.3. Benefits to owners

7.3.3.1. Does auxiliary presence reduce owner workload?

Owners did not appear to benefit from an auxiliary's presence through a reduction in their bower maintenance workload, with auxiliary maintenance contributions showing no correlations with owner maintenance (2009: r_s = -0.16, N = 11, P = 0.65; 2010: r_s = 0.20, N = 13, P = 0.51; 2011: r_s = 0.32, N = 15, P = 0.15). However, in two seasons (2009 and 2011) owners of bowers where auxiliaries maintained for longer tended to spend a higher proportion of their total time at bowers engaged in activities other than maintenance (2009: r_s = -0.59, N = 11, P = 0.06; 2010: r_s = 0.06, N = 13, P = 0.85; 2011: r_s = -0.49, N = 15, P = 0.07).

7.3.3.2. Do auxiliaries contribute to improving bower properties?

Auxiliaries did not bring material benefits to the bower owner in terms of larger or more decorated bowers. Bower structural properties and numbers of decorations did not correlate with rates of auxiliary attendance at bowers (Table 7.3).

Auxiliary maintenance rate:	2009 (N = 11)		2010 (N = 13)		2011 (N = 15)	
Bower Property	r_s	P	r_s	P	r_s	P
Length	0.14	0.69	-0.11	0.72	-0.16	0.57
Width	0.01	0.98	-0.36	0.22	-0.37	0.17
Height	-0.11	0.75	0.53	0.06	-0.22	0.43
Wall thickness	0.17	0.61	-0.22	0.94	-0.21	0.45
Symmetry	0.45	0.17	-0.24	0.43	-0.09	0.74
Decs (without shells)	0.11	0.75	0.99	0.75	-0.20	0.47
Decs (inc shells)	0.06	0.85	-0.14	0.66	0.03	0.92

Table 7.3. Spearman's rank correlations between bower structural and decoration properties and the total amount of time auxiliaries spent engaged in maintenance behaviours at the bower.

7.3.3.3. Does auxiliary attendance at bowers decrease the rate of marauding?

Auxiliary attendance rates had no impact on the rate of marauding at bowers in any of the three seasons (2009: $F_{1,10}$ = 3.30, P = 0.10 (R^2 = 0.27); 2010: $F_{1,12}$ = 0.08, P = 0.78 (R^2 = 0.08); 2011: $F_{1,14}$ = 0.67, P = 0.43 (R^2 = 0.02)). Total combined owner and auxiliary bower attendance rates failed to predict the rate of marauding in two out of three seasons measured (2009: $F_{1,11}$ = 2.83, P = 0.13 (R^2 = 0.24); 2011: $F_{1,14}$ = 1.09, P = 0.32 (R^2 = 0.07)). In 2010 higher attendance rates by both owners and auxiliaries were associated with higher levels of marauding ($F_{1,12}$ = 6.09, P = 0.03 (R^2 = 0.36), Figure 7.3). However, this relationship was lost when the outlier bower was removed ($F_{1,11}$ = 0.04, P = 0.84 (R^2 = 0.10)).
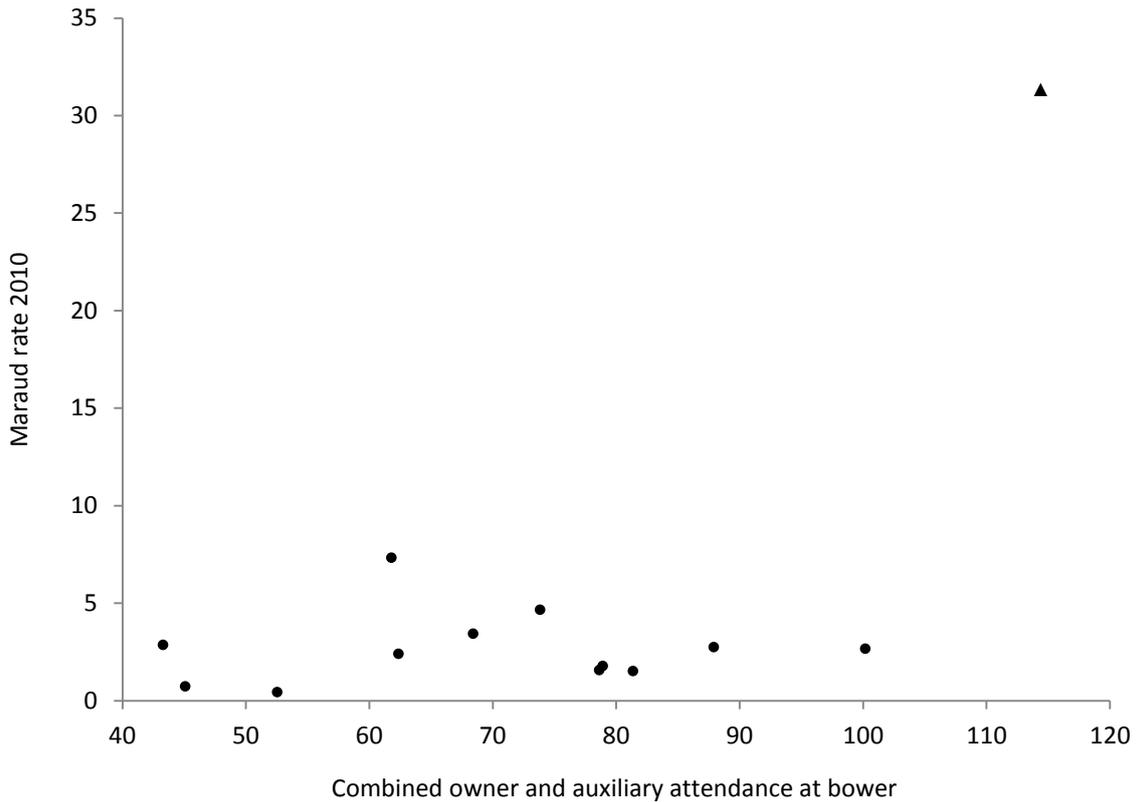
Figure 7.3. Marauding rate (events per camera recording hour *1000) at bowers in 2010 as predicted by the combined owner and auxiliary time spent at the bower. When the outlier value (triangle) was removed from the analysis the relationship was not significant. The outlier represented a bower that suffered exceptional marauding levels, predominantly from a single neighbouring owner.

