The Behavioural Ecology of Forced Copulation in the New Zealand Stitchbird (Hihi)

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"The breed is guileless and innocent of wile in a peculiar degree; the instinct of deception even in a good cause seems not to enter into their scheme of things…They are careless, too, of stranger birds who may happen to have wandered near the family abode…In October and early November, whilst still engaged in the search for nests, it was disheartening work, after believing we had tracked a male to his lair, to find two males engaged in parley – long, low, chattering, very friendly palavers. It seemed then so improbable that one male would tolerate the presence of another close to his breeding quarters…I have reason to believe, however, that although thus friendly, care is taken not to intrude on one another's domains."

H. Guthrie-Smith (1925) describing
the behaviour of the stitchbird in his
book *Bird Life on Island and Shore*

The stitchbird female (left) showing her distinctive white wing-bar and the male (right) displaying the characteristic 'cocked' tail position

'Stitchbird' is this species' pakeha name, thus it is also known by the following Maori names:

hihi*, tihi, ihi, tihe, kotihe, tiora, tiheora, tioro, kotihe-wera (male only), hihi-paka (male only), hihi-matakiore (female only), mata-kiore (female only), tihe-kiore (female only)

* This is the most commonly used Maori name today

Abstract

Although many vertebrate species form stable breeding partnerships, extra-pair copulations are often common in these species, potentially leading to intersexual conflict. Forced copulation or rape is an extreme manifestation of this conflict, occurring when a female is forced to copulate with a male despite her resistance. In this thesis, I report research addressing several questions about forced copulation in stitchbirds (*Notiomystis cincta*), a species with frequent forced copulation attempts. I conducted this research over three years on Tiritiri Matangi Island, off New Zealand's northeast coast. Forced copulation was used opportunistically by all males in the population, and male age and morphometrics did not predict forced copulation success or the likelihood of female consent. A newly proposed hypothesis to explain the function of forced copulation in birds, the 'creation of a dangerous environment' hypothesis, was not supported empirically and in its current form appears to be theoretically unworkable. Male stitchbirds seem able to bypass female choice through adopting a face-to-face forced copulation position. This is effective because their cloacae become engorged with sperm, and act similarly to a penile erection to allow cloacal contact when copulating in this species' unique face-to-face position. Forced copulation attempts occurred mainly during females' fertile periods immediately before egg laying, and this was strongly correlated with an increase in female weight, suggesting that males use the weight of the female to judge her fertility status. Resident males also adjusted their behaviour at this time, switching from a territorial site-specific defence to a mate-guarding tactic localising on the position of the female. While costs associated with forced copulation have been previously documented for females, I show that the resident male also suffers a cost as measured by a 5% loss of bodyweight as a result of extra-pair male territorial intrusions on top of a 2.5% weight loss as a result of mate guarding. The resident male's uncertainty of paternity resulting from extra-pair forced copulation had little effect on provisioning by paired males. The key factors affecting male provisioning were brood size (males did not provision one-chick broods) and whether the male was monogamous or polygynous (males only fed the brood of their primary female). Cross-species comparisons can be useful in understanding the function of forced copulation if carefully undertaken, with previous criticism of this approach based on numerous misunderstandings.

Acknowledgements

So many people to thank and so many self-indulgent in-jokes to reminisce about.

Before I thank the people who helped directly with my research, I'd like to thank a few people who helped me get to a point in my life when I could consider tackling something like a PhD and to whom I owe much gratitude. To my mum and dad who have always believed in me and always supported my decisions. They taught me to think critically and not accept anything at face value (even if they quickly learned to regret teaching me that!). They bought me my first pair of binoculars and put up with my incessant raving about birds for years (then they finally broke down and starting birding themselves). Thanks to dad for a comment many years ago that seeded the idea for me to pursue postgraduate studies, and to mum for dealing with all that needed dealing with back in Australia during the past few years. Thanks also to my brothers, Stu and Date, who have been there when needed, to tell me to "pull my head in" when it needs pulling in, and are able to share with me the latest kiwi joke doing the rounds in Australia; and my nieces and nephew, Madeline, Stephanie and Nathan for keeping me young at heart.

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Life on the island was simply wonderful and this was more to do with the people that I spent time with out there, rather than the fact that it was warm and had a nice beach (although that helped). Thanks Barbara and Ray for always being there to help out, to organise trips on and off, to let me borrow vehicles when I needed them (or was just too lazy to carry my gear across the island), to bring in my washing, for lemons from your tree on pancake mornings and for being my surrogate parents for the past few years. Thanks also to Ian Price and Ian McLeod who were always available to help out with logistical problems around the island, and would grace us researchers with their fine company for drinks and nibbles in the evening.

The data I collected would have been rather patchy if it wasn't for the help of my long-suffering field assistants, Troy (Poopsoid) Makan and Becky (Randy's obsession) Lewis. They rarely grumbled about being tossed out of bed (as long as it was after midday) and being forced to work in all the "evil" bush patches (*i.e.* bush 21) on the island. I'd also like to thank the other people with whom I shared the "research room" over the years, Jason Taylor, Rosalie Stamp, Ian (Mr Poopsie) Fraser, Sandra Jack, Melinda Habgood, Rose Thorogood, Shaun Coutts, Su Sinclair, Angelique Hoffman and Askia Wittern. It was always fun (especially Ian's narcolepsy and Melinda's propensity to whack her head on the top bunk) and I have forever been converted to the medicinal qualities of a nice Gin & Tonic on a hot afternoon. Thanks also to Barbie ™, a doll with whom we all became obsessed during one Christmas period. This lead not only to us having a Barbie ™ advent calendar encouraging us with vignettes of inspiration each day (and some pretty dodgy chocolate), but also to the renaming of a patch of bush on Tiri – "Barbie ™ Bush" which was followed up soon after with "Ken ™ Bush" (I can guarantee that any jokes combining the words "Barbie" ™ and "bush" were well aired, but unfortunately the Barbie ™ pink nest box didn't get beyond the drawing board).

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This project would not have been possible without the generous funding contributions of the New Zealand Lotteries Board (Environment and Heritage), the Supporters of Tiritiri Matangi Inc. and the Massey University Institute of Natural Resources (especially Russ Tillman for granting funding to attend the Australasian Ornithological Conference 2003).

Of course there wouldn't be a study without the birds. They did what they did in a spectacular fashion and allowed me to follow behind them while taking notes and describing their sex lives. Many of these birds I started to see as friends (this is what happens when you are stuck on an island for months at a time) and would enjoy coming back the next season to see if how they were going. They would come and say "hi" at the beginning of each observation session and didn't grumble too much when I had to catch and handle them for measurements (except BM/RY who was always a real bastard). I will miss spending my summers watching these amazing little birds and their dirty little ways.

I would like to express my deep gratitude to Åsa Berggren who has helped and had to put up with more than anyone else during the past few years. Not only has she assisted in the field, joined with me in "bird rescue " missions, patiently listened to my latest ideas and then helped me communicate these to other people, but she has provided support and encouragement when I needed it most. Thank you. It would have been much harder without you by my side.

One final thanks goes to my examination committee; Jim Briskie, Robin Fordham and Andrew Cockburn. I appreciated the time you put in to read and critically review the thesis. I especially appreciated you awarding me my doctorate and the end of it all!

If you are the person who I failed to mention because I only remembered you 5 minutes after I sent this to the printers, I am sorry, but thanks for whatever it was you did – it was great and I couldn't have done it without you.

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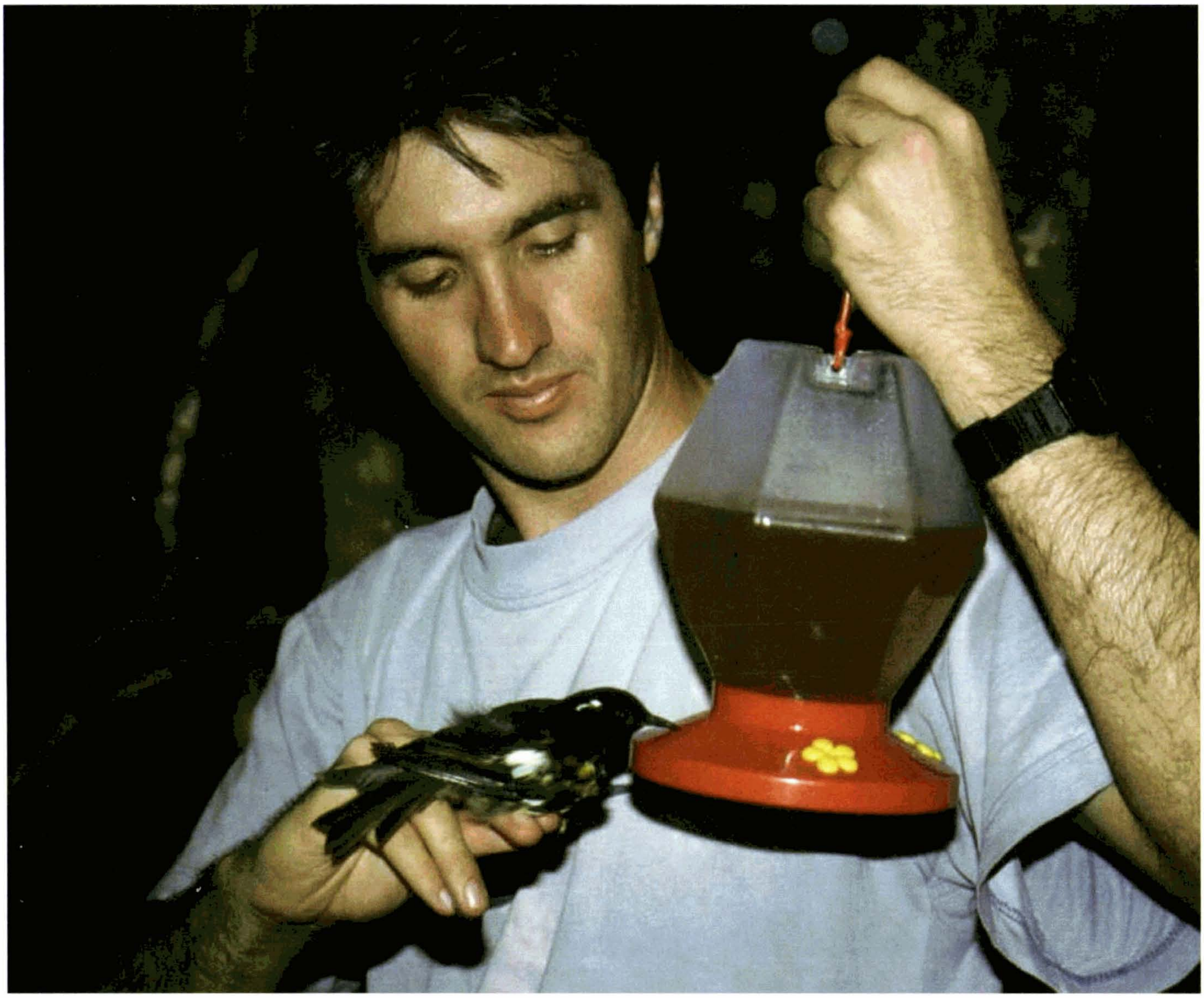
Note on text:

Each chapter is set out in the style of the journal to which it has been submitted. Consequently there is some repetition, particularly in the Methods sections and there are minor stylistic differences between chapters. For the two submitted chapters that include other authors (Chapters 3 and 6), while my input was the greatest, I received assistance from my co-authors. I designed the research, undertook or coordinated the field work, analysed the data and wrote the manuscripts.

Thesis Introduction



Here I give a male stitchbird a drink of sugar water before release after handling

Forced copulation, a set of behaviours characterised by male force and female resistance in a sexual context, is a widespread biological phenomenon occurring in insects (Thornhill 1980), fish (Farr 1980), reptiles (Olsson 1995), birds (McKinney et al. 1983), and mammals (Smuts & Smuts 1993) including primates (Mitani 1985) and humans (Thornhill & Palmer 2000). Forced copulation has generally been considered as a tactic within a male's reproductive strategy where a male uses force to gain additional matings at the expense of the benefits a female may receive through mate choice (Clutton-Brock & Parker 1995; Ligon 1999). However, while in many species their behaviour conforms to predictions from such an interpretation (Birkhead et al. 1985; Jones 1986), in some animals displaying forced copulation behaviours females appear able to prevent males from successfully achieving forced sexual access (Wagner 1991; Gowaty & Buschhaus 1998).

One such group of animals where the 'forced additional insemination' hypothesis has been questioned as the function of forced copulation is in avian species lacking an intromittent organ (phallus). In these birds it is thought that females can control sexual access, meaning males cannot forcibly inseminate an unwilling female (Fitch & Shugart 1984; Weatherhead & McRae 1990; Gowaty & Buschhaus 1998). Additionally it is supposed that females generally gain benefits from extra-pair copulations and thus it seems paradoxical to generally refuse them (Ligon 1999; Cunningham 2003). These ideas suggest that forced copulation in these species must have a function other than a male-driven direct insemination strategy. To account for its existence in these species, two hypotheses have been proposed, the 'resistance-as-a-ploy' hypothesis (Westneat et al. 1990) that predicts females manipulate males into forcibly copulating to measure their quality, and the 'creation of a dangerous environment' or CODE hypothesis (Gowaty & Buschhaus 1998) that predicts males use forced copulation as a form of harassment. These newer hypotheses and a number of their underlying assumptions have rarely been tested empirically, resulting in uncertainty as to the validity of these ideas and the general evolutionary significance of forced copulation in many bird species.

The stitchbird as a model for testing forced copulation hypotheses

The stitchbird or hihi (*Notiomystis cincta*) is a medium sized, forest dwelling passerine that displays significant sexual dimorphism in both size and plumage colour, with males being both larger and more colourful than females (Higgins et al. 2000). Social monogamy is the most common pairing arrangement, although their mating system also includes polygyny, polyandry and polygynandry (Castro et al. 1996). Male stitchbirds engage in a reproductive strategy where both paired and unpaired males pursue extra-pair copulations (EPCs) during the breeding season (Castro et al. 1996; Ewen et al. 1999). The majority of these EPCs are forced (Ewen et al. 1999) and involve a unique face-to-face copulatory position that the female actively and aggressively avoids (Anderson 1993; Castro et al. 1996).

Stitchbirds display many of the qualities required for testing current controversies surrounding the function of avian forced copulation. They lack an intromittent organ but display high levels of extra-pair forced copulation behaviour (Castro et al. 1996; Ewen et al. 1999). They are not shy and are easy to approach, with each pair generally restricting their movements to within a well-delineated territory with an approximate radius of 30 m, allowing close observation over prolonged periods. Stitchbirds exhibit significant breeding asynchrony (Fig 1.), allowing observation of bird movement and forced copulation rates relative to "hotspots" of female fertility, allowing differentiation of a general "copulate with everything" rule, and current forced copulation hypotheses (Birkhead & Biggins 1987).

Behavioural resistance by the female in this species is reportedly obvious, suggesting that it is relatively easy to assess female resistance during successful and attempted copulations. Male investment in the feeding of offspring is highly variable, and this presents an opportunity to measure trade-offs between certainty of paternity, additional mating opportunity and offspring provisioning by the resident male. Male stitchbirds are unique in their positioning of the female for forced copulation, and this raises the question of whether face-to-face copulation in the stitchbird is the behavioural equivalent of the dorsal clamp used for restraining females during forced copulation in the scorpionfly (*Panorpa* sp.) (Thornhill 1980), and thus may allow males to bypass female choice in this species.

The **aim of this study** is to understand the function and mechanics of forced copulation in the stitchbird within the broader context of this species' mating system. In order to address this aim I sought to answer the following specific questions:

1. In what form and context do stitchbirds exhibit sexually coercive behaviours?
2. To what extent do males or females control patterns of extra-pair copulation?
3. Through what method do males evaluate female fertility?
4. Do male stitchbirds possess any anatomical or behavioural features allowing them to bypass female consent?
5. Are males and females affected by costs related to extra-pair forced copulation?

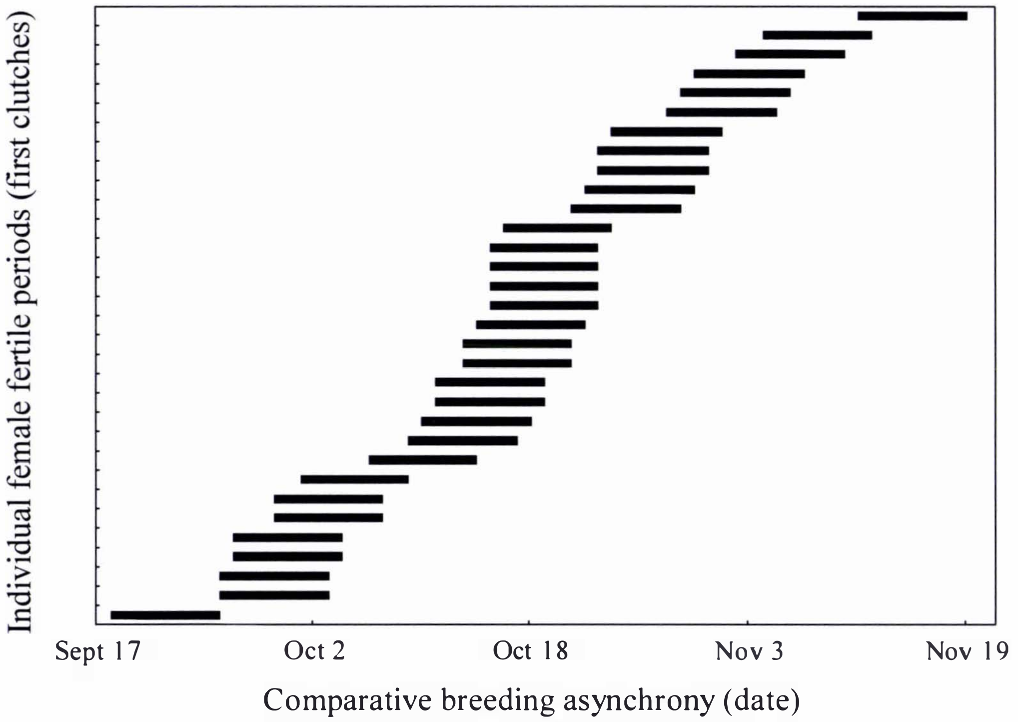


Figure 1. An example of the relative asynchrony of first clutch nesting attempts for 32 females during the 2001/2002 breeding season. Each black bar represents each nest site from the beginning of the female's fertile period (6 days before the laying of the first egg) until the laying of the usually penultimate, third egg.

The study population

Stitchbirds were once found throughout the forests of New Zealand's North Island, but by the 1880s they were considered extinct on the mainland and restricted to a single population on Little Barrier Island (Higgins et al. 2000). In order to increase this species' range and long-term viability, in 1995 the New Zealand Department of Conservation translocated 38 stitchbirds from Little Barrier Island to Tiritiri Matangi Island, commonly referred to as "Tiri" (Fig. 2). A further 13 birds were translocated in 1996 (see Ewen 1998 for details). Since this time, the population has expanded, with the September census recording 45 adults in 2000, 62 adults in 2001, 92 adults in 2002 and 109 adults in 2003, with nesting attempts and the number of chicks fledged per year increasing accordingly (Fig. 3).

The Tiri population was chosen for this study as it had several unique features making it ideal for a study looking to distinguish competing hypotheses relating to the function of forced copulation. These included;

1. Population size. The population was small enough to be comprehensively monitored but large enough for meaningful results to be collected.
2. Patchy distribution. The birds were not uniformly distributed across the island (see Fig. 2) allowing parameters associated with local population density to be assessed.
3. Individual colour banding. Since the initial translocations, all birds have been individually banded with their ages and social parentage recorded.
4. Nesting in artificial boxes. Because the stitchbird is a cavity nesting species, nest boxes must be provided for successful nesting on Tiri. This allowed all nesting attempts to be easily and accurately monitored
5. Reliance on supplementary food. Stitchbirds are reliant on supplementary feeding stations for a percentage of their daily caloric intake, allowing birds to be easily caught or automatically weighed at these locations. These feeders also present an opportunity to study behavioural interactions between birds outside of their territorial areas.
6. Gentle topography and low canopy (by New Zealand standards). The island is easy to traverse, with low canopy and minimal understorey. This allows the birds to be visually monitored with relative ease during observation periods.

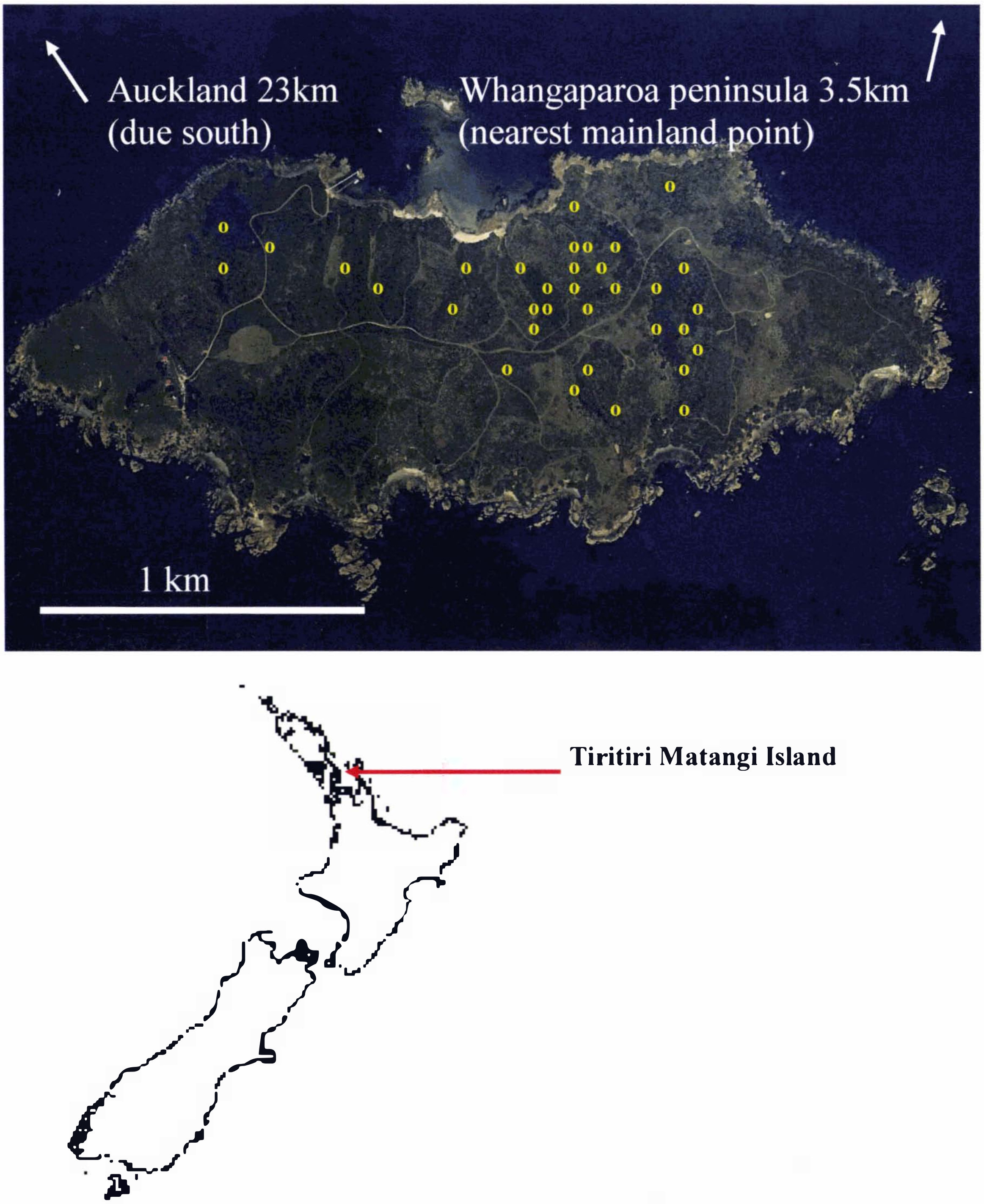


Figure 2. Tiritiri Matangi Island (top) is located in the Hauraki Gulf, approximately 23 km north of Auckland, New Zealand. The island's area is approximately 220 ha and is a patchwork of remnant forest and regenerating forest and shrub-lands. The yellow dots represent stitchbird nesting sites, with these generally restricted to the remnant forest and older revegetated areas.