7.3.3.4. Does auxiliary attendance increase mating success for bower owners?

Bower owners did not benefit through increased mating success through the presence of auxiliary males at their bowers. We found no relationship between owner copulation rates and (i) auxiliary attendance ($F_{1,31}$ = 1.90, P = 0.18), (ii) combined owner and auxiliary attendance ($F_{1,31}$ = 2.81, P = 0.10) or (iii) owner display to auxiliary rates ($F_{1,31}$ = 1.48, P = 0.23).

7.4. DISCUSSION

The sexual displays of male spotted bowerbirds are frequently not the product of a single male, but instead are constructed and adjusted by several different, unrelated individuals. Auxiliary males were identified at almost all bowers in our study population, and were defined by their repeated presence at specific bowers over the course of the breeding season. Auxiliaries engaged in bower maintenance behaviour, but a considerable proportion of their time at bowers was also spent as passive observers, watching the owner as he built and decorated the bower, and performed displays in the absence of females. Auxiliary attendance rates were highest in the period before owners started to copulate, and reduced considerably during the copulation season. We searched for benefits accruing to either party (owners or auxiliaries) that might explain this novel occurrence of collaboration in sexual display. Auxiliaries did not gain direct benefits in the form of copulations, nor did they gain kin selected benefits, as they were not more related to the bower owner than random pairings in the population. Instead, auxiliaries gained delayed benefits in the form of an elevated chance of inheriting the bower they attended, or a nearest neighbour, once an owner disappeared. We suspect that auxiliaries may also gain delayed benefits from learning about bower construction, decoration and display processes whilst observing owners, which they could then deploy once they themselves became owners. In contrast, we found no obvious benefits to bower owners from the presence of auxiliary males. Owners with higher rates of auxiliary attendance and/or maintenance contributions did not experience a reduction in how much time they spend maintaining or attending their bower. Surprisingly, owners at bowers where the auxiliaries spend more time in attendance actually spent more time at their bower, potentially reducing opportunities for them to forage or maraud neighbours. The attendance rates of auxiliaries did not improve bower qualities in terms of avenue size or structural properties or numbers of decorations, nor lower marauding rates. Crucially, variation in auxiliary attendance rates did not influence owner mating success, making it difficult to ascertain the reasons for owners accepting the presence of these extra males at their sites of sexual display.

7.4.1. Benefits to auxiliaries

Why should males serve as auxiliaries at the bower of another male rather than holding their own? First, there may be limitations on the availability of bower locations or suitable sites for bower establishment, suggesting saturation in the bower carrying capacity in our study population. We do not expect that there are physical limitations on suitable habitat (see Miles and Madden 2002), especially considering that bowers in this species are widely spaced at approximately 1km apart, compared to the more densely spaced bowers of other species (Frith and Frith 2004). However, social factors may limit the spacing of bowers, with bowers that are too close together suffering higher rates of destruction by rivalling males (Pruett-Jones and Pruett-Jones 1994). Hence, despite suitable habitat, opportunities for bower establishment are limited, and males may compete for existing bower locations. Second, bower building may be a complex and cognitively demanding process, a certain degree of which may be necessary to learn through experience and practice (Madden 2001a). These factors may suggest that males attend the bowers of established bower owners when they are unable to secure ownership themselves. Becoming an auxiliary could potentially bring four opportunities to benefit; (i) directly, by gaining a share in copulations at sites of sexual display owned by other males, (ii) indirectly, via kin selection by specifically assisting bowers owned by relatives, (iii) delayed, through benefitting by an increased chance of inheriting a bower site via some form of social queuing or hierarchy, and (iv) delayed, by developing skills and experience, learning and/or practicing bower construction or display behaviour. We tested each of these potential benefits in our study population.

Copulations that are observed at the bower have proved to be an accurate predictor of male paternity in a congeneric species of bowerbird, the satins (Reynolds et al. 2007). Therefore, if we had observed auxiliaries copulating at bower sites we could have inferred direct benefits to auxiliary males. The benefits of copulating with subordinate males for choosy females have been explored in several lekking systems, where copulations may occur sneakily, against the owner's interest, or via concessions by owners that gain increased reciprocity or kin selected benefits (Beehler and Foster 1988, Höglund et al. 1993, Kokko and Johnstone 1999). Polyandry in collaborative display may provide females with genetic benefits (Jennions and Petrie 2000), diversification of offspring phenotype (Lank et al. 2002), or the minimisation of sexually transmitted disease (Lombardo 1998). Whilst we

observed no instances of auxiliaries gaining copulations at bowers, the dramatic reduction in their attendance rates during the copulation season may suggest that bower owners were responding to either a tangible or perceived risk of auxiliaries gaining copulations, and subsequently decreased their tolerance for auxiliary presence during this time. However, alternative explanations for this reduction in auxiliary attendance, such as an increased foraging demand or reduction in male condition, may support our evidence suggesting that auxiliaries do not gain direct benefits.

We found no evidence that auxiliaries attend the bowers of related owners, and therefore it is unlikely that auxiliaries gain indirect benefits through bower attendance. Kin selected benefits in many displays can, at least partially, explain collaboration by males that do not gain direct benefits (Hamilton 1964, Kokko and Lindstrom 1996). For example, collaborating with kin has been observed in wild turkeys (Krakauer et al. 2005), black grouse (Höglund et al. 1999), and white-bearded manakins (Shorey et al. 2000). Display sites in one population of male satin bowerbirds appeared to be distributed around related individuals, reducing the level of aggressive encounters between neighbouring bowers (Reynolds et al. 2009). However, relatedness is not always necessary for collaboration to evolve (see Cockburn 1998, West et al. 2002, Gibson et al. 2005). In long-tailed manakins, *Chiroxiphia linearis,* a lekking species in which males form display partnerships, secondary males are not related to alphas and thus gain no inclusive fitness benefits from their collaboration (McDonald and Potts 1994). A further study of four species of manakin species, Pipridae, also found a lack of kin selected benefits in aggregated groups of reproducing and non-reproducing males (Loiselle et al. 2006). Spotted bowerbird auxiliaries were not more closely related to bower owners than expected by chance, which corresponds with previous evidence showing a lack of kin structuring between neighbouring bower owners (Madden et al. 2004b). Bowerbirds exhibit several important differences to many of the mating systems where inclusive benefits have been demonstrated. For example, auxiliaries do not build their own courtship displays alongside alpha male displays, and auxiliary attendance decreases as copulations began, suggesting that their presence at bowers did not function to enhance female visitation rates. The lack of relatedness between owner-auxiliary pairs may not be surprising, as several factors suggest there is no reason to expect offspring to associate with other related males; males play no parental role beyond copulation, and

females are not thought to nest in the vicinity of the bower at which they copulated (Frith and Frith 2004). There may be a long developmental period prior to sexual maturity (Collis and Borgia 1993), and small brood sizes (Frith and Frith 2004) reduce the chance that brothers raised together would later aggregate.

One potentially important benefit auxiliary males gain by attending existing sexual displays owned by other males is the opportunity to gain a position in the social queue to inherit a bower site. Delayed breeding beyond sexual maturity may accrue males delayed direct benefits, which increase future fitness (Zack and Stutchbury 1992). The limited number of established display sites coupled with the longevity of male tenure suggests that inheriting a bower offers auxiliaries substantial benefits later in life. Benefits to male bowerbirds of inheriting established bower sites are likely to include the acquirement of existing, non-perishable decorations (Doerr 2012), experience of increased female fidelity (Uy et al. 2000; 2001) and increased access to propagated decoration fruits (Madden et al. 2012). Delayed direct benefits of territory inheritance have been demonstrated in male clownfish, *Amphiprion percula*, which form uncontested queues for attaining breeding territories without the presence of direct or indirect benefits (Buston 2004). Similarly, in black grouse, *Tetrao tetrix*, gaining central display territories is partially explained by queuing, although as a condition-dependent trait is also determined by aspects of male quality, such as fighting ability and age (Kokko et al. 1998). Auxiliary bowerbirds were approximately five times more likely to inherit a display site than was expected by chance, given our conservative model. Auxiliaries often frequent several bowers within a short distance, and were also more likely to inherit neighbouring bowers. Bower inheritance may not be a complicated process. We have no evidence to suggest that auxiliaries are able to displace owners (e.g. Kokko et al. 1998); owners were never re-sighted following their loss of bower ownership, strongly suggesting that this loss of tenure was due to death from predation or natural causes rather than queue-jumping auxiliaries. Auxiliaries may simply benefit by being the most likely individual to first arrive at a vacant bower, although our data didi not allow us to rule out other, more complex systems of social queuing (e.g. Wiley and Rabenold 1984). Regardless of the mechanism, bower inheritance was the most conspicuous benefit gained by an auxiliary male, and given that reproductive success is

dependent on possession of a bower, is likely to be vital, and highly discriminatory between individuals.

Delayed direct benefits to auxiliaries may occur in ways not examined here. By attending the established bowers of owners, spending considerable time as passive observers and engaging in bower maintenance activities, auxiliary males may be gaining valuable skills and experience that they may not be able to acquire singly (Brown 1987). Evidence supporting the skills hypothesis in other multi-male display systems is mixed, with one of the main problems in assessing this hypothesis being the ability to separate delayed benefits against direct and indirect benefits which may be more strongly selected for (Koenig and Walters 2011). The bowerbird system has potential to lend itself ideally to further investigation in this area, due to the apparent lack of direct and indirect benefits to auxiliaries, the longevity of their lifespan and bower ownership (>10years, Frith and Frith 2004), the delay in maturation in males and the propensity of younger males to engage in behaviours at 'practice bowers' (Borgia 1985b, Collis and Borgia 1992). These factors, coupled with the complex nature of these multi-component displays, are suggestive of a strong element of learning and experience (Madden 2001a). However, our ability to examine the skills hypothesis was confounded by the lack of bowers without an auxiliary male, and many owners were identified as previous auxiliaries themselves. Thus, comparing breeding success between individuals with and without auxiliary experience, as has been achieved with Seychelles warblers, *Acrocephalus sechellensis*, (Korndeur 1996) and red-cockaded woodpeckers, *Picoides borealis,* (Khan and Walters 1997) would be challenging. The current lack of information regarding the prevalence and behaviour of auxiliaries in other bowerbird species may be masking opportunities for such studies. One way in which to overcome some of these limitations and test whether auxiliaries are influenced by their experiences at bowers would be to experimentally manipulate bower properties, and ask whether novel styles were taken up by newly established owners.

7.4.2. Benefits to owners

Whilst the benefits to auxiliaries from attending bowers that are not their own may be realised through an increased likelihood of bower inheritance, explanations for why an

owner should accept the presence of an unrelated male at his bower are harder to determine. Although we did not observe auxiliary copulations at bowers, owners may risk auxiliary males gaining sneaky copulations away from the bower itself, or performing a less attractive courtship display to females that visit whilst the owner is absent. Similarly, owners also risk having their intricately constructed bowers disrupted by less experienced males, or males with different aesthetic preferences to them. The acceptance of auxiliary males suggests that owners may receive benefits from their repeated presence at the sites of sexual display (e.g. Jennions and Petrie 1997). We explored four potential benefit opportunities for owners; (i) auxiliaries reduce the maintenance workload required by owners, (ii) auxiliaries enhance bower display properties, (iii), auxiliaries act as extra guards against marauding, and (iv) auxiliaries otherwise provide benefits that enhance owner mating success.

Owners spend large proportions of time at their bowers, which may reduce their opportunity to forage, collect decorations or maraud rivals (see Chapter 3). Auxiliary attendance at the bower, particularly when he is contributing to bower maintenance, may increase the ability of the owner to leave the bower. We predicted that an increase in auxiliary maintenance would decrease owner attendance and maintenance (there is a strong positive correlation between these two measures for male owners, see Chapter 4.3.1). Auxiliary maintenance did not reduce the total time an owner engaged in maintenance, although we did find a reduction in the relative proportion of time an owner maintained, suggesting that auxiliaries may allow owners to devote greater proportions of time to other bower activities.

As auxiliary maintenance did not appear to compensate owner attendance rates, perhaps auxiliaries provide additive benefits to a male's display by enhancing bower properties which increase the attractiveness of the bower to females. However, the structural and decoration properties of bowers were not significantly altered at bowers with increased rates of auxiliary attendance. Although we found no such relationship, our results do not imply that auxiliary attendance makes no or negligible contributions; our measures of variation in auxiliary input ma not capture absolute benefits gained by their presence. It is possible auxiliaries make significant contributions to bower maintenance and display

properties, but only relative to the input by the owner, thus not necessarily leading to any enhancement of the bower itself. Males are suggested to actively display optimum, rather than maximum, numbers of decorations via a trade-off mechanism that prevents social punishment via increased marauding (Madden 2002). Hence, auxiliary presence may not be expected to lead to an increase in overall bower quality beyond the social status of the male owner.