Stitchbirds on Tiri breed during the spring/summer between September and February, with the first eggs laid in late September or early October (Fig. 1), and the last eggs laid in early to mid January. I studied various aspects of the birds' behaviour and morphology from the onset of nest-site selection in September, through to the fledging of the last chicks in late February for three breeding seasons (2000–2003).

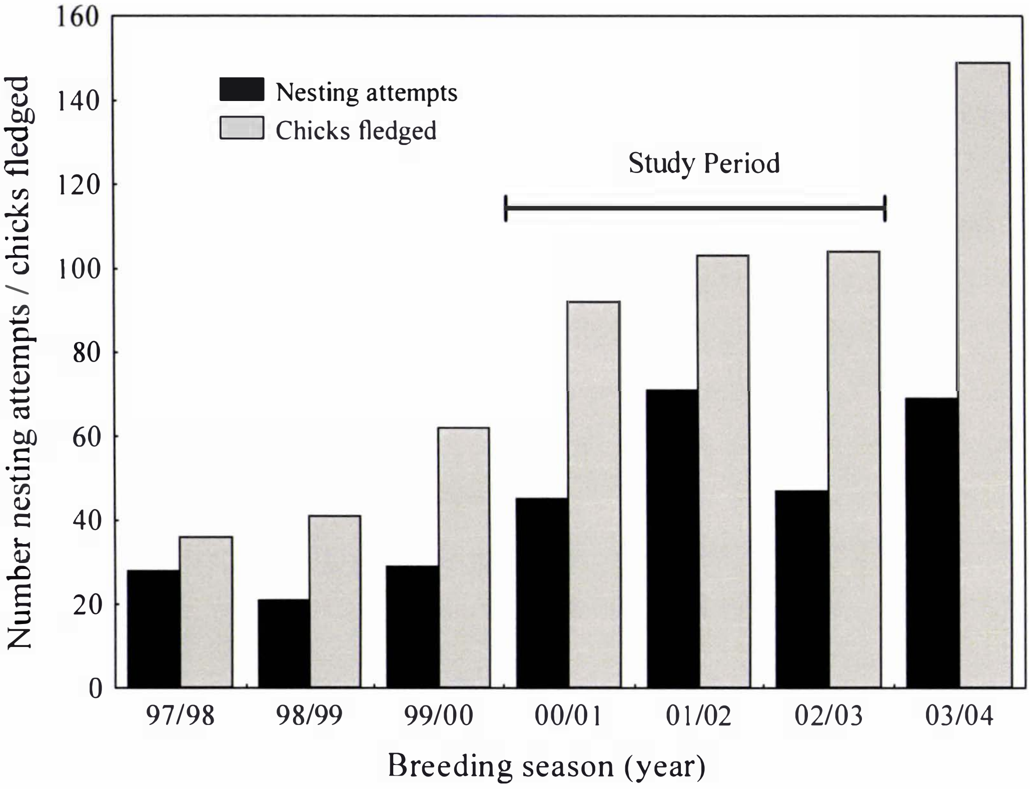


Figure 3. Total number of nesting attempts and chicks successfully fledged for seven breeding seasons from 1997 until 2004. The period of population monitoring for this study is highlighted. (Data for the breeding seasons 97/98, 98/99, 99/00, 03/04 are taken from internal Department of Conservation reports).

Research approach

In order to empirically test and compare competing explanations for forced copulation in the stitchbird (male direct insemination, resistance-as-a-ploy, CODE hypothesis), I look at the temporal patterns of both within-pair and extra-pair copulations relative to each female's fertile period. I also compare the characteristics of males that were successful at forcing copulations with those of resident males that were unsuccessful at preventing these, as well as patterns of female resistance and its influence on extra-pair copulation success (Chapter 1). The robustness of the CODE hypothesis is further examined in Chapter 2 where the verbal game theoretic argument as proposed by Gowaty & Buschhaus (1998) is formally modelled and the model outcomes compared to the CODE hypothesis predictions.

In order to better understand how face-to-face copulation may bypass female mate choice and successfully lead to cloacal contact and forced insemination in the stitchbird, I examine the seasonal changes in the male's cloacal protuberance. Previous studies have generally failed to find support for the 'copulation efficiency' hypothesis of the cloacal protuberance (Wolfson 1952). Because previous tests of this hypothesis have not evaluated the relationship between male and female cloacal openings, I document the relationship between spermatic engorgement of the cloacal protuberance and its angular position in males and the corresponding seasonal cloacal changes in females (Chapter 3).

Males in many species, including stitchbirds, appear able to accurately predict the timing of each female's fertile period as witnessed by their congregations around fertile females (Emlen & Wrege 1986; Castro et al. 1996; Komdeur 2001). The mechanism by which male birds may assess female fertility has been suggested to come from cues directly from the female (flight behaviour, nest building, egg-laying, or female solicitation) or indirectly from the resident male (within pair copulation, mate guarding intensity, or song rate or quality) (Birkhead et al. 1987; Komdeur et al. 1999). To assess which of these proposed cues best predicts the patterns of extra-pair male forced copulation attempts; I use a correlational approach to evaluate which fertility cue is most likely to explain patterns of extra-pair male activity in this species (Chapter 4).

Because of its life history characteristics (high levels of extra-pair forced copulation and extra-pair paternity), mate guarding in the stitchbird is predicted to be intense (Komdeur 2001). However, previous published accounts of mate guarding in this species have suggested that males may not always adopt a mate guarding strategy as predicted (Ewen 1998; Castro et al. 1996). In Chapter 5 I evaluate mate guarding intensity by measuring 1) male proximity to the female, 2) the identity of the bird that re-establishes pair contact, and 3) the location and size of the area defended by the male, relative to the fertile period of the resident female.

Costs associated with forced copulation usually focus on the female (Smuts & Smuts 1993; Olsson 1995), however the possibility that forced copulation exerts costs on males through increased mate guarding has rarely been explored. I evaluated costs for the resident male by measuring his weight changes relative to his female's fertile period and associated extra-pair forced copulation attempts (Chapter 5). Females are thought to pay a cost of consorting with other males, in that the resident male reduces his investment in offspring provisioning proportionally to his certainty of paternity (Ewen & Armstrong 2000). Using a hierarchical model, I evaluate the relative cost of this when compared to other factors influencing male provisioning of offspring (Chapter 6).

Because forced copulation behaviour in non-human animals appears similar to rape in humans, this has lead to cross-species comparisons and the application of hypotheses developed in one field being used to explore the other (Gowaty & Buschhaus 1998; Thornhill & Palmer 2000). This exercise has been controversial and elements of this controversy are explored in Appendices 1 and 2.

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CHAPTER I

Female resistance and male force:
Context and patterns of copulation in the New Zealand stitchbird

Face-to-face forced copulation in the stitchbird

In this photo the male is lying face down on top of the female, who is lying on her back. The female's tail, lower abdomen and a banded leg can be seen.

Does a stitchbird, in time, rape nine?

Chapter reference:
Low, M. Female resistance and male force: context and patterns of copulation in the New Zealand stitchbird. Submitted to *Journal of Avian Biology*

Abstract

The New Zealand stitchbird or hihi: *Notiomystis cincta* is unique in that it has two distinct mating positions; in addition to the male standing on the female's back, as is seen in all other birds, it also copulates face-to-face. In this study, all males first attracted a female to their territory and supplemented their within-pair matings by intruding into other territories and attempting forced copulations. I recorded the temporal variation of both attempted and successful copulations relative to the female's fertile period in order to understand the function of copulation variability in this species. Each of 105 observed copulations were classified according to whether they were: 1) within-pair or extra-pair, 2) forced or unforced, and 3) face-to-face or standing. Together, 'within-pair unforced standing' and 'extra-pair forced face-to-face' copulations accounted for 77% of all observed copulations. The next most frequent classes of copulation were 'extra-pair forced standing' (10%) and 'extra-pair unforced standing' (7%). The peak in copulation frequency centred around two days prior to the laying of the first egg and occurred within a period of six days before and seven days after the first egg was laid. Unsuccessful extra-pair forced copulation attempts closely followed the distribution of all copulations. Male age and morphometrics did not predict whether a female would resist or accept extra-pair copulation attempts, and female resistance did not appear to select for male quality. In the stitchbird, it appears that males use forced copulation as a tactic to gain additional fertilizations within a wider reproductive strategy, and females resist these forced copulations because of some associated cost.

INTRODUCTION

Copulations performed outside of the pair bond have been reported in many bird species, with both males and females recorded as actively engaging in these extra-pair copulations (EPCs) (see Westneat et al. 1990, Griffith et al. 2002 for review). While males gain an obvious benefit from EPCs through fathering additional young, recent work has focussed on the active role females may play in securing EPCs to: (1) gain access to better resources (Gray 1996, Hunter and Davis 1998), (2) guard against infertility of their social mate (Sheldon 1994), (3) maximise genetic diversity of their brood (Westneat et al. 1990), (4) maximise genetic compatibility with the father of their offspring (Kempenaers et al. 1999), and (5) obtain 'good genes' from higher quality males (Møller 1988). Because the relative costs and benefits, as well as motivations, for engaging in EPCs differs between the sexes, this can lead to intersexual conflict (Trivers 1972, Clutton-Brock and Parker 1995). Female attempts to engage in EPCs may be thwarted by their partner implementing a paternity guarding tactic such as mate guarding (Komdeur et al. 1999) or frequent copulation (Birkhead and Møller 1992). Alternatively, females who are unwilling to copulate with an extra-pair male may be forced to do so, with the males of some species able to overpower or restrain an unwilling female for copulation despite her obvious resistance.

Forced copulation has been reported in a wide variety of animal species, including birds (reviewed in Thornhill and Palmer 2000), and is generally characterized by male force and female resistance. However, overt female resistance may be lacking in some cases where males gain sexual access through threat of force and females passively accept because the costs of resistance are high (Palmer 1989, Smuts and Smuts 1993). Despite the possibility that males may win arms races associated with forcible insemination (Clutton-Brock and Parker 1995), and thus influence patterns of extra-pair paternity in some species, this has been ignored in recent attempts to understand the adaptive function of extra-pair paternity in birds (for example Griffith et al. 2002, but see Westneat and Stewart 2003).

While overt female resistance suggests that the female is trying to avoid a particular copulation, it has been suggested that this behaviour could be a ploy to test the copulating male's quality (Westneat et al. 1990). This could evolve as a deliberate female strategy where females actively incite competition to choose the best male (Hoi 1997), or be selected for indirectly, as the competition between males simply leads to females being inseminated by the most competitive male who is strong enough to overpower her (Cox and Le Boeuf 1977, Wiley and Poston 1996). Determining the motivation of females who show behavioural signs of resistance may be difficult (Estep and Bruce 1981); however, if females resist as a ploy there should be some evidence of females inciting male competition (Hoi 1997, Westneat and Stewart 2003). This form of female choice has the potential to operate at a pre-copulatory level through male – male competition, or at a post-copulatory level through sperm competition (Cunningham 2003). Recently, however, the prevailing view that females generally benefit from and therefore should encourage EPCs has been questioned (Westneat and Stewart 2003), raising the possibility that in some cases females may generally resist EPCs. The New Zealand stitchbird or hihi: *Notiomystis cincta* is an ideal species to examine sexual conflict and female control of EPCs because of its overt and common forced copulation behaviours.

The stitchbird is an endangered endemic New Zealand passerine with a distribution restricted to offshore island sanctuaries (Higgins et al. 2001). Stitchbirds usually breed monogamously or polygynously, although occasional polyandry and polygynandry have been noted (Castro et al. 1996). During the breeding season both paired and unpaired males move into other birds' territories seeking extra-pair copulations (Ewen et al. 1999, Low in press), with 35 – 46% of offspring the result of extra-pair paternity (Ewen et al. 1999, Castro et al. in press). The stitchbird is unique in that it can copulate in two different positions: the common avian male-standing-on-the-female's-back as well as face-to-face (Anderson 1993, Castro et al. 1996). Copulations in the face-to-face position are generally considered to be forced, with females avoiding these by giving a specific forced copulation call and fleeing, and resorting to grappling with the male if caught and forced onto her back (Castro et al. 1996, Higgins et al. 2001). If EPCs are generally resisted by female stitchbirds, as has been previously observed (Ewen 1998), this places the stitchbird alongside waterfowl as an exception to the prevailing view that females should benefit from and therefore encourage EPCs (Cunningham 2003).

This study was designed to answer three questions regarding the context and patterns of within-pair and extra-pair copulations in the stitchbird. The first, why do males force copulations? To answer this, behavioural data were collected in order differentiate between four functional hypotheses of forced copulation: (1) as a tactic to gain fertilizations in addition to within-pair matings (Birkhead et al. 1985), (2) as a best-of-a-bad-job mating scenario for reproductively isolated males (Thornhill 1980), (3) as a non-inseminating manipulation of the mating system; the creation-of-a-dangerous-environment (CODE) hypothesis (Gowaty and Buschhaus 1998), (4) because females manipulate males in order to test their quality (Hoi 1997) (for hypothesis predictions see Table 1).

	Predictions					
Hypotheses	FC distributed randomly among males?	Which males attempt FC?	Quality of successful FC male relative to female's mate?	Which females are targeted for FC?	Female reaction to FC?	Extra-pair paternity from FC?
Additional Fertilization	Yes	Potentially all males	Random	All females. Primarily when fertile	Avoid	Yes
Best-of-a-Bad-Job	No	Only males lacking a social mate	Lower	All females. Primarily when fertile	Avoid	Yes
Dangerous Environment	No	Only males lacking a social mate	Lower	Generally non-fertile unpaired or unguarded females	Avoid	No
Female Manipulation	Yes	Potentially all males	Higher	All females. Primarily when fertile	Encourage	Yes

Table 1. Predictions arising from four hypotheses regarding the function of forced copulation (FC) in birds.

Secondly, why do females resist copulations, and how does this relate to current theories of female control of extra-pair paternity (Griffith et al. 2002)? If females are resisting to avoid costs of forced extra-pair copulation, and these forced copulation can result in extra-pair paternity, this suggests that females do not control extra-pair paternity in the stitchbird. I evaluated this by comparing observations of female behaviour to predictions from the theory that females use forced copulation to test male quality; and examine the evidence for forced copulation resulting in extra-pair paternity. Thirdly, do intermediate patterns of force and resistance lie between the previously described behavioural extremes of female-solicited standing copulation and face-to-face forced copulation? In other words, is there evidence for force and resistance in circumstances where females do not overtly struggle? I examined this by documenting all behaviours seen during copulation attempts and relating these to species-specific indicators of resistance.

METHODS

Study population

The birds in this study were observed during three breeding seasons in 2000/01, 2001/02 and 2002/03, and comprise a closed population on Tiritiri Matangi Island (36°36'S, 174°53'E), located off the northeast coast of New Zealand's North Island. Stitchbirds were translocated to the island in 1995 as part of the ongoing species' management programme. The population is small (between 26 and 34 breeding females per year) and restricted to a small portion of the island (30 out of 220 ha), allowing all breeding attempts to be monitored. The population sex ratio was biased towards females during the first two years of the study (1:1.7 and 1:1.1) and biased towards males during the final year (1.1:1). All birds on the island were uniquely colour banded with their ages and social parentage known.

Because the stitchbird is a cavity nesting species and the island is mostly young regenerating forest, approximately 100 wooden nest boxes were provided throughout likely nesting areas. With only one exception during the study, all birds nested in boxes and this allowed nesting behaviour to be easily monitored. Supplementary food was also provided in the form of a 20% (by mass) sugar solution, fed from up to nine feeding stations located around the island. These feeders were not contained within any stitchbirds' territories and did not confound measures of extra-pair male intrusion rates. Stitchbirds on Tiritiri Matangi Island breed during the spring and summer (September to February) and often successfully raise two broods of between one and five chicks. In this study, out of 121 nesting attempts, females were either paired to a monogamous (79%) or a polygynous male (21%). In one nest, two females simultaneously laid their eggs, but this failed soon into incubation due to ongoing aggression between the two females.

Copulation behaviour in stitchbirds

Stitchbirds have been described as copulating in two distinct positions: male-standing-on-the-female's-back (from now referred to as a standing copulation) (Castro et al. 1996) and face-to-face (Anderson 1993, Castro et al. 1996). Standing copulations are similar to those described for other avian species (Birkhead and Møller 1992). Both birds approach one another and engage in a neck-rubbing pre-copulatory sequence while vibrating their wings. The female then turns, the male hovers onto her back, the female moves her tail to one side and the male presses his cloaca towards hers. The male then dismounts, and may neck-rub with the female again, before calling and flying away. Face-to-face copulation is described as the female being chased to the ground by between one and five males, whereupon she is grasped by one of the males and forced onto her back. The male then positions himself on top of the female, with his wings outstretched, and prevents her from escaping, despite her vigorous attempts to do so. During face-to-face copulation attempts, the female emits a distress call during the chase until she is forced to the ground (Castro et al. 1996, Higgins et al. 2001). Anti-predator alarm calls have also been described for this species, and because they differ significantly from the forced copulation alarm call (Higgins et al. 2001, M. Low personal observation), to avoid confusion, these two calls will be referred to as the anti-predator call and forced copulation (FC) call.

Defining force and resistance in the stitchbird

Previously, face-to-face copulations in the stitchbird have been considered to be forced, and standing copulations considered consensual (Castro et al. 1996, Ewen 1998). To evaluate the validity of this dichotomy I observed all behaviours observed during copulations and paid particular attention to those that indicated a copulating bird was either using force or was resisting.

I defined resistance as any female act that reduced the likelihood of successful sperm transfer from a given copulation attempt (Westneat et al. 1990). This included flight from the male, FC calling, hiding, and fighting or struggling with the male. Force is considered in the context of sexual coercion (Smuts and Smuts 1993) or rape (Palmer 1989), whereby a male can use force or the threat of force to increase his chances of successfully mating with a female, at some cost to the female. Including "the threat of force" when assessing copulation motivation was deemed important, as this allowed for the possibility that forced copulations could exist in this species where males did not overtly use force. This approach is necessary for recognizing whether a continuum of sexual coerciveness exists in this species, as elements of force and resistance may be subtle in particular circumstances. In cases where motivations changed during a sexual encounter, the behaviour was categorised by considering the initial motivational state (resistance or active consent). A copulation was considered successful if the male mounted the female and it appeared as if he successfully made cloacal contact.

Behavioural observations

Stitchbird pairs were identified in September and October when females were beginning nest building. Each observation at a pair's territory lasted between 30 and 60 minutes and an attempt was made to monitor each site daily. Particular attention was paid to identifying any birds involved in a copulation or copulation attempt, describing all copulation behavioural sequences, the presence and behaviour of extra-pair males and females, and the reaction of resident birds to them. Nest boxes in each territory were monitored daily to establish the date the first egg was laid. Territorial boundaries were determined by observing the foraging behaviour of resident birds and interactions between resident and neighbouring pairs. The territory boundary was defined as the line beyond which an extra-pair male could call or be visible to the resident male, without the resident male making an attempt to chase him away. Birds were also observed at supplementary communal feeders during 2002/03, to compare to copulation behaviours observed within territories. Additional details can be found in Low (in press).

Age and morphometric data

The age of all birds in this study was determined from banding records held by the New Zealand Department of Conservation. In February 2002, at the end of the breeding season, all adult birds (n = 52) were captured in cage traps near supplementary feeding stations. Upon capture, birds were weighed using Pesola scales (± 0.5g), and their tarsus and head-bill lengths were measured using vernier callipers (± 0.05mm). Age, morphometrics and territory ownership were used as indicators of male quality in the absence of any validated quality measurement.

Analyses

The identity of birds and the timing of copulations were recorded during all three years of the study. However, comprehensive data on unsuccessful copulation attempts, male intrusion rates and female responses were only collected during the 2000/01 and 2001/02 breeding seasons. The identity of the copulating male could not be verified in some forced copulations, and these data are not used in tests requiring knowledge of male identity. Nesting attempts were highly asynchronous, thus all dates associated with collected data were converted to a number relative to the date of first egg lay for that female (= day 0) to allow comparisons between territories. Females were considered fertile between day -6 and the day the penultimate egg was laid (Low, in press). With the exception of morphometric measures, data were not normally distributed or were significantly heterogeneous and thus non-parametric statistics were used for these analyses.

The success of each copulation attempt, upon a given female, was assumed to be independent of the success of any previous attempts, and thus absolute numbers were compared. For the comparison between 1) the number of males involved in chases at the feeder and within the territory, and 2) for female FC call comparisons, a mean was generated for each female if more than one record existed per period, and these were compared using a Mann-Whitney U test. The number of extra-pair males visiting a territory was calculated by recording each male as having been present or absent during observations. This also applied when calculating the mean distances travelled by males when visiting extra-pair females' territories during their own female's fertile and non-fertile periods. For successful extra-pair copulations, males were recorded only once for comparison to unsuccessful males with their ages compared using a Mann-Whitney *U* test and morphometrics compared using a t-test. Where comparisons were made between age and morphometrics of the extra-pair and within-pair male, extra-pair males were recorded only once per female and were compared for age using a Wilcoxon signed-ranks test and for morphometrics using a paired t-test.

I used a sequential Bonferroni correction to adjust p-value significance when performing more than one test on the same dataset (Rice 1989). Means are expressed with standard errors, probability values are two-tailed and statistical significance recognized at $P < 0.05$.

RESULTS

During the three breeding seasons of this study, 121 nesting attempts by 50 females were monitored. Face-to-face forced copulations were generally as previously described, with the female struggling intensely against the grasp of the male, but in three instances the female was successful at struggling out from under the male and flying away. Males behaved very aggressively during these encounters. A male would hold the female down by grasping her legs with his claws and he would use his outstretched wings to restrict her body movements and control his balance. Males would often peck violently at the head and neck of the female as she struggled under them. As was observed by Castro et al. (1996), only one male of the chasing group ever successfully achieved cloacal contact with the female during each forced copulation event.

Temporal patterns of copulation

All 105 observed copulations (58 within-pair, 47 extra-pair) occurred between day -6 and +7, and were grouped around day -2 (Figure 1). No copulations were observed outside of this time even though 66% of territory observations from day -40 to +39 occurred outside of the female's fertile period. Most copulations were observed between the hours of 0700 and 1300, with the hourly copulation rate gradually declining during the afternoon (Figure 2). This pattern was similar for both within-pair and extra-pair copulations.