Assuming auxiliary presence does not reduce owner workload or improve bower quality beyond an optimum level, owners may accept the presence of auxiliaries as they act as deterrents against marauding attacks. We asked whether increased auxiliary attendance was associated with a decrease in the attack rate experienced at their bowers. Marauding is a unique form of intra-sexual competition, where males target the sexual signals of rivals but usually only do so in the absence of the rival himself (Pruett-Jones and Pruett-Jones 1994, Wojcieszek et al. 2007, Pruett-Jones and Heifetz 2012). Therefore, this detrimental act on a male's sexual display could be cheaply and effectively prevented simply by attending the bower, whether that attendance is by the owner or an auxiliary. Despite this, there was no relationship between auxiliary attendance and marauding levels at bowers, and, following the removal of an outlier, combined owner and auxiliary presence also showed no positive correlation with the marauding suffered at their bower. This outlier male endured an exceptional rate of both bower attendance and marauding by a particular neighbouring bower owner, which may have been due to his recent ascension from an auxiliary in the previous season to bower owner at the start of 2010. However, other individuals observed to gain ownership did not suffer such intense marauding by a rival male, and we are unable to offer any reason for the observed pattern in this case. One explanation for the lack of relationship found between auxiliary attendance and marauding rate may be due to our bower monitoring technique. Our data were based on the attendance rates of auxiliaries in the immediate vicinity of the bower, which may omit auxiliary presence in areas outside the coverage of our cameras but still within meaningful proximity of the bower. For example, auxiliaries may sit in the canopy above the bower, serving equally efficiently as a deterrent to marauders. The same may apply for owner attendance rates and marauding (see Chapter 3).

Crucially, regardless of the exact mechanism, we did not detect any direct benefit to the owner in terms of enhanced mating success attributable to the relative presence of auxiliaries. Dominant individuals may not have to gain benefits from the presence of subordinates in order for such collaborations to evolve (Trivers 1971). Auxiliary males may simply be accepted at the bower because the cost of suppressing them is greater than the cost of tolerance, especially given our lack of evidence for immediate benefits such as copulations or hostile takeovers. Behaviours required to remove auxiliaries may be energetically and physically demanding, or may encourage auxiliaries to build their own bowers and thus increase local competition. If exclusion is costly, owners may strategically invest in excluding them at particularly important stages of the breeding cycle; this would provide one explanation for the decrease in auxiliary attendance when copulations began. Sneaky copulations were not observed, but this does not necessarily imply that they are not a real or perceived threat for owners. Our observations cannot separate whether owner tolerance decreases, auxiliary ability to sustain the costs of bower attendance, or both explanations lead to this decrease.

Our current study is further limited by our inability to determine the absolute contributions made by auxiliary males. Observational studies such as this do not allow us to tease apart causes and effects for each of the cost/benefits that we explore. As previously discussed, our finding that almost all bowers have auxiliary males, and most owners were previously auxiliaries themselves, makes direct comparisons of the impact of auxiliary presence difficult. However, such limitations may not be limited to us as observers, but may pose similar problems for female bowerbirds. Our discovery of a clear collaboration between owners and auxiliaries in bowerbird display is novel, but poses two puzzles. First, whilst examples of collaborative, and even cooperative, multi-male displays are now well established, in the cases we are aware of females retain the opportunity to assess the trait of, or contributions to the trait made by, a single male (e.g. Gibson et al. 1991, Hovi et al. 1994, Alonso et al. 2010). In contrast, females visiting male spotted bowerbird bowers may have little indication of what aspects of it are the products of the owner, with whom she will mate, versus potential contributions by auxiliary males; thus, she too may be limited by an inability to determine absolute contributions by several individuals. The separation of trait from the male may benefit the male in terms of unrestricted movement, reduced predation

or other natural selection pressures (Schaedelin and Taborsky 2009), yet increase ambiguity in trait assessment for the female. The consequences of this disconnect between sexual trait and male contribution poses problems for traditional models of sexual selection, and the consequent evolution of female strategies employed to control for this confound demand further exploration.

A second puzzle is how collaborations emerge and persist. Auxiliary presence at bowers is typically short term, lasting over 1-2 seasons, and may not be due to random assortment of owner-auxiliary pairs. To test this, it would be informative to understand how auxiliaries select a bower at which to serve at, and how owners determine whether to accept an auxiliary or not. Several important questions could be proposed; what do auxiliaries do in the time leading up to being accepted as auxiliaries, do they sample bowers and is their assortative selection based on auxiliary-owner quality and what mechanism (other than inheritance) causes them to leave? This form of collaboration may have been previously overlooked in bowerbirds, especially species in which the males and females are monomorphic and auxiliary males may be easily mistaken for visiting females. We suspect that owner-auxiliary relationships may be operating in other bowerbird species, and may also extend to other systems with extended phenotypic traits, making answers to these questions paramount for our understanding of exactly how benefits accrue to the various parties within multi-male collaborations.

Chapter Eight

General Discussion

8.1. WHY CAN'T ALL MALES BE ATTRACTIVE?

One of the greatest conundrums facing evolutionary biologists is how variation between individuals is maintained in situations where there is expected to be strong directional selection on an elaborate male trait. In this thesis, I investigated factors that may maintain inter-individual variation in the spotted bowerbird, a species exhibiting a highly unusual and extravagant sexually selected trait. Choosy females base mate choice decisions on multiple aspects of male display, and gain no material benefits from their choice, yet exert strong selection pressure through disproportionate mating (Lande 1981, Tomkins et al. 2004, Kotiaho et al. 2008). Despite high levels of reproductive skew, which may act to decrease trait variation over time, I observed high variation in the individual features and quality of bowers; structures that males build, maintain and decorate to attract females (Frith and Frith 2004). Bowers are described as extended phenotypic traits, separated from the body of the male and constructed from materials gathered from the local environment, yet functioning in the same way as many sexually selected morphological traits to advertise male quality (Schaedelin and Taborsky 2009). As an extended phenotype, bowers may be particularly susceptible to a range of external factors that influence their expression, and may therefore be expected to show a high level of intra- and inter-individual variation. The first question posed in this thesis was therefore to ask whether individual males maintained consistent displays over short and long time periods (**Chapter Three**). I then identified four mechanisms which may contribute to the maintenance of variation in male spotted bowerbird display; the ability of males to pay physical costs of bower attendance (**Chapter Four**), the cognitive ability of males (**Chapter Five**), the social interactions describing male-male conflicts (**Chapter Six**), and the role that auxiliary males may play in trait enhancement or disruption (**Chapter Seven**). In this discussion I summarise and examine the implications of my findings for models of sexual selection in bowerbirds, and also more generally in species exhibiting elaborate male traits.