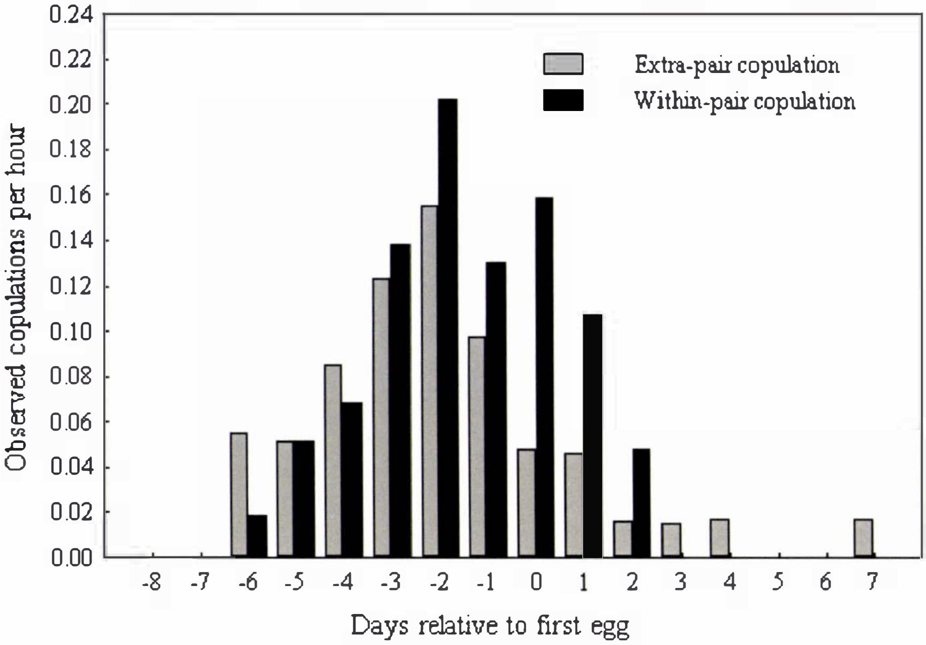

Figure 1. Temporal pattern of successful within-pair and extra-pair copulation relative to the laying of the first egg (= day 0).

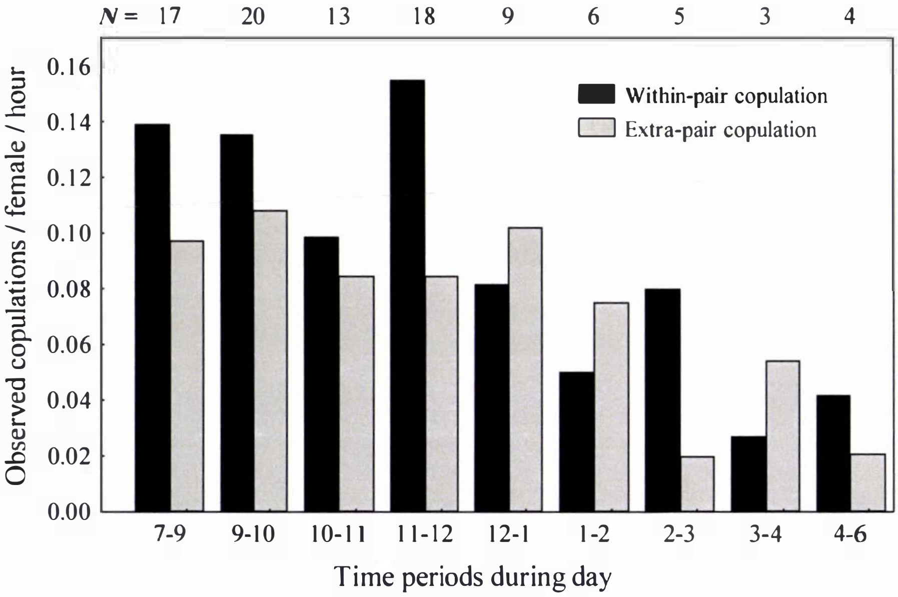

Figure 2. Temporal pattern of the rate of successful within-pair and extra-pair copulations relative to the time of day (between 0700 and 1800 hours) during the fertile period of the female (day –6 to +2).

Copulation categories

The majority of observed copulations (84%) could be placed into two categories – forced face-to-face and unforced standing. However, this strong association between the use of force and the copulatory position became ambiguous or reversed for the remaining 16% of observed copulations (Figure 3). In 11 instances where an extra-pair male copulated with a female in a standing position, the female had either been chased or the extra-pair male suddenly landed next to her prior to the copulation. The female did not approach the male, and began FC calling either during the chase or upon the appearance of the male, and this continued during the pre-copulation sequence and mounting. The extra-pair male went through an abbreviated copulation sequence (usually only a brief neck-rub and then mount) and, unlike within-pair copulations, he never called as he dismounted. During five of these resisted standing copulations, the female's FC calls attracted the attention of the resident male who arrived during or just after the extra-pair male had mounted, and then aggressively chased him away.

In six instances of copulation by mutual consent (five within-pair and one extra-pair), the female and male would begin neck-rubbing and turn as if the male was about to mount, but then the female would be pushed onto her side (on three occasions it appeared as if she overbalanced) and the male would flip her onto her back. At this point the motivation of the female usually changed abruptly and she emitted an aggressive call and struggled against the male. However, in one case she continued neck-rubbing with the male despite being on her back and did not obviously resist the encounter. The male would hold the female on her back and the rest of the sequence resembled a forced face-to-face copulation. I considered these to be consenting face-to-face copulations, as the female had actively approached the male and consented to copulate but only resisted in the middle of the sequence once flipped onto her back. It should be noted that on one occasion the female flipped the male onto his back, before he struggled to his feet and mounted the female in a standing position. On three occasions females were observed mounting the male, after he dismounted, during a standing copulation.

	Male on female's back	Face-to-face
Resisted by female	Within-pair 0 11 Extra-pair	0 28
Female consent	53 7	5 1

Figure 3. Eight-way breakdown of copulation categories relative to three factors, 1) copulatory position, 2) evidence of behavioural resistance by the female at copulation initiation, and 3) within-pair versus extra-pair copulatory partners.

Male – female chases

Extra-pair males

For both first and second clutches, forced copulation attempts made by the extra-pair male within the female's territory coincided with the female's fertile period and the timing of successful forced copulations (Figs 4a, b). The number of males involved in a forced copulation attempt ranged from 1 to 7, although the majority (61%) involved only a single extra-pair male. The mean number of extra-pair males involved in an unsuccessful forced copulation attempt (1.78 ± 0.11 extra-pair males per attempt, n =39) was significantly higher than the number involved in a successful forced copulation (1.28 ± 0.12 extra-pair males per attempt, n = 298; Mann-Whitney U: Z = 2.44, n_1 = 39, n_2 = 298, P = 0.014); with 80% of successful attempts involving only one extra-pair male.

The mean number of extra-pair males involved in chases of females was significantly higher at communal sites (2.89 ± 0.34 extra-pair males per chase, n = 14) than within the female's territory (1.50 ± 0.15, Z = 3.47, n_1 = 14, n_2 = 33, P = 0.0005).

This appeared due to the high concentration of males at these sites opportunistically taking advantage of the arrival of a fertile female.

Within-pair males

On 31 occasions in 24 territories, the resident male was observed chasing his mate in what superficially appeared to be a forced copulation chase. These chases differed from forced copulation chases by extra-pair males in: a) their timing relative to the laying of the first egg (day –18 ± 3; range –55 to –1), b) the response of the female as measured by FC calling rate (1 call per 1.3 ± 0.2 seconds; 20% were 'silent' chases – see below for comparison), c) their length (93 ± 12 seconds; range 20 – 305 seconds – see below for comparison), and d) the character of the chase (while not quantified, they always appeared to be less urgent). Most of these chases (90%) finished with either the birds simply landing in a tree and feeding or preening, or the male flying under the female in full display (Higgins et al. 2001). On two occasions the female became agitated as the sequence progressed and began hissing at the male while in flight, and on another two occasions, the male physically brought the female to the ground but did not copulate with her. On three occasions when the entire behavioural sequence was witnessed, it appeared that the female initiated the chase by hopping in front of the male for up to 2 minutes while giving a slow FC call, then took off with the resident male in pursuit. This initiation behaviour was never witnessed for extra-pair chases.

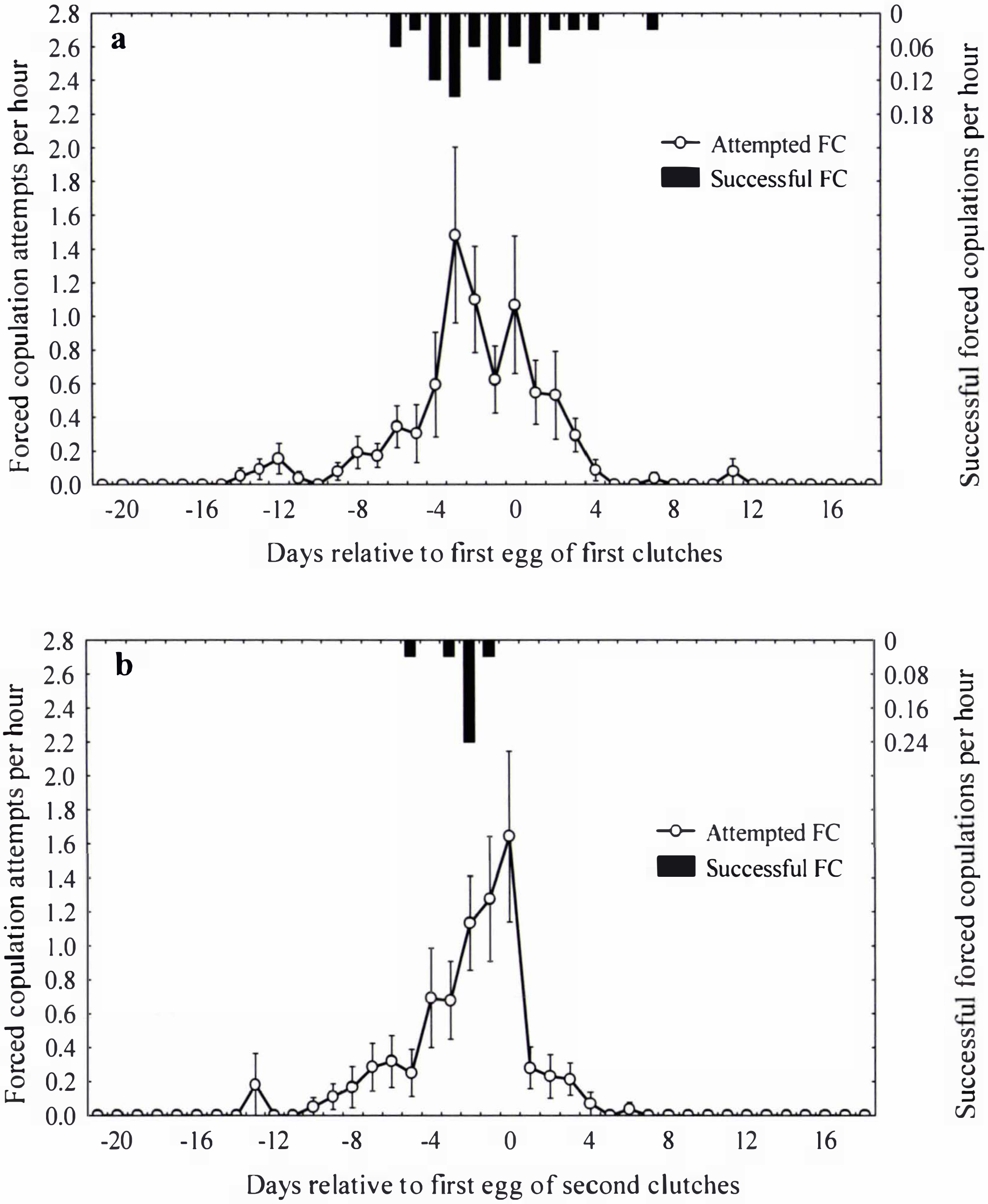

Figure 4. Temporal pattern of the rate of both successful forced copulations and unsuccessful forced copulation attempts per hour relative to the laying of the first egg (= day 0) for both **(a)** first clutches (n = 41 territories surveyed) and **(b)** second clutches (n = 31), in 2000/01 and 2001/02.

Female resistance tactics

Forced copulation (FC) call

Females emitted a series of single high frequency "seep" calls when confronted by an extra-pair male (between 0.25 and 7 'seeps' per second). The occurrence of this call is sensitive and specific to the context of an extra-pair male making sexual advances towards the female. Ignoring the cases of within-pair 'chases' mentioned above, 487 FC calls were noted during the 2000/01 and 2001/02 breeding seasons. These calls were delivered in three contexts: 1) extra-pair male chase or display (98.9%), 2) female-female chase (0.2%) and 3) bellbird-female chase (0.9%). When female stitchbirds are chased by another female or a bellbird, *Anthornis melanura*, they usually remained silent. Forced copulation calls were only heard only once (2.9%) during 34 female-female chases, and four times (2.1%) during 189 bellbird-female chases. In contrast, FC calls were emitted on almost every occasion an extra-pair male approached a female inside her territory (97.9%, $n = 497$).

The frequency of the FC call ('seeps' per second) varied according to circumstance. During a chase, females called at a rate of 3.07 ± 0.26 seep calls per second ($n = 33$, range 2-7) and this lasted for an average of 8 ± 2 seconds ($n = 58$, range 2 – 35). The frequency of the FC call was significantly lower when an extra-pair male was perched near to the female (0.49 ± 0.06 calls per second, Mann-Whitney U test: $Z = 5.23$, $n_1 = 33$, $n_2 = 13$, $P < 0.0001$). The rate increased if the extra-pair male approached the perching female, with it reaching its peak as she flew off or went to ground to evade the male. During observations at feeding stations in 2002/03, fertile females were seen to feed silently alongside extra-pair males unless a male made a sexual display by facing her and raising his ear-tuft feathers. At this point the female would begin FC calling and would leave the feeder, often FC calling all the way back to her territory with the male(s) in pursuit.

The FC call attracted the attention of the resident male. In 135 observations where the resident male was away from the female when she emitted the FC call, he immediately flew in the direction of the call and was seen chasing an extra-pair male from her vicinity. If the female was in flight and being chased, the resident male joined the chase and either diverted away the extra-pair male or waited until the group went to ground, whereupon he physically attacked the male nearest to his mate. In 17 cases where a female was surprised by an extra-pair male and forced to the ground, the resident male arrived before the extra-pair male could mount and either physically knocked him off the female or chased him away. In the five instances where the female was emitting a FC call while being chased by another female or a bellbird, the male arrived but did not interfere in the chase. In three cases where a neighbouring female was chased into the observed male's territory while emitting an FC call, the resident male remained with his own female and ignored the neighbouring female.

Evasion

In addition to emitting the FC call, females reacted in one of two ways to evade sexual contact with an extra-pair male. Females would fly within the boundaries of their territory while performing rapid changes of direction. Females would also go to ground, sometimes immediately, and sometimes after being chased in flight. Once on the ground the female would always attempt to scramble under vegetation or leaf litter, whereupon she would often freeze and become silent for several minutes. If successful, this tactic worked because males either couldn't find the female or it was now impossible to reposition her for copulation. The female would usually recommence the FC call if she was found and the extra-pair male was attempting to mount her.

Which males attempt forced copulations?

Of the 15 males in 2000/01 and the 28 males in 2001/02, all were observed intruding into other male's territories and attempting forced copulations while also being paired to a female within their own territory. These intrusions were centred around the resident female's fertile period, with a male being 20 times more likely to be seen in a territory during the female's fertile period (1.02 ± 0.08 extra-pair males / territory / observation hour) than outside of this time (0.05 ± 0.01 extra-pair males / territory / observation hour). In 2000/01 each male (n = 15) was seen on average in 6.1 ± 0.6 territories (range 1-11) and 20001/02 (n = 28), in 8.8 ± 0.8 territories (range 3-18) other than his own. While all males were seen in other territories during their own female's non-fertile period, only 53% of males were observed intruding when their own female was fertile. Males intruding during this time were significantly more likely to be seen in territories near their own (108 ± 20 m from extra-pair to own nest box), compared to when their own female was non-fertile (168 ± 31 m, Wilcoxon signed-ranks: $Z = 3.29$, $n = 15$, $P < 0.001$).

There was no correlation between the age of a male and the number of territories he visited (Spearman rank-order correlation: $r_s = 0.04$, $n = 43$, $P = 0.76$). The age of extra-pair males who were observed successfully forcing copulations was not significantly different from males observed unsuccessfully forcing copulations in 2000/01 (2.50 ± 0.50 versus 2.54 ± 0.52, Mann-Whitney U: $Z = 0.2$, $n_1 = 4$, $n_2 = 11$, $P = 0.84$), and the age and morphometrics of these two groups of males did not differ significantly in 2001/02 (Table 2).

Trait	Mean ± SE	*t*	*P*
Age (years)	2.3 ± 0.5 (a) 1.7 ± 0.4 (b)	1.17 *	0.24
Tarsus length (mm)	32.93 ± 0.25 (a) 33.01 ± 0.27 (b)	0.21	0.82
Head-bill length (mm)	42.58 ± 0.18 (a) 43.07 ± 0.30 (b)	1.37	0.18
Weight (grams)	39.2 ± 0.6 (a) 38.8 ± 0.6 (b)	0.48	0.63

* For the variable 'age' this value is a *Z* statistic from a Mann-Whitney U test

Table 2. Group comparison of males who were observed (a) successfully forcibly copulating with extra-pair females ($n = 15$) and (b) those that were not ($n = 13$) in 2001/02.

When do females solicit or resist?

During the study all females (n = 50) were observed resisting extra-pair males' copulation attempts, with only five females (eight copulations) seen to consent to copulate with an extra-pair male. The age and morphometric traits of the extra-pair male relative to the resident male were not a factor in predicting whether a female resisted copulation (Table 3). Contrary to expectations, females usually accepted an extra-pair copulation from a male younger than her social partner (1.4 ± 0.24 years versus 2.8 ± 0.96 years), although the sample size was small and the comparison non-significant (Wilcoxon signed-ranks: $Z = 1.06$, $n = 5$, $P = 0.29$). All females who accepted these EPCs were first-year breeders and also secondary females of a polygynous male. On two occasions, primary females were observed silently perching within their territory beside a displaying extra-pair male, but on neither occasion did they copulate.

It seems unlikely that females leave their territory to solicit copulations from extra-pair males, as all within-pair and extra-pair copulations took place within 15 m of the female's nest, with the exception of two forced face-to-face copulations that occurred at a communal feeding site. Furthermore, on only 1/146 occasions when a female was seen in an extra-pair male's territory was she fertile, and on this solitary occasion the female was foraging near the territory boundary.

Trait	Mean ± SE	*t*	*p*
Age (years)	2.4 ± 0.3 (a) 2.7 ± 0.4 (b)	0.82 *	0.41
Tarsus length (mm)	33.08 ± 0.11 (a) 33.15 ± 0.16 (b)	0.05	0.95
Head-bill length (mm)	42.75 ± 0.18 (a) 42.72 ± 0.13 (b)	0.20	0.83
Weight (grams)	38.6 ± 0.4 (a) 39.6 ± 0.4 (b)	1.55	0.14

* For the variable 'age' this value is a Z statistic from a Wilcoxon matched-pairs test

Table 3. Pair-wise comparison of age and morphometric traits of 19 (a) resident males and (b) extra-pair males at sites where the extra-pair male was successful at forcibly copulating with the resident female in 2001/02.

DISCUSSION

Female resistance behaviours

Female resistance appears to be an effective means of limiting the success of EPCs in the stitchbird. Females that fly from an extra-pair male and emit a specialised forced copulation call, alert their social mates who can then intervene and repel the male before he is able to copulate. The rapidly repeating structure of the FC call, may act to continuously update the female's position, and allow her mate to find her quickly. An FC call with a similar structure is used by female indigo buntings *Passerina cyanea* during forced copulation chases (Westneat 1987). Short rapidly repeating notes may be an optimal solution to attracting the mate's attention, and thus represent a convergence of call function in these two species.

Sexual coercion, where a male uses intimidation rather than overt force to achieve copulation, has been documented in mammals (Palmer 1989, Smuts and Smuts 1993) and explored theoretically (Clutton-Brock and Parker 1995). In this study, female stitchbirds were sometimes intimidated or coerced into copulating with little apparent force by the male and with the female only displaying subtle signs of resistance. While face-to-face copulations are obviously forced due to their aggressive nature, resisted standing copulations might easily be interpreted as consensual, as the only evidence of resistance is the species-specific FC call. This suggests that in other species, female resistance behaviours may be subtle and species-specific. A failure to recognize resistance other than overt struggle, may lead to an underestimation of sexual coercion in other species (Smuts and Smuts 1993).

Why do females accept some extra-pair copulations and not others?

When faced with the opportunity of an extra-pair mating, females may actively solicit the EPC, they may accept an EPC solicited by an extra-pair male, or they may resist the male's advances (Westneat et al. 1990). In this study, females were never observed leaving their territory to actively solicit an EPC, nor were they ever observed initiating an EPC with a male who intruded into their territory. During the study, all females were seen to resist copulation attempts from extra-pair males. Five females on a total of eight occasions appeared to consent to an EPC when approached by an extra-pair male, which represented only 17% of all successful EPCs. The elements uniting these five females were: 1) the females were all in their first breeding season, 2) they were all secondary females of a polygynous male, 3) they tended to copulate with a male younger than their partner, who was also a near neighbour and 4) they all resisted multiple forced copulation attempts at other times during their fertile period. One explanation for the females' behaviour under these circumstances is that they are seeking a direct benefit from the EPC by increasing their access to resources (Gray 1996, Hunter and Davis 1998). While male stitchbirds do invest in offspring (Castro et al. 1996, Ewen and Armstrong 2000), they rarely invest in the offspring of secondary females (M Low unpublished data). It is likely that these females are aware of their secondary status due to harassment from the primary female (M. Low personal observation). If males do not invest in secondary females' offspring, they cannot threaten to withhold parental care (Ewen and Armstrong 2000), and thus females can pursue EPCs without significant cost. Because both paired and unpaired male stitchbirds will congregate around fertile females, it might pay females under these conditions to copulate with the resident male as well as potentially unpaired males in an attempt to attract investment for her offspring, or attract a social mate for future clutches.

With the exception of these few consensual EPCs, females resisted both successful and unsuccessful EPCs. It has been suggested that female resistance may be a ploy to test the strength males in an attempt to facilitate mating with a higher quality male (Westneat et al. 1990). If female stitchbirds were promoting pre-copulatory mate choice through resistance of male copulatory attempts, then successful males should differ in quality from a) the resident male and/or b) unsuccessful males. In this study, males that successfully copulated despite female resistance did not differ in age or morphometrics from either of these two groups. The majority (80%) of successful forced copulations involved only a single extra-pair male; this was also found in mallards *Anas platyrhynchos* (Cunningham 2003) and guillemots *Uria aalge* (Hatchwell 1988), and thus there was little pre-copulatory male-male competition in most cases. Residents that intervened in forced EPC attempts, repelled the extra-pair male on every occasion, and were never observed to copulate with the female at this time. This is in contrast to the bearded tit *Panurus biarmicus*, a species believed to exhibit resistance-as-a-ploy behaviour, where the female mates with whichever male catches her first (Hoi 1997). Stitchbirds also differed in that females were never seen inciting chases from extra-pair males, and generally remained quiet and inconspicuous during their fertile period. This suggests that the function of female resistance in the stitchbird is cost limitation rather than female manipulation (Westneat & Stewart 2003).