8.2. FACTORS INFLUENCING MALE DISPLAY

Male bowerbird's bowers may be expected to be under strong directional selection, but as traits that are extended from the physical body of the male they may also be individually susceptible to a wide range of factors that disrupt a male's display. In **Chapter**

Three I asked to what extent males maintained a consistent display over time, given the range of environmental, stochastic and social factors that were likely to cause variation. Whilst bowers varied in their display of perishable decorations, most likely due to the impact of fluctuating environmental conditions, particularly rainfall levels, individual males were remarkably consistent in their display of decorations both within a season, and across multiple seasons of bower ownership. This consistency persisted despite several periods of time when males appeared to semi-abandon their bowers (for example, in **Chapter Four** I show that during periods of drought male attendance at their bowers was significantly reduced). This may suggest that bowers are fairly resilient in themselves, perhaps partly due to their display of non-perishable decorations and use of structural materials that do not degrade quickly, and that male effort required to maintain consistency may have been over-estimated. However, the high level of opportunity for bower decorations to change over time, for example, with the impact of stochastic factors and environmental fluctuation, suggests that, to a certain degree, males actively maintained consistent numbers of decorations on their bowers. Yet, I found no evidence for an adaptive benefit for doing so. The consistency of a male's decorations did not predict male mating success nor did it appear to signal other aspects of male quality, such as length of bower tenure. However, my results are limited by several factors. First, I was unable to assess to what extent the consistency exhibited at a male's bower was down to the individual male himself, as opposed to any factors associated with the physical location of his bower. Male spotted bowerbirds can retain ownership of their bowers over many seasons, and I never observed a male bower owner switch the location of his bower. Thus, I was not able to fully separate aspects of the individual from his location. The interplay between these two factors, however, may not be important given the lack of adaptive benefit consistency appears to have. Male bowerbirds may commence bower ownership with an innate or learned preconception of how their bower should be displayed, and be rigid to that perception over time. The implications of such inflexibility may include increased mate choice costs of females.

The physical costs associated with male bower building and maintenance may provide insight into bower evolution, due to the opportunity for condition-dependent signalling (Rowe and Houle 1996). Several previous studies have considered the costs

associated with bower decorations, including their rarity in the environment and reuse across seasons (e.g. Borgia 1993; 1996, Madden and Balmford 2004). Less was known about the physical cost of spending time attending the bower, although this factor was suggested to be influential on determining bower marauding rates (Pruett-Jones and Pruett-Jones 1994) and may limit opportunities for foraging. In **Chapter Four**, I showed that males varied widely in the amount of time they attended their bowers, but this did not appear to reflect differences in bower properties or influence male mating success. The conclusions drawn in this chapter may have been confounded by the extreme variation in environmental conditions experienced during my study period, which is also likely to have impacted on other aspects of my investigation. However, I used the environmental variation encountered to assess the costs of bower ownership during times of environmental stress. The opportunity to experimentally manipulate access to food resources in a season with uncharacteristically low rainfall suggested that bower attendance does impose metabolic constraints on males, which is perhaps not surprising for a species exhibiting extreme sexual traits (Cockburn et al. 2008). However, these costs were not apparent in seasons ofaverage rainfall. My results concur with previous studies that have indicated that high signalling costs are not necessarily required for honest elaborate trait signalling and have not been found in other bowerbird species (e.g. Borgia 1993; 1996), and I suggest that bower attendance may be a relatively low cost activity for male bower owners when food resources are not limited, compared to alternatives which may expose them to increased predation risk or risk of rival interactions.

The cognitive dimension of male bowerbird display is an intriguing one. Several factors suggest that bower-building species offer an ideal opportunity to investigate the exciting, but currently under-investigated, prospect of sexual selection for cognitive processes (see Madden 2001a; 2006, Madden et al. 2011). Prior to the beginning of my field research, Keagy et al. (2009) published a pioneering paper suggesting that male satin bowerbird performance in problem-solving tasks correlated with male mating success. However, as demonstrated in **Chapter Five**, I was unable to replicate these results in the spotted bowerbird. This may suggest that different cognitive processes are exhibited/selected for across different bowerbird species, perhaps reflecting differences in their physical or social environment (e.g. opportunities to experience novel situations or in

social learning). I then developed a series of psychometric-based tests that specifically aimed to test different, pre-defined cognitive domains. The limitations associated with carrying out such tests in the wild are numerous, but importantly include the lack of control of motivation and distraction during testing. I developed tests with the aim of minimising the impact of such limitations, whilst still allowing males to make measurable decisions based on the task presented, under natural conditions. Whilst males varied in their cognitive performance scores, I again found no relationship between these measures and male mating success. This result could suggest that male bower-building is not cognitively constrained, with all males bearing the cognitive capacity to build a high quality bower. As not all males in the population are likely to become bower owners, any variation in cognitive ability may play a more important role in establishing which males are able to attain bower ownership, rather than determine variation in their ability to build a high quality bower.

Considering the apparent lack of high physical and cognitive constraints on bower-building, I expected that the social environment male spotted bowerbirds inhabited may have helped explain variation in mating success. Males experience an unusual form of intrasexual display; marauding, which impacts on multiple aspects of their sexually selected signal (Borgia 1985a, Borgia and Mueller 1992, Madden 2002). In **Chapter Six** I focused on the impact of bower destructions, as opposed to decoration theft, and asked whether variation in marauding events experienced by male bower owners influenced their display and, ultimately, their mating success. In accordance with previous reports in the literature, I found that males predominantly target their neighbours (e.g. Borgia and Gore 1986, Lenz 1994, Madden 2004a). However, marauding was not evenly distributed between all males that were equidistant to the marauder, and, in contrast to many other reports, male spotted bowerbirds appear to target specific individuals in a non-reciprocated flow of attack. Such targeted intrasexual competition demands explanations on how males are selected as marauders or victims. I looked at differences in pairs of males that were likely to engage in marauding and asked what individual or bower characteristics might distinguish between these relationships. Like Wojcieszek (2007) previously, I could not identify any particular differences in characteristics between males that might provide insight on the nature of these relationships. Although often not reported in previous studies (e.g. Borgia 1985a, Borgia and Gore 1986, Lenz 1994, Wojcieszek 2007), it was possible that not all bowers in

this study population had been located, and not all male bower owners were identifiable. Madden (2004a) reports that in his analysis of marauding behaviour in the same population, 41 of the 51 (80.4%) cases of bower marauds were carried out by unidentified individuals. I believe that I located, and was able to individually identify, the vast majority of bower owners in my study area (on average <45% of marauds were carried out by unidentified individuals, decreasing to <25% in the final season), however, it would not be feasible to suggest that I had a completely accurate measure of all male social interactions. Furthermore, Borgia (1985a) suggested that male social dominance hierarchies were established outside of the breeding season, during multi-male feeding flocks. My data were restricted to interactions occurring within the breeding season, but further detail on male interactions outside of these periods may be likely to uncover important determinants of male social order, such as aggression at feeding sites (Collis and Borgia 1992).