Females might judge male quality by their ability to catch and overpower the female rather than by their ability to compete with other males (Wiley and Poston 1996). This is improbable however, considering the ease with which males can catch females at this time due to the female's average 31% increase in body weight as a result of egg production (Low in press). If a female wanted to test a male's quality, a more accurate assessment of this would be earlier in the nesting cycle. This is because females become handicapped during their fertile period by the additional weight they are carrying and the physiological weakening of their flight muscles due to egg production (Houston et al. 1995). This results in relatively poorer flight performances and an increased likelihood of being caught by predators, and presumably, extra-pair males (Kullberg et al. 2002).

Post-copulatory mate choice, where females encourage multiple copulations to promote sperm competition (Cunningham 2003), also appears to be an unlikely explanation for female resistance in the stitchbird. This is because the majority of copulations involved only one male, copulation frequency was low, and resistance behaviours reduced the likelihood of copulation success rather than acting to increase the number of copulations. These factors suggest that, in the stitchbird, females are resisting to avoid some cost associated with copulating with extra-pair males, such as a reduction in offspring care by her social mate (Ewen and Armstrong 2000) or transmission of disease (Kokko et al. 2002).

Why do male stitchbirds sexually coerce females?

Behavioural evidence supports the hypothesis that sexual coercion acts as a conditional tactic within a wider mating strategy in male stitchbirds. Males preferentially established a territory and called to attract females. Unpaired males have only been observed moving between fertile females and attempting forced copulations when the sex-ratio is male biased (Ewen et al. 1999; M Low unpublished data). When the population sex ratio is female biased or even, all intruding males have a social mate. In this study, males were less likely to intrude into other males' territories and remained nearer their own when their own female was fertile. If males are assumed to have a certain amount of mating effort to expend each day, males stitchbirds will devote more effort towards their own female at times when she is fertile, and on fertile extra-pair females outside of this time. Unpaired males direct the majority of their effort pursuing extra-pair copulations as a best-of-a-bad-job tactic (Ewen et al. 1999).

This interpretation is supported by genetic evidence from other stitchbird studies showing that males with territories father more offspring and have a lower variance in reproductive success than males without territories (Castro et al. in press). These paternity data illustrate that while the average territorial male only fathers approximately two thirds of the chicks in his nest, he compensates for his losses by fathering extra-pair offspring at other sites. Unpaired males however, while gaining similar extra-pair paternity as paired males, cannot compensate for the lack of paternity at their own nest.

In this study, just over one third of all successful copulations were coerced through force or threat of force by an extra-pair male. If this proportion translates directly into paternity, we would expect to see a similar level of extra-pair paternity (approx. 40%). In a previous study on Tiritiri Matangi, where only forced EPCs were observed, the level of extra-pair paternity was 35% (Ewen et al. 1999).In a study of a separate population, extra-pair paternity was 46% (Castro et al. in press). These genetic data suggest that sexual coercion is successful at achieving extra-pair fertilization, with males being at a selective disadvantage if they did not seek out extra-pair forced copulations in addition to within-pair paternity.

The 'creation of a dangerous environment' or CODE hypothesis (Gowaty and Buschhaus 1998), proposed to explain patterns of forced copulation in birds such as the stitchbird, is not supported by the data from this study. The CODE hypothesis makes a number of novel predictions such as 1) forced copulation is directed at both fertile and non-fertile females, 2) forced copulation does not result in fertilization and is negatively correlated with extra-pair paternity, 3) males specifically direct forced copulations at unguarded and unmated females, and 4) male aggression directly alters the mating strategy from polygyny to monogamy. In the stitchbird, none of these predictions are upheld and thus it appears unlikely that Gowaty and Buschhaus' (1998) hypothesis explains the existence of forced copulation in this species.

The adaptive function of extra-pair paternity

The finding that male stitchbirds can force EPCs, and presumably extra-pair paternity, has implications for understanding the adaptive function of extra-pair paternity in avian species. In a recent review of extra-pair paternity in birds (Griffith et al. 2002), consideration was only given to hypotheses that assumed extra-pair paternity is a female strategy and therefore benefits females. While females have been shown to control extra-pair paternity in some studies (e.g. Gray 1996), the possibility that males may be able to subvert female choice (Clutton-Brock and Parker 1995) is currently being largely ignored. Westneat and Stewart (2003) argue that the widespread assumption of extra-pair paternity being a female strategy is unsupported, with it generally ignoring the impact, on female fitness, of the other two players in the game: her social mate and the extra-pair male. In the stitchbird, it seems likely that the function of extra-pair paternity is primarily driven by male reproductive interests, with females only able to minimise the costs involved. Thus future empirical and theoretical assessments of extra-pair paternity in birds need to account for the conflicting interests of both the social mate and extra-pair males on female fitness outcomes.

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CHAPTER II

Intimidate or inseminate?
Modelling the CODE hypothesis

Female foraging for insects on a tree trunk

The female M/RO keeps an eye on me (an extra-pair male within her territory) during an observation session at site b22/14

Chapter reference:

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Abstract

Gowaty and Buschhaus' creation of a dangerous environment or CODE hypothesis (Am. Zool. 38:207-225) adopts the standard feminist explanation for rape in humans and adapts it to explain the existence of forced copulation in bird species where males lack an intromittent organ. The authors argue that rape / forced copulation should be seen as a non-inseminating aggressive act, rather than it being sexually coercive. In examining their verbal game theoretic argument in support of the CODE hypothesis, I conclude that it is based upon two errors. The first is an incorrect assignment of phenotypes to competing strategy groups and the second is a failure to consider relative payoffs when determining evolutionary stability. By modelling the CODE hypothesis I show that forced copulation cannot invade either as part of a mixed strategy or by operating conditionally under the constraints imposed on the model by Gowaty and Buschhaus. Birds engaging in non-inseminating forced copulation are unable to escape the costs that they incur, while at the same time 'altruistically' sharing any benefits of monogamy with the competing strategy males.

INTRODUCTION

Until recently, the standard feminist interpretation that rape in human culture is about power and not sex has been generally accepted (Brownmiller, 1975; Grant, 1993). However, more recent examinations of rape data have lead to the opposite conclusion, that sex is a significant motivating factor in most rapes (reviewed in Jones 1999; Thornhill and Palmer 2000; Alcock, 2001; Pinker, 2002). Evolutionary analyses of these data are showing promise in explaining rape trends (Thornhill and Thornhill, 1983; Thornhill and Palmer, 2000) and there is evidence that pregnancy from rape is at least equal to, and perhaps higher than those arising from consensual sex (Gottschall and Gottschall 1999). In non-human behavioural ecology, forced copulation (or as it will be referred to for the remainder of this paper, "rape") has generally been accepted as being a male sexual strategy (Thornhill, 1980; Clutton-Brock and Parker, 1995). Recently however, Brownmiller's (1975) ideas that rape is about power and not sex have been applied to understand the function of rape in birds (Gowaty and Buschhaus, 1998).

Gowaty and Buschhaus (1998) see rape in birds lacking an intromittent organ (phallus) as a problem case, as it is relatively common but often seems to be a poor way of securing successful copulations and fertilisations. They criticise the standard adaptive explanation of rape being a male sexual strategy whereby males can increase their fitness by forcibly inseminating unwilling females (Morton, 1987). Gowaty and Buschhaus (1998) (from here referred to as G&B) believe that for rape to be adaptive, fertilisation success from rape should be as frequent as from copulations with preferred partners in which females do not resist. Because this is often not the case, they conclude that the function of rape in birds must have some non-sexual function, and it is here that they apply the feminist theory of human rape (Brownmiller, 1975) to avian behavioural ecology. This synthesis has males raping not to inseminate, but to intimidate, and has been titled the 'Creation Of a Dangerous Environment' or CODE hypothesis. Under this hypothesis rape is a non-sexual act of aggression used by a small percentage of reproductively isolated males to modify female behaviour. This creation of a dangerous environment is thought to benefit males because females eventually trade sexual access for protection, thus favouring the evolution of social monogamy. Gowaty and Buschhaus aim to demonstrate the benefits to males of non-inseminating rape by examining its impact on a group of birds mating polygynously. According to the CODE hypothesis, a small number of males who do not have access to females under polygyny, start to rape females (as a form of aggression only) and this adds a cost to females that choose to consort polygynously. If aggressive attacks are common enough to pose a cost that outweighs the benefits of staying with a polygynous male, then the mating system should shift to monogamy where each female can rely on her partner to protect her from those costs of aggression. Gowaty and Buschhaus claim that this behaviour is selected for because the rapist males that otherwise would not have had an opportunity to mate under polygyny now have a partner, and this acts as a selective force that favours the tactic of using rape to increase the reproductive costs of polygynous females.

Who is competing against whom?

To demonstrate the robustness of their CODE hypothesis, G&B present a verbal game theoretical argument. This defines the competing strategies in terms of reproductive outcomes under polygyny. The two contestants within the game are identified as P-males (males with sexual access under polygyny) and Z-males (males with no sexual access under polygyny). Gowaty and Buschhaus assess what happens if a proportion of the Z-males adopt a new strategy of raping females to modify female behaviour. Support for the CODE hypothesis is then derived from two assumptions. Firstly, Z-males via the act of rape can increase the reproductive costs to females that consort polygynously (exclusively with P-males) to such an extent that it becomes more profitable for them to consort monogamously (with all males). Secondly, Z-males' fitness increases as they move from polygyny to monogamy (i.e. they move from reproductive exclusion to having a sexual partner), while P-males reproductive success decreases. Gowaty and Buschhaus claim that Z-males benefit under individual selection as their actions (rape) result in a simple fitness increase as females trade sex for protection.

While superficially this appears a logical outcome of the CODE hypothesis, on closer examination two serious problems become apparent. The first is that in comparing the outcomes of strategies competing within the CODE hypothesis framework, G&B assume two strategies are competing with one another and have identified these as P-males and Z-males (as defined above). This means that having sexual partners under polygyny (P-males) is one strategy and having no sexual partners under polygyny (Z-males) is the other. Explicitly defining each strategy in this way makes it immediately obvious that the competing strategies have been incorrectly defined. Whenever there is a zero-sum contest for resources there must be a winner and a loser but this does not mean that the contestants are following different strategies. It is expected that within a polygynous mating system a single reproductive strategy will produce differential sexual access for males. Under polygyny both G&B's P-males and Z-males are likely to be obeying the same strategy. That is, they are both competing for resources or displaying in such a way as to attract female sexual partners, with some males winning (P) and some losing (Z). Because of this incorrect strategy group definition, when the behavioural strategy of rape is introduced into the model, G&B incorrectly assume that all Z-males (Z-male rapists and non-rapists) are to be treated as a single group. The authors are correct in assuming that two strategies are now to be compared, but it is not simply Z-males versus P-males. The second problem with G&B's interpretation of the CODE model is that in order to determine if the rapist strategy will be successful, it is not enough to simply show that the fitness of rapists increases as the mating system moves from polygyny to monogamy. If game theory is to be utilised to demonstrate the success of rapists, then at the very least it must be shown that rapist strategy payoffs achieve a value greater than or equal to the incumbent strategy payoffs at some point between polygyny and monogamy.

To evaluate the CODE hypothesis game theoretic model as verbally described by G&B, it needs to be determined whether rape and consensual sex conform to a mixed or conditional strategy. The form of the game will determine the makeup of the competitors within each strategy group and will affect the predictions of strategy payoffs (Maynard Smith, 1982). The various behavioural options available to an animal may be classified as a 'strategy' (a description of the overall rule) or a 'tactic' (a description of a behavioural component of the strategy). It has been suggested that this separation of terms can generally be ignored in practice (Krebs and Davies, 1993). However, if an effort is not made to keep 'strategies' and 'tactics' separate in discussions of animal competition, it can easily lead to the situation where the success of different behaviours within a strategy are being erroneously considered to be competing strategies. The consequences of this are seen in G&B's dismissal of the standard sociobiological explanation of rape being a sexual strategy. Gowaty and Buschhaus state that rape must have the same payoffs as consensual sex for it to be adaptive, thus meaning that rape must always be a 'strategy' and therefore to be evolutionarily stable it must conform to the payoffs within a mixed strategy game. This mistake is understandable especially when conditional tactics are routinely discussed as if they are alternative strategies (Krebs and Davies, 1993). What needs to be remembered is that behaviours can operate as tactics within a strategy of the form, 'when strong, do the successful thing, and when weak make the best of a bad job'. This is a singular strategy that can be seen as competing with the strategy of an animal that attempts to do the successful thing, but does not adopt the best of a bad job tactic when prudent. Thus the poor tactic (in this case, rape) should not be compared to the successful tactic (or even to doing nothing), but rather needs to be seen as an additional component of a successful wider strategy rule.

The concerns with G&B's formulation of the CODE model do not mean that the idea of males conditioning females through rape is necessarily invalid. In order to determine whether the CODE hypothesis in its current form is feasible, the rest of this paper will define the variables and assumptions of their model. Once these are made explicit, a game theoretic approach as advocated by G&B will be used to test the evolutionary stability of the outcomes predicted by the authors.

Rape as a component of a mixed strategy

One interpretation of the CODE hypothesis is that rape operates as part of a mixed strategy where the payoffs to all behavioural alternatives are equal. In this form of the game one strategy is that of males who display and compete for female choice with some having sexual access to several females and others having none. These can be called 'displayers' and include all of G&B's P-males and any Z-males that do not engage in rape. The second strategy is the male who is not selected by females under polygyny and resorts to rape to attempt a shift in mating system to monogamy. These can be called 'rapists' and include only those Z-males that rape. This means that within the mixed strategy game, not all of G&B's Z-males are competing under the same strategy. To assess the CODE hypothesis as a form of mixed ESS, it is assumed that the following conditions in the game are met.

1. Within the game there are three male phenotypes. The first type of male (*P*) is the male who successfully gains sexual access to females under polygyny (G&B's P-males). The second type of male (*Zp*) is the male who fails to gain sexual access under polygyny but does not rape (some of G&B's Z-males). The third is the male (*Zrape*) who would not gain sexual access under polygyny and instead rapes (the remainder of G&B's Z-males).

2. There are two male strategies contesting the game. These are the ‘displayer’ males whose strategy is to display or defend resources to attract females to mate with and never rape ($P + Zp$ males), and the ‘rapist’ males whose strategy is to rape females and attempt to mate with any females who seek protection from aggression (*Zrape* males).
3. Rape does not result in successful insemination and is an aggressive behaviour only. This means that rapists have zero reproductive success under polygyny.
4. Rape effort by an individual is independent of the number of females and other rapists in the population.
5. Female behaviour is plastic in ecological time. When the numbers of rapists in the population is zero, females will mate polygynously. As the number of rapists increase, so does the number of females switching to monogamy.
6. All females are fertile at the same time or distributed in space so that males cannot defend more than one female at the same time.
7. The population has a 50:50 sex ratio and all females are equally fecund and breed once in every round of the game.

If there are N_f females in the population and for every rapist, a proportion of females m switch to monogamy, then the average payoff calculated in terms of female access to each male phenotype can be represented as:

$$P = \frac{N_f - (N_{zr} \times m \times N_f)}{N_p}$$

$$Zp = \frac{N_{zr} \times m \times N_f}{N_{zr} + N_{zp}}$$

$$Zrape = \frac{N_{zr} \times m \times N_f}{N_{zr} + N_{zp}} - C$$

Where N_{zr} is the number of *Zrape* males in the population, N_{zp} is the number *Zp* males (together these make up G&B's Z-males), N_p is the number of *P* males (G&B's P-males), and C is the cost of rape to males. In this game the payoffs to each phenotype and thus each strategy change as the population shifts from polygyny to monogamy (Figure 1 a, b). When there are no rapists in the population ($N_{zr} = 0$), the payoff to *Zp* and *Zrape* males is zero, while *P* male access to females is dependent only on the number of *P* males in the population (N_f / N_p). As N_{zr} increases, so do the numbers of females being shifted away from *P* males to the benefits of all *Z* males (both *Zp* and *Zrape*). The assumption in the model is that monogamy is a built-in limiting factor, stabilising the payoffs for all male phenotypes when the population reaches this point.

Figure 1a shows the relative payoffs to the three male phenotypes and Figure 1b shows the payoffs to the rapist and displayer strategies as the number of *Zrape* males increase and the mating system shifts from polygyny to monogamy. In Figure 1a it can be seen that as the population shifts to monogamy, the number of females a *P* male has sexual access to gradually drops to one, while *Zp* males that under polygyny have no access to females, gradually increase their average female access towards one. The *Zrape* male never quite gets to one, if we factor in their additional cost, the cost of rape.

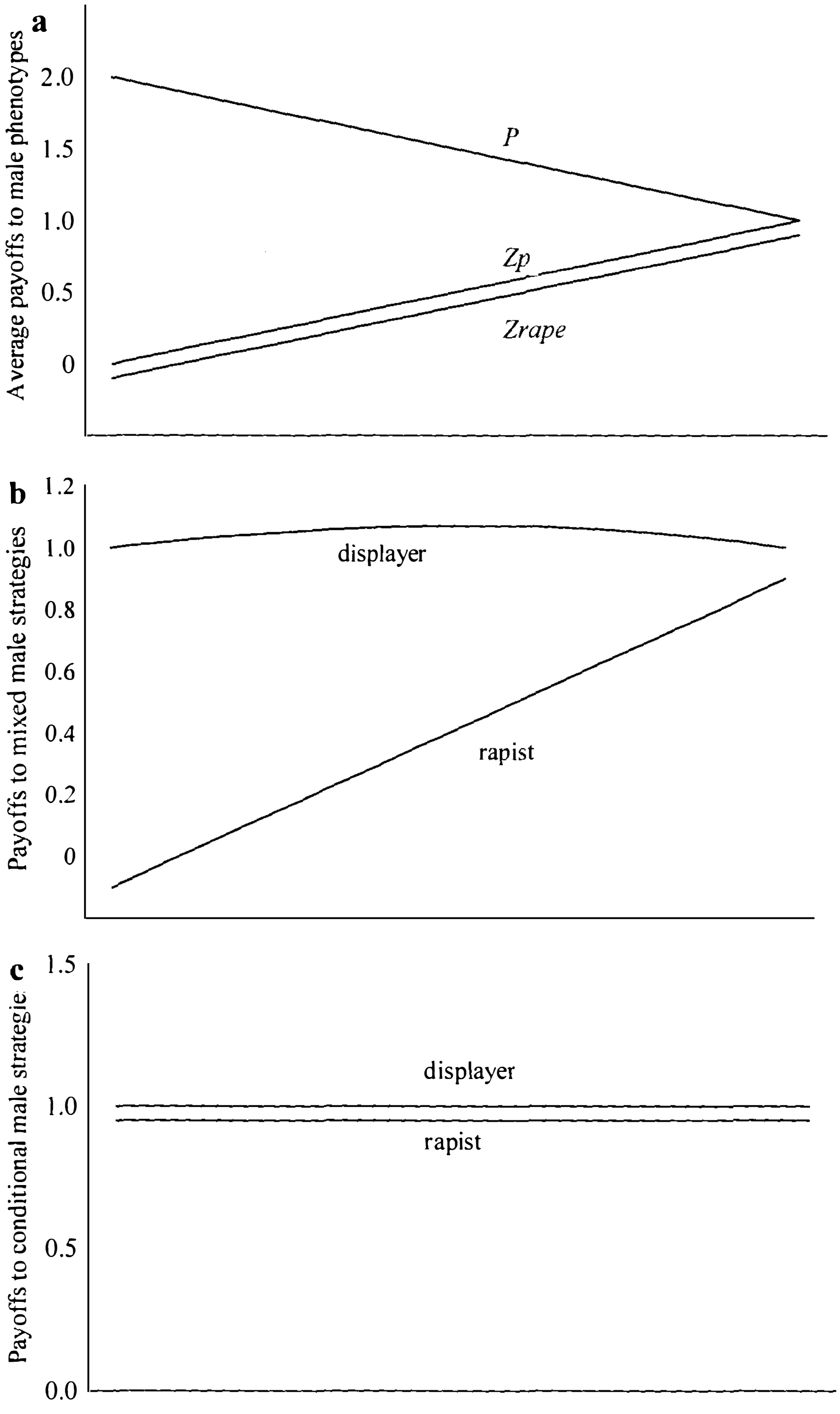

Fig. 1. Average male fitness payoffs on a continuum between polygyny and monogamy for **(a)** the three male phenotypes (*P*, *Zp* and *Zrape*), **(b)** displayer ($P + Zp$) and rapist (*Zrape*) strategies when rape is acting within a mixed strategy framework, **(c)** displayer ($P_p + Zp$) and rapist ($P_r + Zrape$) strategies when rape is operating as a conditional strategy. Fitness payoffs are calculated relative to the average number of sexually accessible females minus the cost of rape (if applicable).

If we examine strategy payoffs as shown in Figure 1b, as rapists (and their payoffs) increase, so do the average payoffs for the displayer strategy until approximately the halfway point between polygyny and monogamy. It appears counterintuitive that as rapists steal females away from the displayer strategy, the payoffs to both strategies should increase. However, what is happening is that as an individual male shifts from displaying to the rape strategy he loses fitness and the remaining displayers have gained this loss. This is difficult to see because it is easy to confuse the fitness of a male phenotype with average strategy payoffs. Consider a population of polygynous displayers consisting of 100 males and 100 females where only 20 of the males gain sexual access to females. This means that the males with sexual access have five females each and the rest have zero. But the average payoff for the displayer strategy is one female for every one male. Now imagine that one of these males becomes a rapist. Assume that by himself he is able to harass two females into mating monogamously with two of the 80 spare males. He has one chance in 40 of getting one of those females to mate with him and thus the payoff for this strategy is 0.025. What must be remembered is that until he shifted strategy his payoff was not zero but 1.0 (which is the average payoff for the displayer strategy). Thus in switching to a raping strategy the male has reduced his chances of gaining sexual access to females from a one in five chance of mating with five females, to a one in 40 chance of mating with one female. The displayer payoffs increase because now they are not dividing 100 females across 100 males, but rather 99.975 females between 99 males. Every male that shifts to the rapist strategy is similarly adopting a strategy with a lower average fitness payoff until monogamy is reached. At monogamy, all males now have access to one female each, but rapist males must contend with incurring the additional cost of rape. Under these conditions, rapists cannot invade a population of displayers when considered as a mixed strategy game.

Rape as a tactic within a conditional strategy

The second interpretation of the CODE model is that rapists are expressing a conditional behavioural tactic within the strategy, ‘display first and if fail to attract female partners, then rape’. For the conditional game the assumptions from the previous game hold, with the exception of the distribution of male phenotypes into the competing strategy groups. For this game the *Zp* males and *Zrape* males are still competing against each other, but the *P* male phenotype is now divided between each strategy. The first strategy is the same as the displayer males from before; that is they attempt to attract female partners with some successful (P_p) and others not (*Zp*). The strategy attempting to invade this group is made up of males who are successful at attracting female partners (P_r) and some who are not but then resort to rape (*Zrape*). If we assume that each strategy is equally successful at attracting females, then *P* males can be divided into each strategy at the same ratio as the *Z* males. Utilising the payoff equations for the three male phenotypes from the previous game, we can see the relative payoffs to each strategy represented in Figure 1c. The rapist strategy always lags behind the displayer strategy because while the rapists achieve the same sexual access to females at all stages from polygyny to monogamy, they always have the additional rape cost reducing their payoffs.

If we abandon the underlying assumption behind the CODE hypothesis and assume that rape can achieve fertilisation, rape can work as a conditional strategy because it adds to the lifetime reproductive success of the animal (Birkhead et al., 1985; Clutton-Brock and Parker 1995). At very low densities rapists could invade a population of non-rapists, as they gain offspring through rape at times when they otherwise would have no sexual access to females. Thus, all else being equal, the rapist strategy can steal fitness from the other strategy for themselves and this presents a fitness payoff greater than the non-rapists and allows them to invade, as they are an ESS (Birkhead et al. 1985). In contrast, rapist males under constraints of the CODE hypothesis force polygynous females away from the *P* males of *both* strategies. The fitness gains from these 'stolen' females are then not added to the rapist strategy, but are 'altruistically' shared equally with the competing strategy *Z* males. This is because any female that abandons polygyny for monogamy, may partner herself with either a *Zp* or a *Zrape* male. This means that *Zrape* males incur the cost of rape for an average net gain of zero to their strategy. It is this that prevents rape in the CODE hypothesis from working as a conditional tactic and thus rapists cannot invade a population of non-rapists under these conditions.

Counter-adaptations and rape costs

Gowaty (1997) and Gowaty and Buschhaus (1998) have rightly argued that females are not passive reactors to male reproductive interests and should respond with counter-adaptations to minimise the impact of mating system manipulation. They discuss the various anatomical and physiological structures and behavioural methods that females may employ to limit the negative impacts of rape. When considered in context, the presence of these counter-adaptations poses two problems for the CODE hypothesis. The first is that the presence of structures and mechanisms in females to reduce the efficacy of forced insemination suggests the opposite to what G&B conclude. Rather than it demonstrating that rape is ineffective and thus must have some non-sexual function, it shows that insemination from rape has been effective enough to promote the selection of female counter-adaptations. From this it seems logical to conclude that rape primarily evolved to forcibly inseminate females. The second problem for CODE comes from the impact of female choice on the payoffs to the competing strategies. Female mate choice was operating under polygyny and there is no reason to believe it will suddenly cease to operate as the system moves towards monogamy (at the very least females need to choose a male not already paired). Gowaty and Buschhaus argue that under enforced monogamy, females would be selected to engage in assortative mating to minimise their reproductive costs. This would occur either through (or as a combination of) better quality females competing to pair up with better quality males, and females seeking extra-pair copulations with better quality males than they are partnered with. As the better quality females pair up with the most preferred males (*P* males), poorer quality females would be left to pair with the rapists. Fitness losses to rapists would be further compounded by the loss of paternity if their females engaged in extra-pair copulation with *P* males, also predicted by G&B. If any of these female choice variables are factored into the mixed strategy game, displayer payoffs rise with a corresponding fall in the payoffs to rapists, thus widening an already impassable gap.

It could be argued that the relative costs of rape may be negated by some unilateral cost that other males incur. The most obvious is that of a display cost to males that are attempting to attract a female partner. In the conditional game all males display to attract females and only once a rapist has failed in this does he attempt to rape. Both rapist and non-rapist *P* males will incur identical costs, leaving the rapist *Z* males to fully absorb the additional costs of rape, while the non-rapist *Z* males avoid this. Thus under a conditional strategy, rapists' costs will always be higher than non-rapists, but without any relative increase in sexual access. In a mixed strategy situation it becomes more complex as female choice is expected to affect display rates. As the system shifts towards monogamy, there is a pressure on all *Z* males (including rapists) to attract one of the monogamous females to mate with them through some form of display. Monogamous females will attempt to pair up with the best male they can (within the constraints imposed on choice by rape) and this will drive rapists to display. If the *Zrape* males fail to display, they will disproportionately lose females to non-paired displayer males (*Zp*). This means that once rapists achieve any shift towards monogamy, they are forced to display for female choice. This gives them a display cost equal to that of the other males and still leaves them relatively worse off with the cost of rape. If rape acted to prevent females from choosing, then it is reasonable to assume that selection would run in the other direction and displayers would stop displaying. This would have the same effect in the game as adding the display costs to the rapist strategy. Thus as rapists approach monogamy (Figure 1b) and their access to females approaches that of displayer males, they will lose any relative advantage in display costs and yet will still be encumbered with the costs of rape.

Gowaty & Buschhaus recognise that this problem exists when they state, "the fitness payoff to a lone aggressor seems less likely to result in a positive function compared to other Z males". However they manoeuvre around this by stating that the fitness payoff to males that rape in groups will result in a positive payoff for all the males in the group because the costs and benefits would be equalised if reciprocity were practiced. No explanation as to how this might work is offered. How would birds monitor who had done their fair share of raping and how would they punish birds that were simply exploiting the 'altruistic' rapists for their own selfish reproductive ends? Even if we suppose that reciprocal altruism can operate under these conditions, the problem has not been solved but rather moved sideways. All that has been done is shift the focus from a single rapist to a single group of rapists. Any birds outside the group (all displayer males, including those that under polygyny have zero fitness) would still get the same sexual access without the costs of rape. The problem of a lower fitness payoff to rapists when compared to other males has not gone away.

The fact that rapists' costs under the constraints of the CODE hypothesis exceed those of the displayers while often their reproductive output is relatively lower means that at any level of monogamy the reproductive payoffs to rapists are less than those of all other males. Thus over time any tendency to rape will decrease as the population is not evolutionarily stable, and the number of rapists falls (in the mixed strategy scenario it accelerates) back towards polygyny. Any rapists at that point would be driven to extinction by the severe costs imposed by their tactics and the lack of any reproductive benefits.

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CHAPTER III

Cloacal erection in the stitchbird:

Functional convergence with mammalian genitalia promotes stiff competition

The comparative size of a testicle and the brain of a male stitchbird

The male WM/G helps to answer the age-old question, “What do guys think with?”

Chapter reference:

Low, M., Castro, I. & Berggren, Å. Avian cloacal erection: Functional convergence with mammalian genitalia. Submitted as a report to *Science*.

Abstract

Cloacal protuberances (CP) in birds result from spermatic engorgement of storage tubules during the breeding season. We describe a method by which CPs improve the efficacy of sperm delivery by acting functionally like a penile erection. In the male stitchbird, not only are CPs greatly enlarged during the breeding season, but they also significantly alter their angular position. This 'erection' favours male-female cloacal contact during this species' unique face-to-face forced copulation. Evidence of CP angular changes in an unrelated species suggests this phenomenon is widespread and important for understanding copulation efficiency, sperm competition and constraints on the evolution of the avian intromittent organ.

Sperm competition intensity is positively associated with massive enlargements of sperm storage organs in avian cloacae during the breeding season (*1*). These cloacal protuberances (CPs) function in a similar manner as the mammalian epididymis and scrotum in that they store large numbers of spermatozoa under ideal conditions (*2*). The stitchbird or hihi (*Notiomystis cincta*) is an endangered endemic New Zealand passerine and is reported to have one of the largest cloacal protuberances (CP) of any bird species (*3*). Extra-pair copulations are common and this is reflected in the high numbers of extra-pair young found in nests (*4*). Stitchbirds are unique in that they may either copulate in the standard avian position (male standing on the female's back) or face-to-face (*3, 5*). Face-to-face copulation is always forced, with the male wrestling the female onto her back before mounting her to achieve cloacal contact (*3*) (Figure 1). It is currently thought that birds lacking intromittent organs should not be able to achieve cloacal contact and successful sperm transfer without female cooperation (*6, 7*). In stitchbirds, 80% of all extra-pair copulations are forced (*8*) and have been significantly correlated with extra-pair paternity (*9*).

Figure 1. In this rare photo of a forced face-to-face copulation, the male is lying on top of the female with his head to the right of the picture. The female is on her back under the male and her lower abdomen, tail and a banded leg can be seen (red arrow). This behavioural sequence occurs on the ground by necessity, is noisy and prolonged, and is a time when both birds are at a likely increased predation risk (*20*). Predation risk may explain why this effective means of forcible mating has only evolved once, in New Zealand where ground-predators were relatively rare during this species' evolution. Photo by ML.

Because male stitchbirds appear able to overcome female resistance without possessing an intromittent organ, we were interested in examining if the face-to-face position and CP functioned analogously to the intromittent organ of waterfowl (*10*), that have similarly high levels of forced copulation (*11*).

We measured a number of male and female cloacal parameters (CP length, width, height and angle) from a well-studied, banded stitchbird population (*8*). In males, these measurements were repeated four times within the year to provide CP parameters for the periods of just prior to breeding (September), during breeding (November), immediately post-breeding (February) and non-breeding (June). Female measurements were collected during the non-breeding season (June) as well as when the female was within a few days of laying her first egg (October – November). Cloacal protuberance volumes were calculated from these measurements and clearly demonstrate that the male stitchbird possesses one of the largest recorded breeding CPs whether calculated as total volume (*12*) (1193 ± 34 mm^3 (mean ± SE), $n = 27$, max. = 1570 mm^3) or a volume index of body weight (*13*) (40.0 ± 1.1 mm^3/g, $n = 27$, max. = 51.1 mm^3/g). Male breeding CP volumes were found to differ significantly from volumes calculated from measures collected at pre, post or non-breeding times ($F_{3,100} = 143.5$, $P < 0.0001$). The CP angle also differed significantly between breeding and all non-breeding season measures ($F_{3,86} = 98.3$, $P < 0.0001$) (Figure 2).

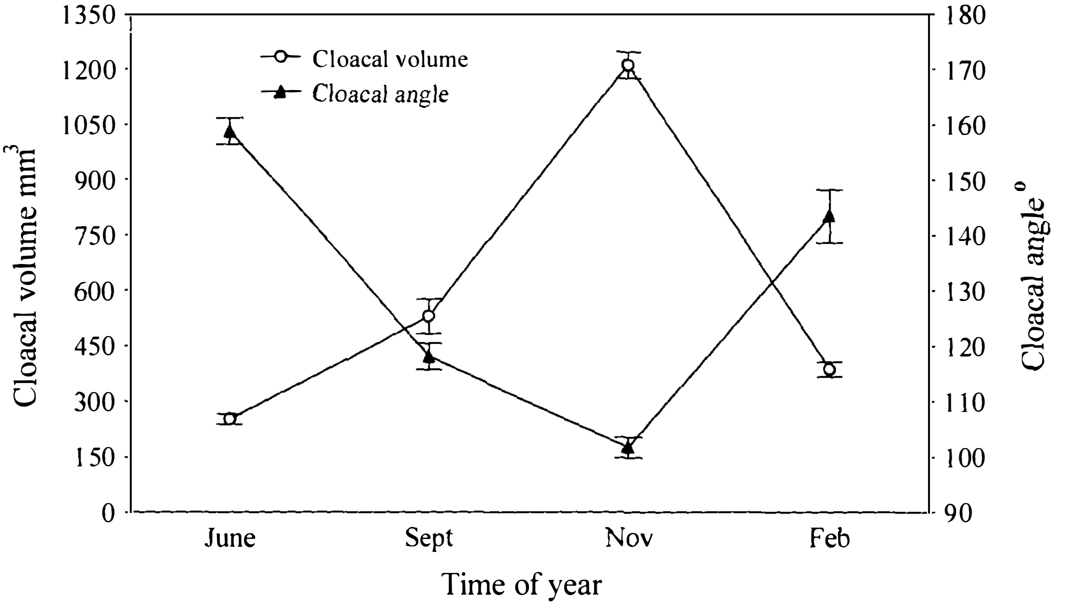

Figure 2 Relationship of male stitchbird cloacal volumes and angles (mean ± SE) during non-breeding (June, $n = 33$), pre-breeding (Sept, $n = 19$), breeding (Nov, $n = 27$) and post-breeding (Feb, $n = 25$).

The primary cause of the volume and angular changes in the CP was due to enlargement of the sperm-storing distal seminal glomera, just under the skin in the posterior CP (Figure 3). There was a strong highly significant negative correlation between the CP volume and CP angle (Pearson correlation $r = -0.8$, $t = 12.4$, $P < 0.0001$) (see Figure 2). Female breeding CP volumes (522 ± 38 mm^3, $n = 6$) were also significantly greater when compared to measures collected during non-breeding (176 ± 6 mm^3, $n = 46$; $t = 15.6$, $P < 0.0001$). This change appeared to be due to a uniform swelling of the tissues surrounding the cloacal opening, and therefore unlike males, mean female CP angles remained relatively constant throughout the year (non-breeding CP angle: 158 ± 2 degrees, CP angle prior to egg laying: 166 ± 1 degrees, $t = 1.5$, $P = 0.13$).

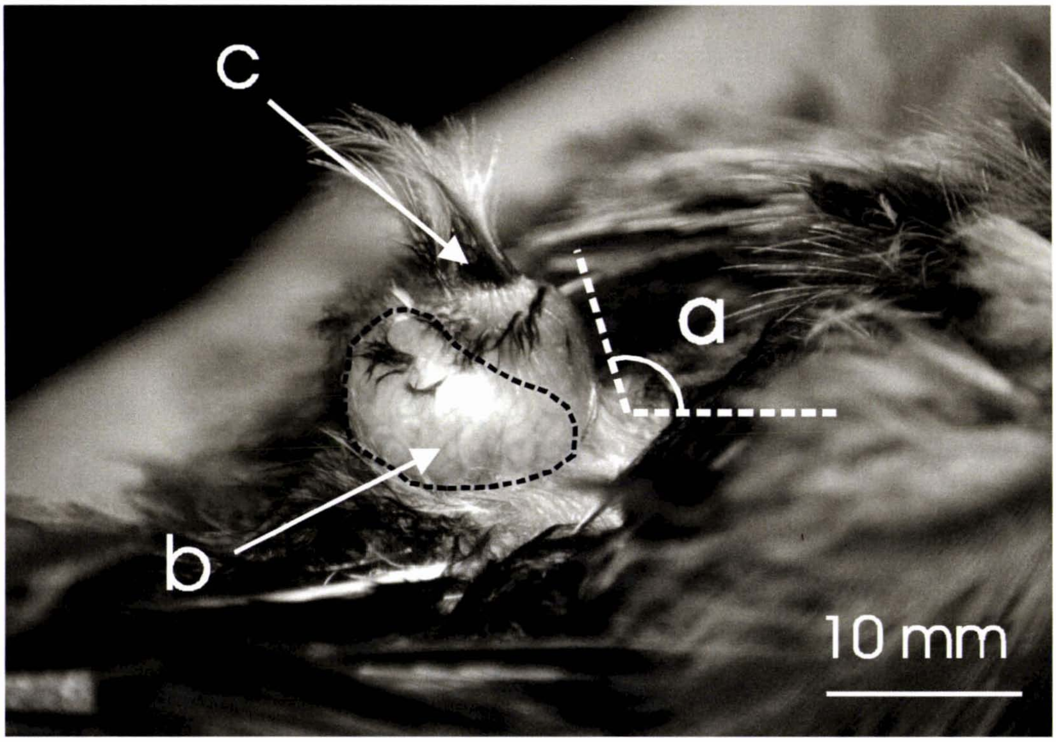

Figure 3 Lateral view of the breeding male stitchbird CP. The bird is on its back with its head to the right of the picture. **a.** The CP angle is calculated from the intersection of the line drawn parallel to the spine of the bird with the line drawn from the midpoint of the cloacal attachment to the body wall to the midpoint of the vent opening. **b.** The enlargement of the CP and the cause of its displacement is due to hypertrophy and sperm storage of the distal seminal glomera (outlined). **c.** The cloacal opening points almost perpendicular to the spine in the sexually active male. Photo by ML.

Three functional hypotheses have been proposed to explain the existence of CPs in birds (*1*). Empirical support has been presented for the 'sperm competition' and 'sperm size' hypotheses by showing a positive relationship with these factors and the size and storage capability of the avian CP (*1*). The 'efficient copulation' hypothesis has often been cited since being proposed over 50 years ago (*2*) but any correlation between the size of the avian CP and copulation efficiency (as defined by cloacal contact time) has not been demonstrated (*1, 12*). It has been suggested that massive CP sperm reserves act in one of two ways; either to allow multiple copulations or to increase ejaculate volume (or both) (*14*). Our findings suggest that in stitchbirds and probably other species, the large sperm stores act in a third way, by changing the angular position of the CP to improve copulation efficiency. To our knowledge, in no previous studies of CP size and variation have the positions of the male and female cloacal openings been measured relative to the breeding cycle. We believe that the changing angle of the cloaca is analogous to achieving a penile erection, and thus any investigation into the efficacy of the CP as a copulatory organ must take into account the CP's orientation.

Cloacal contact time is one factor positively related to successful insemination (*1, 15*). During face-to-face copulation the male stitchbird maintains cloacal contact for an average of 10 seconds (with a maximum of up to several minutes) (*3, 9*). This is in contrast to the much briefer cloacal 'kiss' seen during consensual stitchbird copulation. The face-to-face cloacal contact time is extremely long by avian standards (*15*) and would be almost impossible to achieve from a 'male-on-the-female's-back' position. We compared the relative CP position for the male and female when in a forced face-to-face copulatory position under two circumstances. The first was for a hypothetical male where the CP angle did not change in the breeding season from its non-breeding angular position (Figure 4a), and the second was for a male where the CP angle changed with engorgement of the seminal glomera, as was observed in this study (Figure 4b). From this can be seen the relative advantage a male with a more forward pointing CP has over a male where the CP enlarges but does not alter its angular position, when forcibly copulating with a female. This advantage is also expected to transfer to the standard 'male-on-the-female's-back' copulation, as the male should more easily be able to deliver sperm to the female's cloaca with a more forward pointing CP.

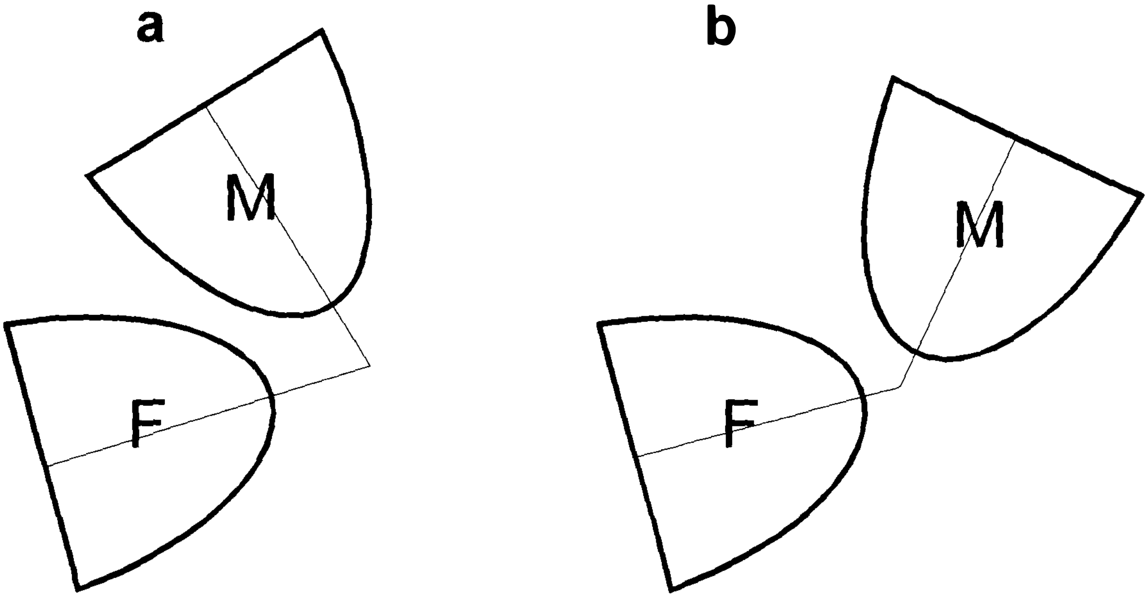

Figure 4 Diagrammatic representation of the relative position of male (M) and female (F) cloacae during a face-to-face sexual encounter. The angle of the female CP is fixed at the breeding angle of 166 degrees. For males, the two CP angles shown are, **a.** at the mean non-breeding angle (158 degrees) despite development of the breeding CP, and **b.** where the male's cloaca alters its angular position as the breeding CP develops (101 degrees). To account for the rotation of the male's body to achieve cloacal contact with the female, we measured the distance from the contact pivot point of the two birds (the lower breast carina) to the top of the CP, relative to a line drawn parallel to the bird's spine. From this information the amount of rotation necessary to bring the cloacal openings together could be calculated using basic trigonometry (37.5 degrees), and this was factored into the male CP angles in **a** and **b**. In the face-to-face copulatory position of the stitchbird, the change in CP angle from non-breeding to breeding alters the male's cloacal position relative to the female's by almost 60 degrees, leaving the male and female cloacae relatively well apposed at 130 degrees to each other (**b**).

In a number of bird species, females press their tails to the ground to prevent male cloacal contact during attempted forced copulation (*16*) or may struggle or eject sperm from the cloaca to minimise sperm uptake (*17, 18*). Only in waterfowl, where males possess an intromittent organ, is forced copulation widespread and relatively successful (*10, 11*). By forcing the female onto her back and pressing an 'erect' CP over the female's cloacal opening, male stitchbirds have developed a unique way of bypassing a number of female resistance mechanisms without possessing an intromittent organ. This is the behavioural equivalent of specific anatomical forced copulation adaptations found in other species, such as the genital claspers of the scorpionfly, *Panorpa* sp. (*19*). This potentially allows the male stitchbird to increase his likelihood of insemination by transferring a large amount of sperm to overcome sperm competition from the resident male and also prevents the female from immediately evacuating his semen from her cloaca. In many cases of stitchbird forced copulation there are a number of competing males also present (up to eight) (*3, 8, 9*) and this ability to prolong cloacal contact with the female prevents other males from immediately mounting, inseminating the female and diluting his ejaculate.

We believe that in the stitchbird, selection has been operating not only on the storage capacity of the seminal glomera, but also on the position of the seminal glomera relative to the cloacal opening. One result being that over evolutionary time as the sperm storage capacity of the CP increased, the ability of males to successfully maintain cloacal contact during extra-pair forced and unforced copulation improved, thus further driving the selection of increased sperm storage because of escalating sperm competition. While the stitchbird is unique in its method of forced copulation, selection should also act on the CP in other species with sperm competition to maximise copulation efficiency. We tested the prediction that CP angular changes will also be seen in species lacking face-to-face or forced mating by taking breeding (n = 16) and non-breeding (n = 14) cloacal measures of male bellbirds (*Anthornis melanura*). As was found with the stitchbird, bellbird CPs significantly increased in volume from non-breeding (49.4 ± 4.7 mm^3 (mean ± SE)) to breeding (204 ± 11 mm^3; $t = 11.6$, $P < 0.0001$), while cloacal angles at the same time, significantly decreased (non-breeding: 153 ± 4 degrees, breeding: 112 ± 2 degrees; $t = 9.2$, $P < 0.0001$). This suggests that a more forward pointing cloacal opening during the breeding season due to differential enlargement of the posterior CP through swelling of the seminal glomera may be a common phenomenon. If so, future assessments of the 'copulation efficiency' hypothesis of the avian CP will need to take into consideration different species' CP orientation, as a more forward pointing cloacal opening in males potentially improves the relative ease of achieving and maintaining cloacal contact in both standard and non-standard avian copulatory positions. This will also be important for the ongoing evaluation of hypotheses regarding the evolutionary "loss" of the avian intromittent organ (*20, 21*).