Finally, I asked whether the presence of auxiliary males at the bowers owned by other individuals may have had a significant impact on the expression of a male trait, and thus his mating success. The occurrence of auxiliary, or secondary, males at bowers has been widely anecdotally reported, but never fully investigated. I observed the presence of these auxiliaries at almost every bower in my study population, leading to questions about their influence on the quality of the owner's trait, confounds of female choice and the mechanisms that underpin this behaviour. In **Chapter Seven** I drew on comparisons with lekking species, where secondary males frequently play a role in male display. In contrast to many lekking species, male auxiliary bowerbirds appear to gain no direct or indirect benefits, but may gain delayed direct benefits via their attendance at bowers. I identified one potentially important delayed benefit to auxiliaries; the increased likelihood of bower inheritance at the bowers they attended. The costs and benefits to the bower owner were less apparent and were restricted by only being able to measure the relative, rather than absolute, input from auxiliaries as almost every bower had at least one identified auxiliary male. It is possible that auxiliaries provide important contributions to male bowers, but that this contribution does not differ widely between them. Similarly, it was difficult to assess the possibility of auxiliary males gaining skills and experience at bowers owned by other males due to our lack of being able to identify bower owners that had not been auxiliaries themselves. The potential benefits of being an auxiliary male may provide important

information regarding his subsequent success as a bower owner, and is an area worthy of greater investigation and comparison across bowerbird species. The impact of unrelated, auxiliary males at the sites of sexual displays owned by other males may have important consequences for models of sexual selection and variation in trait expression.

There is likely to be a high level of interplay between the mechanisms that I have investigated separately in each chapter. For example, early developmental conditions, as determined by the physical environment a male matures in, may determine cognitive development and subsequent performance (Nowicki et al. 2002, Lachlan and Nowicki 2012). Likewise, opportunities for learning and experience as an auxiliary male may affect later social dominance, marauding interactions and cognitive performance in natural conditions (e.g. DuVal 2013). The complex nature of such interactions between mechanisms was beyond the scope of this thesis but is likely to be of importance when considering the complex nature of the display traits exhibited in this species.

8.3. IMPLICATIONS FOR MODELS OF SEXUAL SELECTION

8.3.1. For spotted bowerbirds

The mechanisms identified in this thesis that may contribute to maintaining variation in male spotted bowerbirds did not appear to have fitness consequences for the male, and the measurable inter-individual variation in their expression had no influence on male mating success. For each of my data chapters, I began by identifying inter-individual differences in the display and/or behaviour of bower owners, and found that differences between individuals seemed abundant and apparent. Importantly, even within the confines of my own data collection period, consensus in female choice over consecutive seasons was not always present, despite no obvious change in the study population's social dynamics (due to the rarity of bower ownership changes) and the consistent signalling ability of males across that same time period (see **Chapter Three**). This lack of ability to find repeatable measures of mating success is puzzling. Theories of sexual selection often assume that traits predicting mating success are stable over time (Cornwallis and Uller 2010), yet within this single spotted bowerbird population elements of male display that have previously been described as being good predictors of male mating success (*Solanum* fruits, Madden 2003b)

were not good predictors during subsequent seasons, and such changes appeared to be arbitrary in nature (Dingle et al. *in prep*). However, whilst I am unable to answer why these factors did not consistently relate to male mating success, even within generations of many of the individuals I monitored, there are a number of potential explanations in the current literature that might shed light on the behaviours observed in spotted bowerbirds. The consequences of these potential explanations are likely to be applicable across bowerbird populations and species, and also in other mating systems exhibiting elaborate sexual traits.

8.3.2. Across bowerbird species

The wide range of bowerbird display traits amongst the seventeen bower-building species suggests that different combinations of environmental, physical, social and cognitive factors may have shaped bower evolution (Diamond 1982, Borgia et al. 1985, Borgia and Collis 1989, Kusmierski et al. 1993, Coleman et al. 2004, Coleman 2005, Endler et al. 2005, Borgia et al. 2007, Keagy et al. 2011, Endler 2012, Keagy et al. 2012). Bowerbirds exhibit breeding systems that are considered to be one of the classic examples of trait evolution through sexual selection, appearing frequently in texts as a model example of directional selection and elaborate trait evolution (Alcock 2005, Gould and Gould 2007, Krebs et al. 2012). Despite this, and alongside numerous datasets and investigations that have been reported in the literature, it has still not been possible to reach a consensus on precisely which traits directional selection acts. A plethora of studies now report on multiple correlates of mating success, some of which appear to contradict each other or fail to be repeatable over time, populations or species. For example, correlates have included bower decorations that vary in quantity, relative importance, rarity in the environment or costs of acquisition (Borgia 1985, Borgia and Mueller 1992, Borgia 1995, Madden 2003a, Doerr 2009; 2012, Kelley and Endler 2012, Dingle et al. *in prep*), structural components and maintenance (e.g. Borgia and Mueller 1992, Robson et al. 2005), and behavioural components (e.g. Loffredo and Borgia 1986, Coleman et al. 2007, Keagy et al. 2009). Factors that appear to show strong correlations with male mating success in one species, such as problem-solving ability and cognitive measures (Keagy et al. 2009, 2011) are not repeatable in another, congeneric species (see **Chapter Five**). Contradictory conclusions regarding the population social dynamics also confound our understanding; in many populations marauding is

targeted at unrelated neighbours (e.g. Borgia 1985, Lenz 1994, Madden et al. 2004b and see **Chapter Six**), yet Reynolds et al. (2009) report that in one population of satin bowerbirds related males aggregate and actively avoid competitive interactions with neighbouring, related kin. Doerr (2010b) failed to find support for the social control hypothesis in great bowerbirds, although Madden (2002) suggested active social control in spotteds. In some cases, it is difficult to imagine how certain correlates of male mating success can apply across species, or even across populations within a species. For example, in a single population of great bowerbirds, males created forced perspectives using graded sizes of stones at the entrances to their bower avenues, and males that created higher degrees of forced perspective gained more mates (Endler et al. 2010, Kelley and Endler 2012). However, in other species, this forced perspective would be impossible to create; in the population of spotted bowerbirds used in this study, for example, males decorate the entrances of the bower almost exclusively using white snail shells of uniform size, and in other populations of great bowerbirds males primarily use bones or shells which again do not create this perspective (Frith and Frith 2004).