Methods

Field work was undertaken on Tiritiri Matangi Island (36°36'S, 174°53'E), 20 kilometres north east of Auckland, New Zealand. Male stitchbirds were captured using cage traps at supplementary feeding sites around the island in February (n = 25), September (n = 19) and November (n = 27) 2002 and June (n = 33) 2003. Female stitchbirds were caught using the same methods during non-breeding in June (n = 34) and during their fertile period when breeding in October and November (n = 6) 2003. Stitchbirds are sexually dimorphic and all birds on the island are colour banded thus identification of previously caught individuals prevented any bird from being measured more than once during a capture period. Bellbirds were caught in the same manner as stitchbirds in June and November 2003 to provide individuals for cloacal measurements. Upon capture, all birds were weighed to the nearest 0.5 g and examined to ensure that they were in good health. Birds were held on their backs during cloacal measurements with the feathers around the cloaca wet with alcohol to allow ideal visualisation of the CP. The CP length and width were measured perpendicular to each other using vernier callipers across the mid-point of the CP. The height was measured along the anterior border of the CP using callipers between the anterior cloacal attachment to the body wall and the anterior vent opening. The CP angle was measured by holding the bird in the palm of one hand and laying it on its back. A transparent protractor was superimposed over the bird and viewed from the side, with the angle taken as that between the line running from the cloaca towards the head (parallel to the spine) and a line drawn from the midpoint of the cloacal attachment to the body wall and the middle of the vent opening (Figure 3). Cloacal protuberance volume was calculated as $h\pi r^2$, where h is the CP height and r is 0.5 times the average of the CP length and width. Observations of sexual behaviours and forced copulation were made over three breeding seasons between September 2000 and February 2003 and more details of the study can be found in (*8*). Statistical analyses were carried out using Statistica (*22*).

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CHAPTER IV

Female weight predicts the timing of forced copulation attempts in stitchbirds

Female bringing nest capping material to the nest

Female WR/RM brings a beakful of moss to cover her first egg just after laying

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Chapter reference:

Low, M. In Press. Female weight predicts the timing of forced copulation attempts in the stitchbird. *Animal Behaviour*.

Abstract

Male birds can often accurately gauge the fertile status of females. As is found in other species, the stitchbird manifests this ability through increased mate guarding attentiveness and attempted extra-pair copulations centred on the female's peak fertile period. Males are thought to use various behavioural cues to assess female fertility including: 1) within pair copulation, 2) mate guarding intensity, 3) female solicitation, 4) female flight behaviour, 5) nest building, 6) egg-laying, and 7) paired male song intensity. By using a correlational approach, I examine which behavioural cues are intimately linked with the fertile status of the female stitchbird, as well as being able to account for patterns of extra-pair male behaviour. Increasing female weight appears to be the primary fertility indicator in this species and it is likely that males evaluate this through changes in her flight behaviour, however this requires experimental confirmation. Female stitchbirds increase their body weight by an average of 31 % (max. 43 %) in the three weeks prior to laying. Extra-pair male interest rises sharply as the female's weight increases from 31 g to a peak weight of approximately 41 g, two days before the first egg is laid. Because of potential costs associated with forced copulation, female stitchbirds may attempt to limit the availability of information regarding their fertile state by burying eggs within the lining of their nest.

INTRODUCTION

Male birds often adopt a mixture of behavioural tactics where they combine monogamous pairing while pursuing extra-pair copulations (EPCs) (Birkhead & Møller 1992). To maximise the reproductive outcomes from this strategy, males need to protect paternity at their own nest sites while ensuring that extra-pair fertilisations (EPFs) are a likely result from their own EPCs (Komdeur et al. 1999). In order to achieve this, males need to accurately estimate the fertile status of females. This ability is demonstrated in many species where the paired male increases mate guarding intensity as the female approaches her peak fertile state (Hatchwell & Davies 1992; Komdeur et al. 1999), while extra-pair males seek copulations with females at times of her peak fertility (Emlen & Wrege 1986; Pinxten & Eens 1997; Komdeur 2001). In most species it is unclear what cues males use to evaluate the female's fertile status, but seven have been suggested. These cues come either directly from the female's behaviour (flight, nest building, egg-laying, or female solicitation), or indirectly via the paired male's behaviour (within pair copulation, mate guarding intensity, or song rate or quality) (Birkhead et al. 1987; Komdeur et al. 1999; Tobias & Seddon 2002).

The stitchbird (or hihi: *Notiomystis cincta*) is a medium sized (28 – 43 g) endangered New Zealand passerine and is currently restricted in its distribution to only three islands off the coast of New Zealand. It displays significant sexual dimorphism in both size and plumage colour, with males being both larger and more colourful than females (Craig et al. 1982). Social monogamy is the most common pairing arrangement, although their mating system also includes polygyny, polyandry and polygynandry (Castro et al. 1996). Male stitchbirds engage in a reproductive strategy where they combine nest site defence with a female partner while seeking EPCs (Castro et al. 1996). The majority of these EPCs are forced (Ewen et al. 1999) and involve a unique face-to-face copulatory position that the female actively and aggressively avoids (Castro et al. 1996). Resident males increase their mate guarding attentiveness as females enter their fertile period, along with extra-pair male territorial intrusions and copulation attempts, demonstrating that males can predict when copulations are likely to result in fertilisations (Ewen 1998). Ewen (1998) concluded that because stitchbird males regularly enter each others' nest chambers, they are assessing the state of nest building and use the presence of a completed nest as the primary fertility cue. However, at the Mt Bruce National Wildlife

Centre in New Zealand, where a small captive population of stitchbirds is kept, staff monitor female weights rather than relying on nest building to determine when females are nearing egg-laying (R. Collen and B. Welch pers. com.). Using female weight to assess fertility is supported by the only experimental assessment of avian fertility cues undertaken. In the sand martin (*Riparia riparia*) it was shown that males judge female fertility by observing the impairment of flight performance of the female due to her increasing weight (Jones 1986).

The primary purpose of this study was to compare how 'direct' fertility cues were correlated with extra-pair male interest in the female in a population of free-living stitchbirds, and which of these cues predicted female fertility. The efficacy of cues as accurate fertility predictors in the stitchbird was assessed by comparing predictions of male behaviour if a particular cue was used, to observations of males both within and outside female territorial areas. Indirect cues associated with the paired male's behaviour are examined in light of the birds' general behaviours and the problem of them being confounded with direct cues. Female stitchbirds cover their eggs with nest lining material during laying, and the possibility that this limits information regarding the female's fertile state is also discussed.

METHODS

Study Population

The birds in this study comprise a closed population located on Tiritiri Matangi Island (36°36'S, 174°53'E). The 220 ha island is free from exotic predators and situated off the northeast coast of New Zealand's North Island. All birds are uniquely colour banded and thus provide an excellent opportunity for studying the birds' social behaviours, as the area containing breeding territories (30 ha) is small enough to enable the entire population to be monitored (32 females and 25 males in 2001 and 34 females and 41 males in 2002). Stitchbirds on Tiritiri Matangi Island breed during the spring and summer (September to February) and may lay up to three clutches of between two and six eggs (unpublished data, M Low), with a laying interval of approximately 25 hours (Castro et al.1996). Supplementary food in the form of a 20 % (by mass) sugar solution is fed from up to nine feeding stations which are provided year round and used by all birds on the island. These feeding stations are situated at the forest edge along walking paths and are not contained within birds' territories. Because the stitchbird is a cavity nesting species and the island is mostly comprised of young regenerating forest, wooden nest boxes are provided (86 in 2001, 110 in 2002). These are grouped in twos or threes throughout likely nesting areas and are situated approximately 1.5 metres off the ground with a hinged lid and allow easy monitoring of nesting. For over 200 nesting attempts on the island, the artificial nest boxes were used on all but one occasion. This study was conducted during two breeding seasons between September 2001 and December 2002.

Behavioural Observations

Stitchbird territories were located by following birds in all forested areas on the island during September, to coincide with male territorial calling and female nest site selection. Territorial boundaries for each pair were determined by watching both sexes' movement and their interactions with neighbouring birds. The boundary was defined as the line beyond which an extra-pair male could call or be visible to the resident male, without the resident male making an attempt to chase him away. These boundaries are generally stable outside of the resident female's fertile period and it was the area as defined during the pre-fertile period that was used to judge whether an extra-pair male was intruding during both fertile and non-fertile periods. Thirty-two territories were monitored for a continuous 30 to 60 minute period (mean ± SD, 39 ± 13 minutes), almost daily from the onset of nest site selection until chick hatching. Between day –28 and day +18 (where day '0' = first egg), 988 of these territory observations were undertaken (mean ± SD, 31 ± 8 observations per site; range 11 – 47). During observations the territorial pair was continuously followed (usually within 5 to 10 metres) with no evidence of any disturbance to the birds' behaviour. Most territories are roughly centred on the active nest box, and the observer returned to this point to re-establish contact if the birds were lost. The forest areas inhabited by stitchbirds on the island generally support a limited understorey, and allow observation of much of the bird's territory from most locations. All observations were recorded onto a voice-activated recorder via a lapel microphone, to allow uninterrupted observations.

The general behaviour of the resident pair was recorded, with an emphasis on behaviours relevant to differentiating fertility cue hypotheses. All copulations and female copulation solicitations (Higgins et al. 2001) were described, the identity of the birds involved noted and their timing relative to the date of first egg laying recorded. Territorial calling frequencies of the resident male during his female's fertile period were compared for periods when no extra-pair males were calling on or within his territorial boundary and periods when one or more were present. Also compared was the likelihood of the resident male calling in a 30 second period immediately before and after an extra-pair male called on or within the territorial boundary, after an intruder absence of greater than 5 minutes. This was to allow a measurement of the effect of calling by an extra-pair male on the resident male, after any previous effect of extra-pair male calling was assumed to have disappeared.

To measure when extra-pair males engaged in territorial intrusions relative to the fertile period of the resident female, all birds other than the residents entering the territory had their identity and the time of entry and exit recorded. Extra-pair birds were located by call or by sighting, with them only recorded as being present when their location was known. If more than one intruder was present, then the times of each male were summed giving total male intruder times of more than 60 minutes per observation hour in some territories. To establish whether extra-pair males could judge the fertile status of females without any immediate territory cues being present, 29 additional observations were carried out at an actively used communal site, the main supplementary feeding station. Each of these observations lasted for 60 minutes and the identity of each bird visiting the feeder was recorded. The identity of any birds involved in a forced copulation chase was noted, along with details of the event; including if the chases resulted in successful forced copulation. A forced copulation chase is defined as an event where the female begins to emit a specific high-pitched alarm call and attempts to flee one or more pursuing males. This may end with the female escaping by flying away or hiding under leaf litter, or the female being caught, brought to the ground and being subjected to a forced copulation (Castro et al. 1996).

Weight Measurements

To assess the correlation between female weight and egg laying, all breeding females ($N = 34$) were weighed at a mobile supplementary feeding station on a set of electronic scales (Weighing Systems Ltd.) to an accuracy of ± 0.5 grams at least twice weekly for the three months during the laying of first clutches in 2002. The system was designed so that for birds to drink from the feeder, they needed to stand on a perch linked to the weighing mechanism. An electronic readout of the bird's weight was displayed allowing the identity and weight of each bird to be recorded by the observer. Because the weight of the bird could increase by up to 2 g while drinking the artificial nectar, only the initial weight was recorded. Birds were weighed in the morning between 800 and 1100 hours to minimise the effect of diurnal weight fluctuations (Armstrong & Ewen 2001). Weighing frequency was increased to daily measurements when females became more than 2 g heavier than their recorded basal weights, with daily weighing continuing until incubation. Birds were measured either at a communal feeding station or within their own territories. From these measurements a mean female weight relative to the day of first egg lay was generated for further analyses. On days when females were laying eggs, the female weight was recorded after the egg was laid. Only one weight per bird was recorded on any given day and weights were only collected during first clutch attempts.

Nest Data Collection

All nest boxes were monitored every third day until the beginning of nest building. To determine any correlation between the timing of nest completion and the female's fertile period, boxes were then monitored daily to record the date of nest completion and first egg laying. Nests were defined as complete when soft lining (moss, feathers or tree fern scales) had been incorporated into the entire surface of the nest cup. The presence of eggs in the nest was determined by gently placing a finger into the nest cup and sifting through the soft lining. This was necessary as female stitchbirds usually cover their eggs with additional nest lining material. This covering on the eggs (nest cap) is a collection of moss or tree fern scale up to 2 cm deep that is added to the nest by the female soon after she has laid an egg. I recorded the nest as 'capped' after each egg if there was enough new lining added to prevent the eggs being visible from above. Nests were disturbed only when the location of the female was known and she was not inside the nest box.

Analyses

Nesting attempts were highly asynchronous and thus all dates associated with collected data were converted to a number relative to the date of first egg lay for that female (= day 0) to allow comparisons between females. Females were deemed to be fertile from six days prior to first egg lay until the penultimate egg was laid (Komdeur et al. 1999). This was supported by the observation that within pair copulations were never observed before day –6. The majority of the data were not normally distributed and thus non-parametric statistics were used for most analyses. A Spearman rank correlation was used to examine the relationship between mean female weight and mean extra-pair male territorial intrusion rates from day -28 to +18. For nest completion as a cue, a Kolmogorov-Smirnov one-sample test was used to compare the observed cumulative distribution of nest completion over the four weeks prior to egg lay with two predicted distributions. One distribution assumed that nest completion had no relationship to egg-laying during that period and thus nest completion was equally likely on any day, with the cumulative distribution constantly increasing by 1.14 nests per day from day -28 to day -1. The second distribution compared observations against a predicted pattern where nest completion was clumped just prior to the female's fertile period and would allow males to accurately predict egg laying from nest completion. The percentage of times a female was chased at the communal site during her fertile and non-fertile periods was calculated by dividing the number of days a female was chased by the number of days she was seen for both of those periods and was analysed using a paired Sign test. Calling data obtained for resident males that produced matched pair data for times when intruders were present and absent for each territory, were compared using Wilcoxon matched pairs test. Calculations were carried out in Statistica (StatSoft Inc.1997). Not all sites could be surveyed nor all birds measured in all sampling periods, resulting in uneven numbers in some statistical tests. Means are expressed with standard errors, probability values are two-tailed and statistical significance recognised at $P < 0.05$ unless otherwise stated.

Ethical Note

A minimum distance of 5 metres was kept between birds and observers during observations to minimise any disturbance. Nest boxes were inspected according to Department of Conservation guidelines and no females abandoned their nests during this study. All work undertaken in this study was carried out under a research permit from the New Zealand Department of Conservation and had Massey University animal ethics approval (protocol number 00/80).

RESULTS

Extra-pair Male Intrusions, Chases and Copulations

At territory sites

Intruder male activity within territories increased steadily from day -6, peaking on day 0 at 19.92 ± 5.62 minutes/ territory/ hour (range 0 – 380) and then rapidly declined to zero by day 5 (Figs. 1, 2). The sum of territorial intrusion time by extra-pair males was significantly greater during the female's fertile period (9.05 ± 2.09 minutes/ territory/ hour) when compared to outside of this time (0.35 ± 0.07 minutes/ territory/ hour) (Wilcoxon paired-sample test: $Z = 4.70$, $N = 32$, $P < 0.001$). This was due to a combination of more extra-pair males visiting the site (fertile versus non-fertile, 0.97 ± 0.15 versus 0.06 ± 0.01 extra-pair males/ territory/ hour: $Z = 4.68$, $N = 32$, $P < 0.001$), each male intruding a greater number of times per hour and remaining within the territory for longer periods during the female's fertile period. As extra-pair male activity significantly increased at a site, the ability of the resident male to exclude intruders sometimes diminished to the point where extra-pair males could remain in the territory within a few metres of the female for the entire observation period. In these extreme situations, between 5 and 10 extra-pair males would be recorded per hour, with a group of males following the female every time she moved. In these cases the resident male was forced to sit above or next to the female and physically prevent any of these males gaining access to the female (Chapter 5). All observed extra-pair male copulations with the resident female ($N = 22$) occurred between day -6 and day 7, with all but two during the female's fertile period (Fig. 3). Of all successful EPCs, 78% were vigorously resisted face-to-face forced copulations. At five sites where no male was in residence, intruder male activity was no different during the females' fertile periods when compared to sites where a resident male was present (10.41 ± 3.97 minutes/ territory/ hour) (Mann-Whitney U test: $U = 66$, $N_1 = 30$, $N_2 = 5$, $P = 0.53$). At these sites, a male from another territory would often attempt to mate guard the female, however this was sporadic and did not begin until after significant intruder male activity was noted for that site (approximately day -3). These males were never observed returning to that territory during chick feeding. On 15 occasions a non-resident non-fertile female was observed passing through a fertile female's territory where at least one male intruder was in close proximity. On none of these occasions was the non-fertile female pursued by any of the extra-pair males.

At communal sites

The identity of the chased female was recorded during 108 extra-pair male forced copulation chases during observations at communal feeding sites. While at these sites, it was clear that the likelihood of an individual female being subjected to a forced copulation chase during any 60 minute observation was significantly higher during her fertile period (39 ± 5 %) than during her non-fertile period (3 ± 0.8 %; Paired sign test: $Z = 4.51$, $N = 26$, $P < 0.001$) (Fig. 3), while her rate of visitation remained similar. Of the 26 females sighted during both periods, only 12 individuals were chased when non-fertile compared to 25 being chased when fertile. Of the 108 chases, only 17 were directed at non-fertile females, with 3 occurring during the pre-fertile period (11.6 ± 1.76 days prior to first egg laid) and 14 occurring in the post-fertile period (9.9 ± 1.5 days after first egg laid). Assuming that 'mistakes' in identifying females as fertile should occur equally in both the pre and post-fertile periods, the distribution should reflect this. The fact that the majority of these non-fertile attempts show a clear trend towards the post-fertile period (Fisher exact test: 82 % versus 50 %, $N = 17$, $P = 0.071$), suggests that an aspect of the fertility cue may persist in some individuals after the final egg has been laid.

Female Weight as a Fertility Cue

I recorded 1396 weights from 34 females during an 11-week period in 2002 when females were attempting first clutches (Fig. 1). Female weight appeared to be an excellent predictor of when females would begin to lay eggs, as they gained 31 ± 1.3 % of their body weight (range 15 – 43 %) in the 20 days prior to egg laying. Females reached their peak weight at day -2 (41.24 ± 0.45 g), corresponding to the day prior to ovulation of the first egg and thus their estimated peak fertile period. Mean female weight was strongly correlated to mean male territorial intrusion times between day -28 and +18 (Spearman rank correlation: $r_s = 0.59$, $N = 47$, $P < 0.001$). It appeared that there was an average threshold weight of approximately 36 g, below which males generally ignored females and above which extra-pair male activity increased relative to the female's increasing weight (Fig. 1). Extra-pair male activity appeared to lag approximately 48 hours behind the weight cues of the female with male activity peaking at day 0.

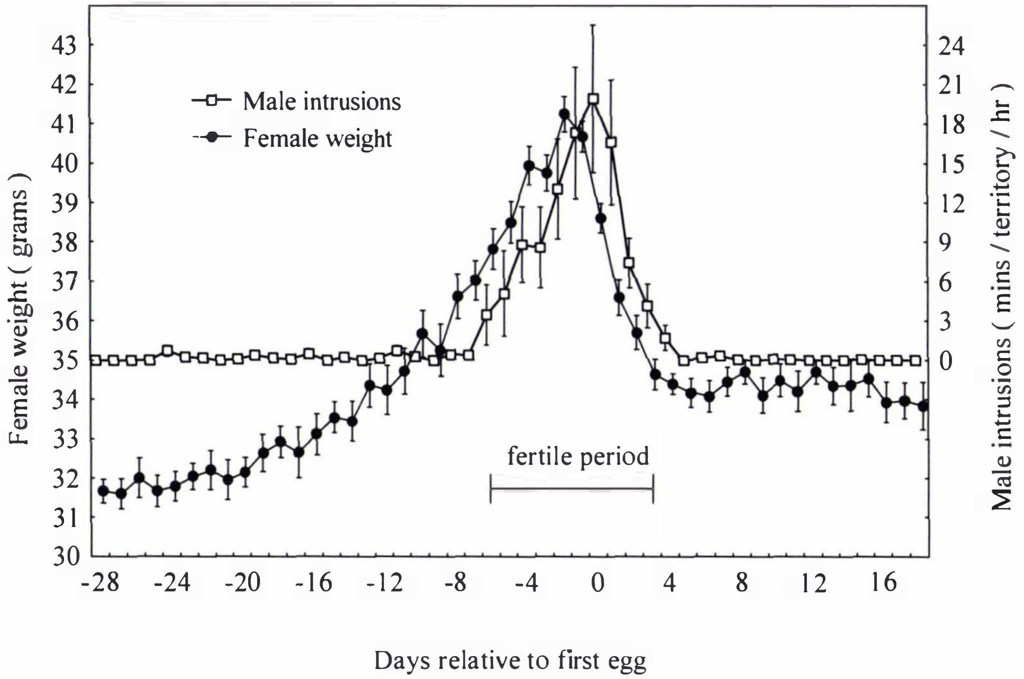

Fig. 1. Temporal pattern of female weight -●- (mean ± SE grams) and extra-pair male intrusions -○- (mean ± SE minutes/territory/hr) relative to the date of first egg lay (= day 0). Not all territories were observed or females weighed on each day and the number (*N*) sampled for each generated mean value ranges from 23 – 31 for male intrusions and 20 – 32 for female weight.

Nest Completion as a Fertility Cue

There was a poor relationship between the date of nest completion and the presence of male intruders in the territory (Fig. 2). Nests were completed between four weeks and one day before the first egg was laid (12.2 ± 1.36 days, $N = 32$). Observed nest completion from day –28 to day –1, did not significantly deviate from a theoretical cumulative distribution where each nest had an equal likelihood of completion on any day (1.14 completed nests per day) during this time period (Kolmogorov-Smirnov one-sample test: $D_{\max} = 0.22$, $N = 32$, $P = 0.10$). This result is supported by the significant deviation of observed nest completion from a theoretical cumulative distribution where nest completion was clustered over a six day period beginning between day –11 and –6 as expected if males used nest completion to accurately predict the onset of the fertile period

($D_{max} > 0.5$, $N = 32$, $P < 0.001$). It should also be noted that for the two nests completed on day –1, extra-pair male activity had been increasing steadily since day –5. For the nine nests completed between two and four weeks before first egg, the earliest significant intruder activity was recorded on day –6.

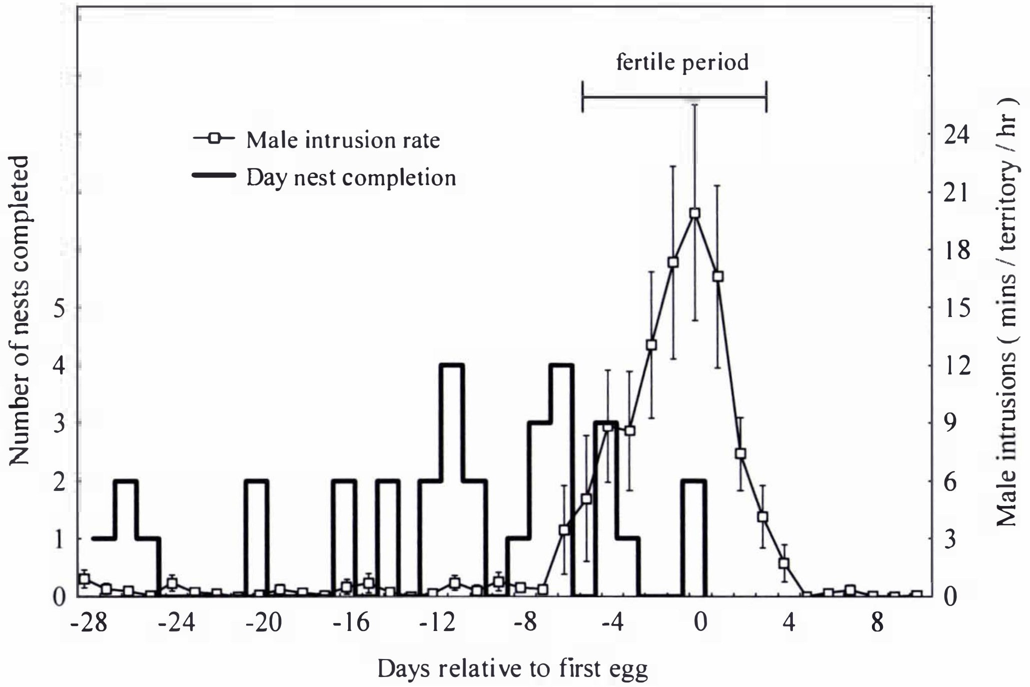

Fig. 2. Temporal pattern of nest completion ($N = 32$) and extra-pair male intrusions -o- (mean ± SE minutes/territory/hr) relative to the date of first egg lay (= day 0). Each step plot represents the number of nests completed on that day. Not all territories were observed every day and the number (N) sampled for each generated mean value for male intrusions ranges from 23 - 31 territories.

Female Solicitation as a Fertility Cue

Female copulation solicitation behaviour was recorded as early as 22 days prior to the first egg being laid. This behaviour was not frequently observed and was highly variable, with 40% of females never seen engaging in the behaviour. Females were significantly more likely to behaviourally solicit to their male partner during the 9 days of their fertile period (0.35 ± 0.09 solicitations per hour) than the 9 days prior to this time (0.18 ± 0.07 solicitations per hour) (Wilcoxon paired-sample test: $Z = 2.11$, $N = 20$, $P = 0.034$).

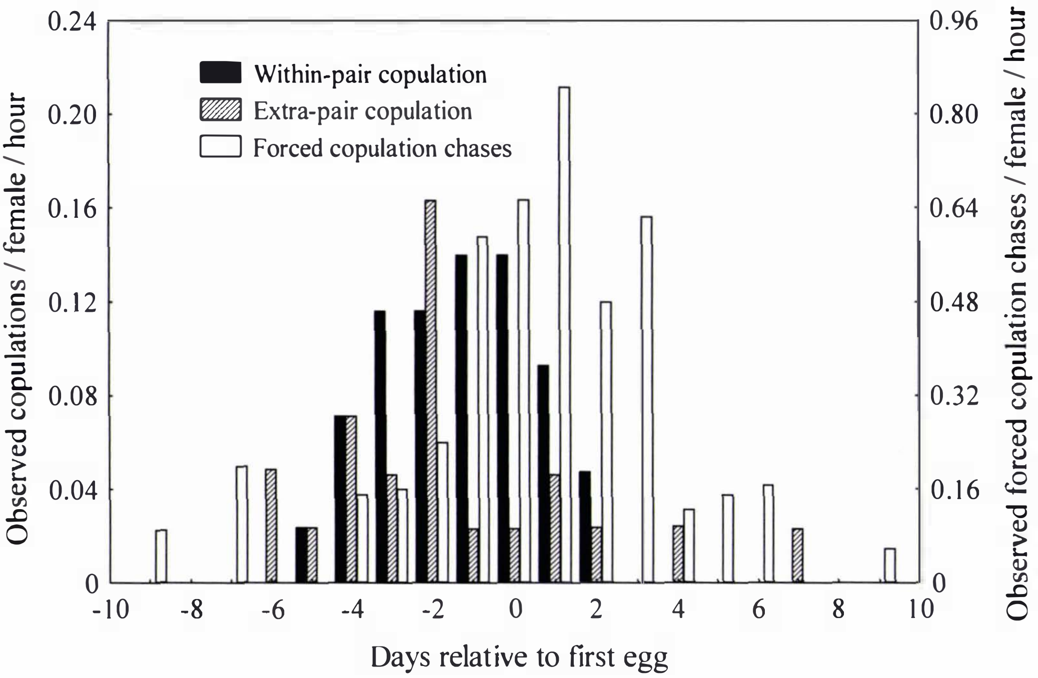

Fig. 3. Incidence of extra-pair copulation (shaded bars), within-pair copulation (black bars) and forced copulation chases of females at communal sites (white bars) per female, per hour of observation time relative to the date of first egg lay (= day 0).

Female Nest Capping Behaviour

The nest capping behaviour of 28 females was monitored relative to their egg laying cycle with clutch sizes ranging from two to five eggs (mean 4.07 ± 0.06). All females capped their first egg, and in 12 out of 28 nests, females capped their eggs up until the final egg was laid (final eggs were never capped due to the onset of incubation). Fifteen females did not cap the penultimate egg and one female with a clutch of 5, only capped the first 2 eggs. In 6 of the 16 cases where the female failed to cap the final 2 eggs, this was due to incubation beginning on the penultimate egg. Females were observed to cap the nest soon after laying the egg. Once emerging from the box, the female made up to six trips collecting a beak full of capping material, before leaving the nest alone. Fresh capping material was collected each day with the previous day's capping material being pushed under the eggs and incorporated into the nest lining.

Indirect Fertility Cues

Resident male calling rates are affected by the presence of calling extra-pair males. Resident males called significantly more frequently during the fertile period of their female when extra-pair males were calling on their boundaries (2.97 ± 0.30 calls per minute) than when the intruders were absent (0.62 ± 0.14 calls per minute) (Paired t-test: $t_{14} = 7.47$, $P < 0.001$). There was also a significant increase in the resident male's likelihood of calling immediately after, rather than before an extra-pair male called on the territorial boundary (17% versus 94%, Paired sign test: $Z = 3.32$, $N = 17$, $P < 0.001$). Resident males were absent in five of the territories prior to extra-pair male activity increasing and thus resident male calling rates could not explain the behaviour of extra-pair males at those sites during the female's fertile period.

During 434 hours of territory observations falling within the female's fertile period, 32 within pair copulations were observed (Fig. 3). Because I was able to closely follow the birds during observations, the majority of copulations were likely to have been observed. This observed within-pair copulation frequency of once every 13.5 hours during the female's fertile period is so low as to be almost invisible to passing extra-pair males who do not spend any significant time in territories other than their own (0.35 ± 0.07 mins/ territory/ hr), until they detect an extra-pair female is fertile.

DISCUSSION

Fertility Cues

Two classes of fertility cues need to be differentiated in discussions of male assessment of female fertility. Direct cues such as female flight, nest building, egg-laying, or female solicitation are potentially available to all males in a population and thus a single cue can be used to explain the behavioural patterns of all males. Indirect cues, where extra-pair males rely on detecting an aspect of the paired male's behaviour (mate guarding, male song and copulation patterns), raise questions regarding the motivation of the paired male (Møller 1991), and are confounded by the possibility that extra-pair males are simply using the same 'direct' cue the paired male is using. This is evident in the stitchbird where even though indirect cues such as resident male calling rates are correlated with female fertility (Castro et al. 1996), extra-pair male activity is similar regardless of a resident male's presence. Resident males may call more frequently during the female's fertile period, but as was found in this study, the calling rate is confounded by the presence of extra-pair males and thus the direction of any cause and effect relationship is currently impossible to determine.

Of the direct cues evaluated in this study, only female body weight accurately predicted the timing of egg laying and was strongly correlated with extra-pair male intrusions in each female's territory (Fig. 1). Males may gather information on female weight either by observing that the female looks 'fat' or by detecting the increase in body mass through its effect on the female's flight behaviour. Female birds undergo dramatic weight fluctuations during the breeding season, associated with the production and laying of eggs (Moreno 1989; and see above). Weight increases and physiological changes associated with egg production have both been shown to have a significant effect on female flight behaviour, manifesting as a trade-off between vertical flight speed (Kullberg et al. 2002) and take-off angle (Lee et al. 1996). This is due to increasing body mass resulting in an increasing wing load for the bird (Kullberg et al. 2002) with a corresponding reduction in flight muscle mass and performance, as proteins are mobilised from the pectoral muscles for incorporation into the egg (Houston et al. 1995; Veasey et al. 2001). Female flight impairment may continue into incubation due to the longer-term effects associated with the loss of pectoral muscle mass (Veasey et al. 2001). These significant changes in female flight performance around the time of egg laying could provide a cue that males use to assess the female's fertile status (Jones 1986).

In sand martins (*Riparia riparia*), a species that appears to have a male mating strategy similar to the stitchbird, females that had their weight artificially increased by an intraperitoneal injection of saline took longer to reach ascending flight and were disproportionately chased by extra-pair males (Jones 1986). These effects were detected with a 20 % increase in body weight. In the starling (*Sturnus vulgaris*), females reduced their escape take-off angle by 30 % when encumbered with a 7 % increase in body weight prior to egg lay (Lee et al. 1996). In blue tits (*Parus caeruleus*), when females were 14 % heavier due to carrying eggs, they flew 20 % slower (Kullberg et al. 2002). If these figures are compared to the average body weight increase of 31 % (max. 43 %) in the female stitchbird, it is likely that in this species, flight performance is more greatly affected and thus more obvious to a male stitchbird.

The possibility of egg production affecting flight performance well into incubation (Veasey et al. 2001), may explain the higher likelihood of non-fertile females being subjected to forced copulation attempts by extra-pair males in the post-fertile period when compared to the pre-fertile period. The use of female weight as a fertility cue may also explain the observations reported in Ewen and Armstrong (2002) where extra-pair males subjected three newly fledged stitchbird juveniles to forced copulation. Juvenile stitchbirds have a female plumage until their first moult and fledge at a weight almost identical to that of a female about to lay her first egg (fledging weight: 41 ± 0.6 grams, unpublished data, M Low). In all three instances, the resident female was in the process of renesting, and it is not surprising that under these circumstances males would attempt to copulate with a female-looking bird with impaired flight ability.

Alternative direct fertility cue hypotheses cannot account for the pattern of extra-pair male activity seen in the stitchbird. The presence of an egg in the nest occurs after the majority of extra-pair male intrusions and copulations have taken place (Figs. 1, 3). The observation that extra-pair males visit other nest chambers and may observe a nest either completed or under construction (Ewen 1998; pers. obs.) would only provide the limited information that a particular female will lay eggs at some point in the next month. The fact that the pattern of nest completion in the four weeks prior to egg laying fails to deviate significantly from a distribution where nests are just as likely to be completed on any day during that time, means that this cue cannot account for the male's ability to know when a female is entering her fertile state and time his attentions to coincide precisely with her peak fertile period.

Female behaviour specific to her fertile period such as copulation solicitation, begging calls and other vocalisations have all been suggested as fertility cues (Komdeur et al. 1999; Tobias & Seddon 2002). During their fertile period, female stitchbirds neither beg nor make specific vocalisations and generally remain silent (pers.obs.). Female stitchbirds sometimes solicit copulations, however this behaviour is observed well before any extra-pair male interest in the female occurs. While these solicitations increase significantly from once per 5.5 hours in the pre-fertile period to once per three hours in the fertile period, because of their low frequency and lack of specificity, they are unlikely to be useful for accurately predicting female fertility. It should also be noted that while females 'solicit copulations' from their partners during the pre-fertile period, no copulations were ever observed at this time, suggesting that resident males are using another cue to assess their female's fertile status.

With the exception of female weight, none of the cues can explain the immediate reaction of males at communal feeding sites to the arrival of a fertile female nor the ability of non-fertile females to pass through a fertile female's territory without harassment. Thus it appears the fertility cue is intrinsic to the female and can be assessed by males in a matter of seconds. However, this does not discount the possibility that extra-pair males use other less accurate 'rules of thumb' to help them decide which sites are likely candidates for further investigation. While the relationship between female weight, female fertility and extra-pair male behaviour in this study is very tight and highly suggestive, only an experimental approach similar to Jones (1986) can properly elucidate the 'cue' used by males to judge female fertility. One cue has been neglected in previous discussions of male assessment of female fertility, and that is the possibility of males gaining information via an olfactory signal. Unfortunately this form of signalling in birds is still largely unexplored and thus it is difficult to gauge the extent to which it might be used by stitchbirds (Hagelin et al. 2003).

Do Females 'Hide' Their Fertility?

Forced EPCs in the stitchbird are aggressive with the female actively resisting the encounter and sometimes being injured in the process (Castro et al. 1996). The possibility that forced EPCs are costly to females in this species suggests that females may attempt to limit broadcasting information about the state of their fertility to extra-pair males. Female stitchbirds generally cover the first two eggs of a clutch under a cap of additional nest lining material. This is unlikely to be a conventional form of egg crypsis because stitchbirds are a cavity nesting species and build their nest on a high platform of sticks, preventing natural predators from reaching the nest cup (Angehr 1985; unpublished data, M Low). One clue as to why female stitchbirds bury their eggs comes from the dunnock (*Prunella modularis*), where males use the arrival of the first egg to fine-tune their assessment of the likelihood of a particular copulation resulting in fertilisation (Hatchwell & Davies 1992). Male stitchbirds regularly investigate nest boxes in other birds' territories and if they fail to observe the resident female, they could potentially gain fertility information by observing an egg in the nest. If so, then egg burying may represent a best-of-a-bad-job tactic designed to limit information to extra-pair males regarding the stage of the female's fertile cycle.

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CHAPTER V

Behavioural tactics and energetic costs of mate guarding in a species with high levels of forced extra-pair copulation

Resident male displaying to extra-pair males during mate guarding

Male stitchbird M/RR showing erect tail and ear-tuft feathers and wing abduction display while defending his female from a group of five extra-pair male intruders

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Chapter reference: This chapter had been split for publication into:
Low, M. Mate guarding tactics in the stitchbird: the impact of intrusion pressure, female location and stage of fertility. Submitted to *New Zealand Journal of Ecology*
Low, M. The energetic cost of mate guarding in stitchbirds is correlated with territorial intrusions. Submitted to *Behavioral Ecology*.

Abstract

Males are predicted to maximise their reproductive success by pursuing extra-pair copulations (EPCs) while engaging in anti-cuckoldry behaviour such as mate guarding. In the stitchbird, males combine nest site defence with high levels of territorial intrusions and forced EPCs; leading to high levels of extra-pair offspring. In this study I demonstrate that stitchbird males exhibit intense mate guarding behaviour centred on the day the female lays her first egg. Territory defence switched from being site-specific during the pre-fertile period to centring on the female's location during her fertile period. In order to quantify the costs associated with this level of mate guarding, resident male weights were measured on a daily basis throughout the study. This showed that males lose 2.5% of their body weight when engaging in territorial defence and general mate guarding behaviours and this cost is compounded by a further 5% loss of body weight if extra-pair male intrusions occur during the female's fertile period at a rate greater than 5 minutes per hour. While the costs of harassment associated with forced extra-pair copulation have previously focused on females, this study is the first to show that harassment costs can also be significant for the resident male.

INTRODUCTION

In order to maximise lifetime reproductive success, males of many bird species adopt a strategy incorporating a mixture of behavioural tactics where they combine monogamous pairing while attempting extra-pair copulations (Birkhead & Møller 1992; Ligon 1999). Offspring from extra-pair fertilisations are common, and may make up as much as 76% of young (Mulder et al. 1994; Ligon 1999). To maximise reproductive output, males should attempt to increase their own extra-pair copulations while minimising the chance of being cuckolded. In birds, mate guarding is one of the most commonly observed forms of paternity defence (Birkhead and Møller 1992; Komdeur et al. 1999). Typically it is described as a male closely following his female partner during her fertile period and may involve a vigorous reaction to extra-pair male territorial intruders (Arvidsson 1992; Komdeur et al. 1999).

The intensity of mate guarding has been negatively correlated with the risk of extra-pair copulations at the defended site (Komdeur et al. 1999; Chuang-Dobbs et al. 2001; Pilastro *et al.* 2002), supporting the idea of it acting as an anti-cuckoldry behaviour. Costs or trade-offs associated with mate guarding have recently been demonstrated and include a reduction in courtship feeding and copulation (Mougeot et al. 2002), reduced male foraging and body weight (Westneat 1994; Komdeur 2001), reduced pursuit of extra-pair copulations (Chuang-Dobbs et al. 2001) and a reduced attraction of secondary females (Pinxten & Eens 1997). Mate guarding intensity is predicted to be high in species where a significant paternity risk exists, when the timing of this risk is short and predictable, and if the potential costs of cuckoldry are high, due to a large male investment in paternal care (Komdeur 2001 and references therein).

The stitchbird (or hihi: *Notiomystis cincta*) is a medium sized (28 – 43 g) endangered passerine and currently restricted in its distribution to three islands off the coast of New Zealand. Stitchbirds are sexually dimorphic in size and plumage colour, with males being both larger and more colourful than females (Craig et al. 1982). Social monogamy is the most common pairing arrangement, but their mating system also includes polygyny, polyandry and polygynandry (Castro et al. 1996). Male stitchbirds defend the nest site with a female partner, and also seek extra-pair copulations (Castro et al. 1996; Ewen et al. in press). The majority of these extra-pair copulations are forced (Ewen et al. 1999; see Chapter 1) and involve a unique face-to-face copulatory position

(Anderson 1993; Castro et al. 1996). Extra-pair male intrusions and copulation attempts have been shown to increase during the female's fertile period, demonstrating that males can predict when females are likely to be fertile (Castro 1995; Ewen et al. in press; Low in press). Testicular and cloacal protuberance sizes are significantly larger than predicted for a bird of its size (Castro et al. 1996) indicating that sperm competition is likely to be significant in this species (Møller 1991; Briskie 1993). The percentage of extra-pair offspring in the population is high (35%), and can be found in the majority (80%) of nests (Ewen et al. 1999). Male stitchbirds do not courtship feed or incubate, but they do contribute to chick feeding, albeit at a lower rate than females (Castro et al. 1996; Ewen & Armstrong 2000).

The combination of high paternity risk, predictable fertile periods and male investment in offspring predicts that stitchbird males should engage in intensive mate guarding as a form of paternity assurance (Komdeur 2001). Castro et al. (1996) report that while a proportion of stitchbird males were observed mate guarding, many did not appear to spend much time with any one female during the pre-laying and laying period. These observations are not quantified, and it is difficult to accurately assess the degree of mate guarding in that population. Ewen et al. (in press) concluded that mate guarding by male stitchbirds is restricted to nest site defence rather than guarding the female directly. However, the timing of that study was during the period immediately after the species was translocated to the study site when an extreme male bias existed in the population due to high post-release female mortality (Ewen 1998). At this time, females were difficult to locate and thus males may have been adopting a best-of-a-bad-job mate guarding tactic. To better establish how mate guarding is expressed in the stitchbird, my study aimed to quantify the form and extent of mate guarding and assess the effect of extra-pair male intrusions on the expression of the resident male's behaviour. This was measured by observing the average distance between the male and female, the reaction of males to separation from the female and the area actively defended by the male during the pre-fertile, fertile and post-fertile periods. Extra-pair male intrusions are known to increase during the female's fertile period and the male responds vigorously to their presence (Castro et al. 1996; Ewen et al. in press). Thus the secondary aim of this study was to quantify the energetic costs of mate guarding as expressed by weight changes in the resident male and determine if costs (weight reduction) increased as a result of increasing extra-pair male intrusions.

METHODS

Study Population

The birds in this study were observed in 2001 and 2002 and comprise a closed population on Tiritiri Matangi Island (36°36’S, 174°53’E), located off the northeast coast of New Zealand’s North Island. The island is approximately 220 ha in area, but stitchbirds are restricted in their distribution to the remnant forest patches comprising approximately 30 ha. All birds on the island are uniquely colour banded with their ages and social parentage known. Stitchbirds on Tiritiri Matangi Island breed during the spring and summer (September to February) and may lay up to three clutches of between 2 and 6 eggs (4.05 ● 0.06, $N = 32$), with a laying interval of approximately 25 hours (Castro et al. 1996). Stitchbirds were translocated to the island in 1995 as part of the ongoing management of the species by the New Zealand Department of Conservation. The population is small (approximately 32 pairs) allowing all breeding attempts to be monitored. During 2001 and 2002 the sex ratio remained relatively constant at approximately 1:1. Supplementary food in the form of a 20 % (by mass) sugar solution was fed from up to nine feeding stations which were provided year round and used by all birds on the island. Because the stitchbird is a cavity nesting species and the island is mostly comprised of young regenerating forest, artificial nest boxes are provided. These are situated approximately 1.5 metres off the ground with a hinged lid and allow easy monitoring of nesting.

The female’s fertile period is estimated to begin six days prior to laying of the first egg and finish the day the penultimate egg is laid (Low in press). This range is estimated from the observation that within-pair and extra-pair copulations begin six days prior to the laying of the first egg, and is consistent with observations from other stitchbird populations (Castro et al. 1996). This period is also known to correspond to the maximum extra-pair male intruder activity in the territory, with this increasing steadily from day –6, peaking on day 0 at approximately 20 minutes/ territory/ hour (range 0 – 380) and then rapidly declining to zero by day 5 (Low in press).

Mate Guarding and General Observations

Stitchbird territories were located and pairs identified by following birds in all forested areas on the island during September, when male territorial calling and female nest site selection began. An attempt was made to observe each territory for a continuous 30 to 60 minute period (mean ± SD, 39 ± 13 minutes) each day from the onset of nest site selection until chick hatching. Although copulation rates remain relatively static from 0700 – 1300 hours [Chapter 1], observation times were randomly distributed with respect to territory to control for possible temporal confounds. Stitchbirds generally ignore human observers within their territories and thus birds could be continuously followed (usually within 5 to 10 m) during each observation period with no evidence of any disturbance to the birds' behaviour. Most territories are roughly centred on the active nest box, and the observer returned to this point to re-establish contact if the birds were lost. Nest boxes were monitored daily to establish the date of first egg laying for each female.

The general behaviour of the resident pair was recorded at all sites including the occurrence and description of copulations, male and female displays, nest building and foraging. For birds other than the residents entering the territory, their sex, identity and time of entry and exit were recorded (see Low in press for more details). The following mate guarding measures of the resident male were recorded for 23 territories during first clutch attempts between day -21 and +18 in 2001 (mean ± SD, 27 ± 6 observations per site; range 10 – 38).

(i) Time observed within the territory. The time the male or female left and re-entered the territory was recorded. From this, the total time that one or both resident birds were present was calculated.

(ii) The distance between the resident male and female. Every two minutes, a recording was taken as to whether the male was within 8 m of the female. Eight metres was chosen as this distance allowed the male to generally maintain visual contact with the female under most circumstances. If the male was visibly chasing an extra-pair male within his territory at the time of recording, because this represents a form of mate guarding in itself, the distance measurement was delayed until the chase was complete and the male alighted. Recording only took place when the location of both birds was known.