There may be several reasons for this failure to reach a consensus: (i) current methods used to measure and quantify bowerbird traits may simply not capture the correct element that female bowerbirds are selecting for. This seems unlikely given the wide range of correlates that have now been investigated (see above), as well as others that are likely to have been considered but do not appear in the literature due to a lack of significance; (ii) female choice captures some element of interaction between multicomponent signals that has not been measured in the particular combination of factors that matters (for a review of female choice in multicomponent displays see Candolin 2003); and (iii) female choice switches over time and space, suggesting that we should not expect to find consistent correlates across studies (Chaine and Lyon 2008). Perhaps it is unsurprising, given the complex nature of male bowerbird displays with an almost infinite combination of factors that might explain female choice, that in some seasons any single measure does show a significant correlation. For example, Madden (2003b) looked at 71 different objects that are used in spotted bowerbird display, so perhaps it might be inevitable that at least one of these will show a relationship with mating success (although robust models and corrections for multiple comparisons were carried out).

Despite these clear differences in bowerbird species behaviour, sexual display and the correlates of mating success, results from studies in the literature are often applied beyond the contexts in which they were investigated, and applied across species in order to justify new hypotheses or explanations. For example, male paternity tests in satin bowerbirds confirmed that observed male mating success at the bower successfully predicted genetic paternity (Reynolds et al. 2007), and this assumption has been applied across species in both spotted and great bowerbird studies (Madden 2002, Doerr 2009a) Similarly, the mate search patterns of female satin bowerbirds as described by (Uy et al. 2000; 2001) have not been replicated in other populations or species, yet are often assumed to be of a similar nature when examining other bowerbird mating behaviours. Such assumptions of between-species commonalities may confound our ability to draw accurate conclusions on the direction of sexual selection pressure.

8.3.3. For models of sexual selection

Variation in the expression of male elaborate traits is a common product of sexual selection, yet the exact mechanisms driving this variation remain unclear in many mating systems. Models of sexual selection often propose that the evolution of elaborate male traits occurs due to female preference for those males exhibiting the most extreme examples (Andersson 1994), and that such preference may occur due to Fisherian run-away processes or good genes theories (e.g. Kokko et al. 2003, Andersson and Simmons 2006). Examining the correlates of mating success across bowerbird species suggests that selection may be variable across space and time. In theory, such variation, particularly in extended phenotypic traits that may be more susceptible to external fluctuations, can maintain genetic variation within a species, especially if fitness ranks differ between environments. This may create genotype x environment interactions that persist in a given environment but vary across populations within a species (reviewed in Byers 2005 and Radwan 2008). Female selection for locally adapted males may also create viable scenarios for the evolution of condition dependent traits that signal male quality (modelled in Reinhold 2004).

The rapid and unpredictable changes in traits that correlate with mating success may complicate our understanding of how strong directional selection leads to the elaboration of sexual display, whilst also offering a potential resolution to the lek paradox (Bussiere et al. 2008). The lack of consistent selection on any particular component of a male's sexual signal is not limited to the complex displays of male bowerbirds. A lack of repeatability in the correlates of male mating success across many species may be underestimated due to a lack of publication of insignificant results. Using two other classic examples of female preference for elaborate male traits, it is possible to see how initial assumptions regarding directional selection pressure have become confused by the addition of data which appear to offer multiple, sometimes conflicting, evidence for trait selection. For example, male barn swallow characteristics and/or behaviours that are reportedly sexually selected traits include the length of tail streamers (Möller 1990, repeated by Smith and Montgomerie 1991a, Möller 1998, Kleven et al. 2006), plumage parasite load and white spots (Kose and Møller 1999), plumage colour (but not streamer length or symmetry in this population, Safran and McGraw 2004), nest building ability (Soler et al. 1998) and brain size (Möller 2010). The sexually selected traits of male peacocks, one of the most flamboyant examples of an exaggerated trait, show similar fluctuations in female preference and time-space variation: early observational and experimental manipulation studies indicated female preference for males with larger trains (Petrie et al. 1991, Petrie and Halliday 1994), but this has since been contested (Takahashi et al. 2008) and the solution for peahen preference is likely to be more complex, involving multiple components and even the loss of signalling traits (Wiens 2001, Loyau et al. 2005). Such observations across time and space may support the hypothesis that elaborate, multi-component male traits can provide different functional information among populations, especially those that are geographically (and therefore genetically) isolated (Candolin 2003). Inter-population variation may ultimately facilitate population divergence and lead to speciation (Uy and Borgia 2000, Safran and McGraw 2004).

8.4. FUTURE DIRECTIONS

Capturing the element, or combination of elements, that female bowerbirds select for when assessing male sexual displays continues to baffle our understanding of elaborate

trait evolution. In this final section, I propose a number of potential ways in which this current study could be extended and expanded to try and address these current limitations. First, in order to fully understand the selection pressures acting on complex, multi-component male traits, studies need to be conducted over longer time periods, in order to assess the consistency of factors/mechanisms that may be influencing such selection. In the spotted bowerbird, the targets of female choice appear to be changeable over time (also see Dingle et al. *in prep*), and my results seem to suggest that aspects of male display that have previously correlated with male mating success may not be consistent over time. Coupled and compared with previous data, my results may suggest that there is no consistent selection on any particular component of a male's signal, but the reasons why females may switch in their targets of male quality remains unclear. Other recent literature also appears to contradict some of the fundamental relationships between male traits and female choice; see Cornwallis and Uller (2009). Cockburn et al. (2008) also points out the discrepancies that may be presented when only considering a short time period; they indicate that the strength of directional selection on male fairy-wrens could be highly contradictory depending on which three-year sample period was selected. Long-term studies looking at the changing components of traits that correlate and predict mating success over successive seasons may allow us to identify common themes, such as long-term environmental change, or subtle, slow-developing changes in the social environment, which cannot be identified through short term investigation. In bowerbirds particularly, the longevity of individual males (up to ten years in my study population), may suggest that the impact of female selection may only fully come to light over multiple generations; a time-scale that few bowerbird studies have managed to span.

The data presented in this thesis was collected from a population of wild, free-living birds, without the need for forced experimental testing. For cognitive studies in particular, the current emphasis on results gathered from captive individuals may introduce biases in the data such that they fail to fully capture an individual's true capabilities in the wild (Thornton and Lukas 2012). For example, problem-solving ability differed between wild and captive spotted hyenas (Benson-Amram et al. 2013) and individual success in great tits' performance in captivity did not predict success in the wild (Morand-Ferron et al. 2011). Both indicate that an individual's performance in captivity significantly differs from its

behaviour under natural conditions. In **Chapter Five** I measured cognitive performance in unforced problem-solving and cognitive tasks, and acknowledged the lack of control in my experimental design. Males may perform differently under captive conditions, although it is difficult to predict the exact nature of these differences; motivation could be increased through temporary food deprivation prior to testing, which may increase a male's performance; alternatively, the stress likely to be induced may compromise performance (Peters et al. 2011). Either way, it might be difficult to envisage how captive, controlled testing might reflect a male's natural performance in the wild. It would also be difficult to bring wild male bower owners into captivity for testing, even for short periods of time, without risking considerable disruption to their social environment; disowned bowers quickly get taken over by other males, usually auxiliaries that are frequently in attendance (Frith and Frith 2004, and see **Chapter Seven**). Therefore, impact of taking several males simultaneously into captivity may have severe consequences on the social hierarchies within the population. One way to overcome such problems may be to compare cognitive performances in wild individuals with those of captive bred birds held in zoos or private collections. However, captive individuals are unlikely to have encountered the equivalent ranges of experiences and opportunities for learning that their wild counterparts have, questioning the relevance of measuring performance under conditions they are unlikely to encounter during their natural lifetime. For example, environmental conditions in captive birds are likely to be highly controlled to avoid severe stresses such as drought and food shortages, which may discourage innovation, Thornton and Lukas 2012. I advocate a greater emphasis on wild cognitive testing, measuring an individual's natural expression of behaviour, as well as in controlled captive conditions, to allow more stringent comparison of the effects of both conditions on performance.

Similarly, another future direction for the study of inter-male variation in cognitive performance may be to increase testing protocols that are built around psychologically grounded criteria (Thornton et al. 2014). Individual variation in cognitive ability may impact reproductive fitness and provide insight into cognitive evolution (Thornton and Lukas 2012). In **Chapter Five**, I report on the cognitive ability of wild male bowerbirds in four classically defined cognitive tests, based on established psychological theory. These may differ in their ability to capture cognitive capacity compared to problem-solving tasks that are based on a

species' standard behavioural repertoire (e.g. Keagy et al. 2009). The ability of problem-solving tasks to accurately and consistently quantify an individuals' cognitive capacity has yet to be established, and such tests may instead be capturing variation in non-cognitive factors, such as exploration, perception, attention, neophobia or motivation (Thornton et al. 2014). I hope that initial attempts to capture cognitive variation in individual performance, such as those carried out by Healy and Hurley (1995), Boogert et al. (2010), and myself with spotted bowerbirds (Isden et al. 2013), can be extended in the future to allow rigorous psychologically-based testing which makes specific predictions about the exact cognitive mechanism under examination.

The impacts of male-male competition on male display traits, and ultimately, male mating success are well founded (Berglund et al. 1996, Kokko and Johnstone 1999). In **Chapter Six** I found no consistent evidence that could predict whether a male bower owner was the target of frequent marauding by a rival male or not. Despite measuring multiple factors that may be indicative of such targeting, the lack of understanding surrounding intra-sexual competition in this species remains intriguing. It would be important for future research to aim to identify these underlying mechanisms that predict marauding rates, and thus to qualify the social impact of marauding on male mating success. Whilst several models of marauding behaviour have provided important parameters for successful strategies that males may adopt (e.g. Pruett-Jones and Pruett Jones 1994, Hunter and Dwyer 1997, Pruett-Jones and Heifetz 2012), exactly how these optimal strategies relate to the behaviours exhibited by males in the wild remains unclear. For example, contrary to Pruett-Jones and Heifetz (2012) predictions that males likely to gain higher rates of copulation should maraud less and guard more, I found no such relationship in my study population. Equally, in **Chapter Three** I show that males that spend a greater proportion of time attending (akin to guarding) their bowers do not enjoy lower marauding rates. Understanding how optimum models relate to realistic measures of natural intrasexual competition in wild populations may increase our understanding of its impact on reproductive fitness.

Finally, the impact of auxiliary males on a bower owner's sexual display demands further investigation. This exciting, yet currently under-examined, behaviour may provide

important insights into the evolution of bowerbird displays, specifically determining what properties of a male are necessary for the elevation to bower ownership status. Many questions remain unanswered; in **Chapter Seven** I investigated a number of potential costs and benefits to both the auxiliary and owner, but my initial results need further examination to determine (i) how male auxiliaries determine which bower to attend, (ii) what factors lead to their acceptance by a bower owner, (iii) what experiences and social learning do auxiliaries gain from their time spent at another male's bower, and (iv) what mechanisms allow a female to decouple a bower owner's contribution to his sexual display from that of its auxiliary? Due to the commonality of auxiliary males in my study population, it was difficult to separate owner versus auxiliary contributions and ask such questions. However, quantification of the occurrence of auxiliary males in other populations and species of bowerbirds may aid our understanding of the relationship between bower owner, auxiliary presence and female mate choice decisions.

8.5. FINAL SUMMARY

In summary, this thesis has shown that the causes of male variation in spotted bowerbirds defy many of the previous assumptions regarding sexual selection on an elaborate and highly unique trait. Bowerbirds provide one of the classic examples of sexual selection, appearing in many textbook case studies identifying the impact of strong directional selection by female choice, yet, following over thirty years of intensive study prior to this thesis, and the contribution made by it, there still lacks an ability to determine exactly which factors selection acts on. This thesis contributes to our current knowledge of sexual selection mechanisms in an elaborate male trait by quantifying and exploring mechanisms of inter-individual male spotted bowerbird variation. It also provides a number of techniques which may benefit from extended periods of investigation and expansion (for example, the observations spanning across generations of factors that predict male mating success, and the increased use of psychometric-based cognitive tests on wild subjects). Understanding why the targets of female choice vary over time and space, and how such variation might be predicted, would help determine how sexual selection pressure has come to shape this elaborate male trait. Bowerbirds remain an ideal model system in which to conduct such studies, and consistent publishing of data from long-term studies may reveal

more about the evolution of one of the most bizarre sexually selected traits exhibited in the animal kingdom (Gillard 1969).

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