(iii) Re-establishment of contact after separation. If the male and female were initially together (< 8m) and contact was broken by a movement of one bird of greater than 10 metres, the identity of the bird that re-established contact within a two minute period was recorded. Re-establishment of contact was chosen as a mate guarding measure as it allowed males to leave the female repeatedly to chase extra-pair males and then return to her without being recorded as initiating movements away from the female. The two minute time period was chosen as most male - male chases are of a shorter duration than this (M Low, unpublished data).

(iv) Presence of the male and female at a communal site. When a female arrived at a supplementary feeding station outside of her territory, the male was recorded as accompanying the female if he was present within 30 seconds of her arrival and within 8 m of the feeder.

Territory Size and Position

The effect of extra-pair male intruders on the size and location of the area actively defended by the resident male was also assessed. The boundary of the defended area for each pair was determined by watching both sexes' movement behaviour and their interaction with neighbouring birds during the pre-fertile period. The boundary was defined as the line beyond which, an extra-pair male could call or be visible to the resident male, without the resident male making an attempt to chase him away. These boundaries are generally stable outside of the fertile period and are used to denote each pair's territory, with the boundary being used to gauge whether an extra-pair male is intruding. This territory area was then compared to the location and size of the area defended by the resident male at the time of peak intruder numbers during the female's fertile period. All territorial boundaries were entered onto digitised maps and their areas were calculated using the area calculation function of GPS mapping software (Ozi-Explorer 2000).

Weight Measurements

To determine costs associated with mate guarding and extra-pair male intrusions on resident male weight, male stitchbirds were weighed on a set of electronic scales

(Weighing Systems Ltd.) to an accuracy of ± 0.5 grams at least twice weekly (with an attempt to weigh them daily) in 2002. The scales were attached to a hummingbird feeder containing artificial nectar so that when birds came to drink, they stood on a perch linked to the weighing mechanism. An electronic readout of the bird's weight was displayed allowing the identity and weight of each bird to be recorded by the observer. Because the weight of the bird could increase by up to 2 g while drinking, only the initial weight was recorded. Males were weighed in the morning between 0800 and 1100 hours to minimise the effect of diurnal weight fluctuations (Armstrong & Ewen 2001). Most measurements were carried out at supplementary feeding stations on the island, with any bird not recorded here being weighed within its territory.

Data Analyses

No bird was weighed or pair observed more than once per day and only first clutch attempts were monitored for this study. Because of the relative nesting asynchrony, data collection dates were converted to a number relative to the day the first egg was laid by the female of that pair (day 0), to allow comparison of results between pairs. The periods before day -6 and after the penultimate egg was laid were labelled the pre-fertile and post-fertile periods respectively.

For all comparisons between stages of fertility (pre-fertile, fertile and post-fertile) for male weights and mate guarding values, a mean value was generated for each bird from a standard interval from each of the three time periods. The pre-fertile period of day -12 to -7 was chosen to represent the time the male was spending a significant amount of time in the territory and with the female, but without any significant extra-pair intrusions. The fertile period of day -3 to +2 corresponded to the peak fertile period of the female and the majority of intruder activity. The post-fertile period of +11 to +16 was used as it occurred one week after the end of the fertile period to allow for any recovery of condition by the male after the fertile period. The mean values for each bird generated for these time periods were compared using matched-pair statistical tests. For evaluating the changes in communal site mate guarding, the number of times each female arrived at the feeder accompanied by their male partner during each of the three fertility periods was converted to a percentage of all arrivals for each female and these values compared using a Sign test. When assessing the correlation between extra-pair male intrusion rates and percentage territorial area defended, data were log transformed prior to parametric analysis.

Not all sites could be surveyed or birds measured in all sampling periods resulting in uneven numbers in some statistical tests. Parametric statistics were only used where data were normally distributed and variances were not significantly heterogeneous. Where more than one test was performed on the same dataset, assessment of P-value significance took into account a modified Bonferroni correction (Rice 1989). Means are expressed with standard errors, probability values are two-tailed and statistical significance recognised at $P < 0.05$. The Statistica software package (StatSoft 1997) was used for all analyses.

RESULTS

The Form and Extent of Mate Guarding

Resident male and female time in territory

Data on male and female absolute presence and their presence relative to each other were collected from 23 territories (Fig. 1). Times recorded assume that both sexes were equally likely to be seen and when not observed were not within their territory, an assumption that may not be valid. During the two weeks prior to the female's fertile period (day -21 to day -8) males were observed for 44.9 ± 0.5 minutes per hour and females 48.5 ± 0.5 mins/hr within the territory. For males, this increased during the fertile period to 53.7 ± 1.3 mins/hr and peaked on day 0 at 58.5 ± 1 mins/hr. Female times within the territory during the fertile period did not increase from the pre-fertile period (49.0 ± 1.1 mins/hr). In the post-fertile period, male times dramatically decreased (19.7 ± 1.8 mins/hr) while female times increased (57.4 ± 0.3 mins/hr) reflecting the fact that the female was incubating and the male most likely seeking extra-pair copulations [Chapter 1].

Females were likely to be seen in their territory without the male being present in the pre-fertile period for 6.9 ± 0.4 mins/hr. This decreased significantly during the fertile period to 0.7 ± 0.3 mins/hr (paired t-test $t = 10.82$, d.f. = 20, $P < 0.001$), and from day -2 to day 0, no female was seen in their territory without the male also being present. Both birds being either present or absent from the territory increased from the pre-fertile period

(49.6 ± 0.5 mins/hr) to the fertile period (53.3 ± 0.8 mins/hr: $t = 3.82$, d.f. $= 21$, $P < 0.001$).

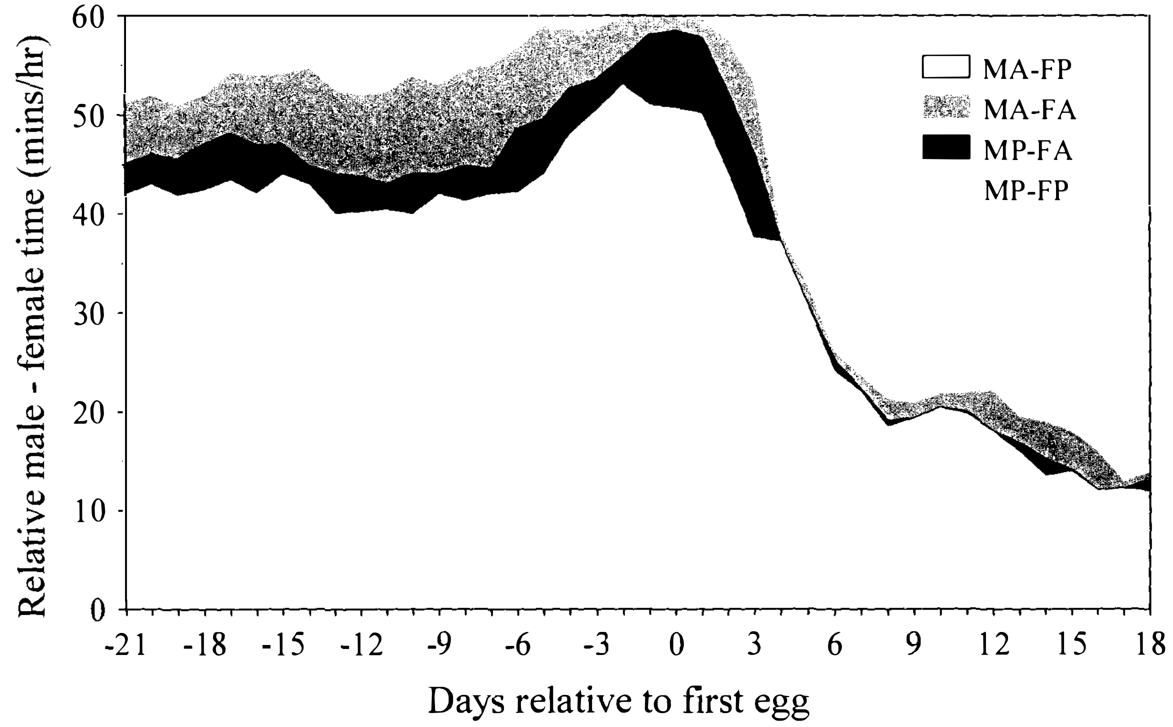

Figure 1. Relative time males and females spend in the territory (mean; mins/hr) relative to egg laying (day 0 is first egg laid). The hour for each day is partitioned into 4 categories; male present – female present (MP – FP), male present – female absent (MP- FA), male absent – female absent (MA – FA) and male absent – female present (MA – FP). Because not all territories were visited every day, the number of territories observed to generate each mean value ranged from 13 – 22.

Time spent within 8 m of female

Males spent significantly longer periods within 8 m of the female during her fertile period than her pre-fertile and post-fertile periods (Wilcoxon paired-sample test $Z = 3.81$, $N = 20$, $P < 0.001$, and $Z = 3.51$, $N = 16$, $P < 0.001$ respectively), with this reaching a maximum mean value of 97 ± 2 % of the time spent together (58 minutes per hour) at day -1 (Fig. 2).

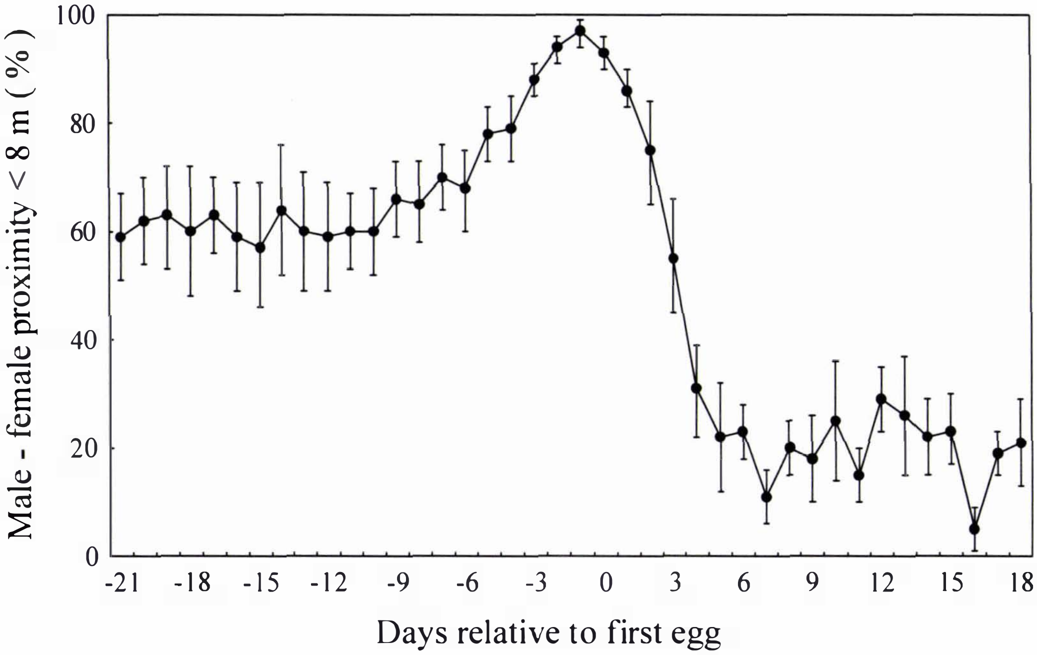

Figure 2. The relationship of male proximity (< 8 metres) to the female when present in the territory together (mean ± 1 SE; %) relative to egg laying (day 0 is first egg laid). Males spent the greatest percentage of their time with the female on day –1 (97 ± 2%). Because not all territories were visited every day, the number of territories observed to generate each mean value ranged from 13 – 22. In the post-fertile period *n* is lower than the territories sampled as no number could be generated if the male was not present in the territory.

Re-establishment of contact after separation

Males were more likely to re-establish contact after separation from the female during the pre-fertile and fertile periods and females took on this role during the post-fertile period (Fig. 3). The likelihood of a male following or returning to a female reached a maximum of 98.7 ± 1.4 % on day -1 and a minimum of 0% on day 9. The percentage of times the male re-established contact with the female after a separation event was significantly higher during the peak fertile period (90.8 ± 2.2 %) than during the pre-fertile (72.7 ± 3.2 %) and post-fertile (18.9 ± 4 %) periods (Wilcoxon paired-sample test $Z = 3.77$, $N = 22$, $P < 0.001$; and $Z = 4.01$, $N = 22$, $P < 0.001$ respectively).

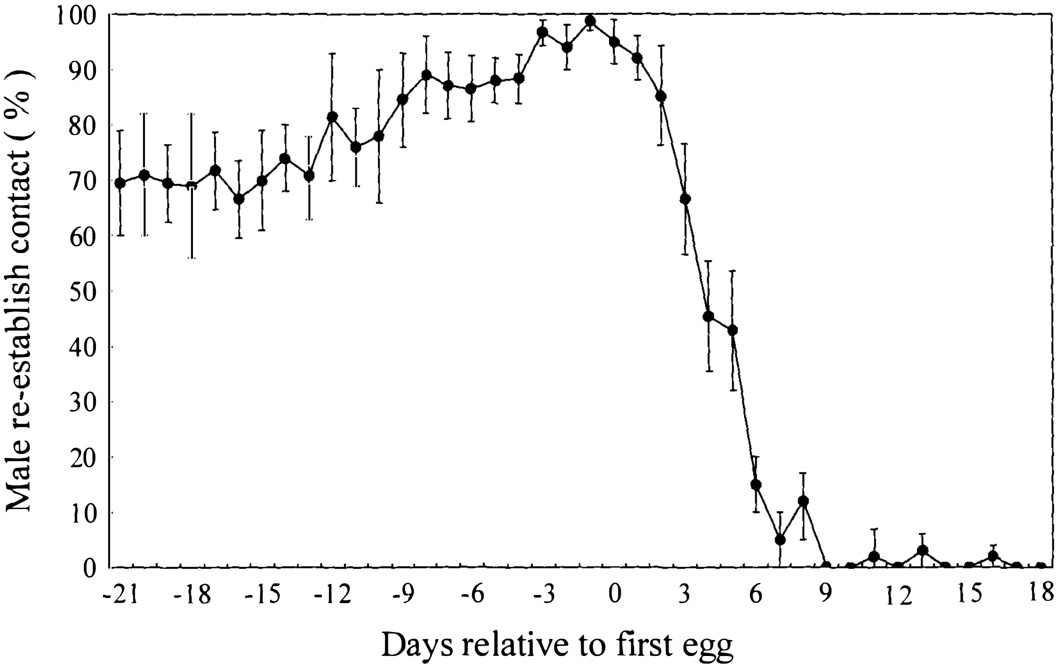

Figure 3. The likelihood of the male being the bird to re-establish contact after a separation event of greater than 10 metres (mean ± 1 SE; male %) relative to egg laying (day 0 is first egg laid). Because not all territories were visited every day, the number of territories observed to generate each mean value ranged from 13 – 22. In the post-fertile period *n* is lower than the territories sampled as no number could be generated if the male was not present in the territory.

Resident male response to extra-pair male intrusion

The resident male responded immediately to any intrusions by extra-pair males with raised head and tail-feather threat displays, calls and aggressive chasing. Any extra-pair male that managed to engage the female in a chase was aggressively chased in turn by the resident male. During forced copulation attempts, if present, the resident male would physically attempt to remove the extra-pair male from on top of the female by pecking and striking at him with his claws, before chasing him away from the female's location. Resident male retaliation in the form of physical aggression or copulating with his female partner after an extra-pair male had been in contact with her was never observed. The reaction of the resident male to other male stitchbirds was in stark contrast to the male's reaction when the female was chased by a bellbird (*Anthornis melanura* – a honeyeater of similar size to the stitchbird). In these cases (N = 119), the male generally ignored the incident and did not actively defend the female. In only 22% of these chases did the male react and follow the chase, but on no occasions was he witnessed engaging the bellbird in any sort of physical encounter.

Male response to a missing female

If the female's position was lost to the resident male, this resulted in an abrupt change in his behaviour. When in her presence, he sat nearby giving a variety of one, two and three-note calls and only leaving her side to chase territorial intruders. If the resident male lost track of the female's location, he would fly in an outward spiral around the last known position of the female giving loud characteristic three-note calls. The male would rapidly move between four or five key locations while vigorously calling and aggressively defending the area around and between these sites. This continued until the female was relocated, when the resident male's behaviour abruptly changed to a silent stationary position usually within a few metres of the female. Males sometimes reacted this way during the pre-fertile period, but it was obvious and consistent during the fertile period, especially when extra-pair male activity around the site was significant. Observation of this response was consistent across all territories and observed during all three years of the study.

Area defended by the resident male

For 16 pairs the mean defended area during the pre-fertile period (3274 ± 175 m^2) and the area defended on the day of peak extra-pair male intruder activity during the fertile period

(1104 ± 352 m^2) were compared relative to the amount of intruder activity recorded for each of those territories. The percentage of the pre-fertile territory that was actively defended during the time of peak intruder activity was negatively correlated to the amount of intruder male activity at that site (Pearson correlation: $r = -0.83$, $t = -5.60$, $N = 16$, $P < 0.001$) (Fig. 4). For the lowest three intrusion rates recorded (< 1 minute per hour), males continued to defend almost all of their pre-fertile territory area (range 86 – 100 %). For the highest three intrusion rates (range 120 – 300 minutes per hour), males defended only the immediate area around the female (range 0.09 – 1.5 % of pre-fertile territory area), which in two cases represented an area with a radius of one to two metres around the female. Under these conditions, the female attempted to continue feeding and the resident male moved with her, displaying to and chasing any of the extra-pair males that approached within one to two metres of her. In all cases of mate guarding during the fertile period the defended area centred on the female and thus moved as the female moved around the territory.

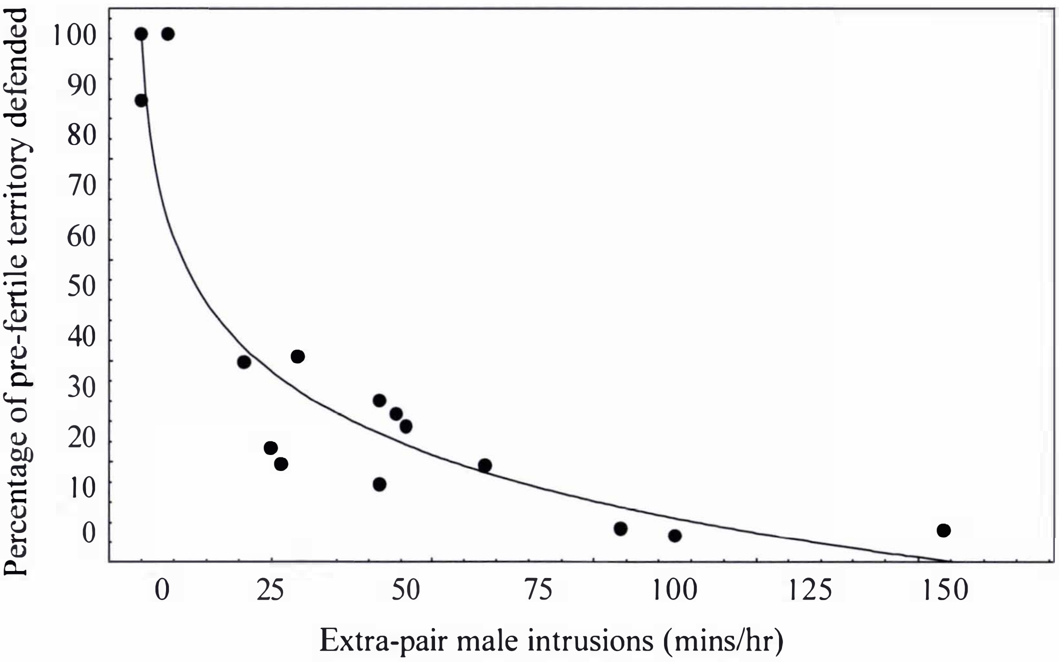

Figure 4. The percentage of the pre-fertile territory that is defended by the resident male during his female's fertile period in relation to the amount of extra-pair male intrusion during that same period. The data in this figure are untransformed with each point representing an individual nesting attempt. Males will continue to actively defend almost 100 % of this area when extra-pair male activity is very low. This area drops exponentially as the male intrusion rate grows.

In two separate territories, involving a total of nine nesting attempts, a different mate guarding tactic was observed. In these cases, males did not actively follow the female around most of the territory, but rather remained in an elevated position in a central location. From here the resident male could observe the female and would chase out any extra-pair males observed entering the local area. The common factor at these two sites was an unusually limited amount of understorey allowing good visibility of the entire territory from a canopy position.

Mate guarding at communal sites

A total of 433 observations of females arriving at feeding areas and the presence or absence of their partnered male were collected during 39 observation periods. Data from 26 females were collected for the pre-fertile period and from 27 females for the fertile and post-fertile periods. The likelihood of a male accompanying his partnered female to a feeding station increased significantly from 37.0 ± 4.8 % in her pre-fertile period to 66.3 ± 4.7 % during her fertile period (Sign test: $Z = 4.58$, $N = 25$, $P < 0.001$). This male accompaniment dropped significantly from both the fertile and pre-fertile percentages soon after incubation began (6.4 ± 1.8%: $Z = 4.69$, $N = 25$, $P < 0.001$ and $Z = 4.58$, $N = 24$, $P < 0.001$ respectively). While at the feeding stations males often fed alongside their female, but on occasions would wait outside the feeder cage and follow the female when she left the site.

Energetic Costs as Measured by Male Weight Change

During the female's fertile period, mean resident male weights dropped from 39.8 ± 0.39 g on day –6 to 38.7 ± 0.35 g on day 0. Because male weight was negatively correlated with both mate guarding intensity and extra-pair male intrusion rates, mean male weights were divided into two groups; those males with high intruder activity during their female's fertile period ($N = 18$) and males with low or zero intruder male activity ($N = 10$) (Fig. 5). Low intruder sites were differentiated from high intruder sites in that while resident males were observed actively mate guarding, they had less than 5 minutes per hour of intruder activity on all days during the fertile period.

Mean male weights during the pre-fertile period were similar for both groups (high intruder: 39.86 ± 0.39 g, low intruder: 40.0 ± 0.28 g) as were weights during the post-fertile period (high intruder: 40.95 ± 0.37 g, low intruder: 41.01 ± 0.36 g). Mean male weights during the fertile period were significantly lower in the high intruder group when compared to the low intruder group (high intruder: 38.44 ± 0.35 g, low intruder: 40.01 ± 0.39 g; *t*-test $t = 2.71$, d.f. = 26, $P = 0.011$), supporting the hypothesis that extra-pair male intrusion increases costs to resident males. For the low intruder group, male weights did not change from the pre-fertile to the fertile period in contrast to the high intruder group where they were significantly lower during the fertile period (paired *t*-test $t = 5.39$, d.f. = 17, $P < 0.001$). Males in the high intruder group reached their minimum weight on day –1 (38.0 ± 0.40 g). Pooled high and low intruder pre-fertile weights were significantly lower than pooled post-fertile weights (paired *t*-test $t = 3.37$, d.f. = 26, $P = 0.002$) supporting the hypothesis that male territorial and mate guarding duties in the pre-fertile period involves a cost to resident males.

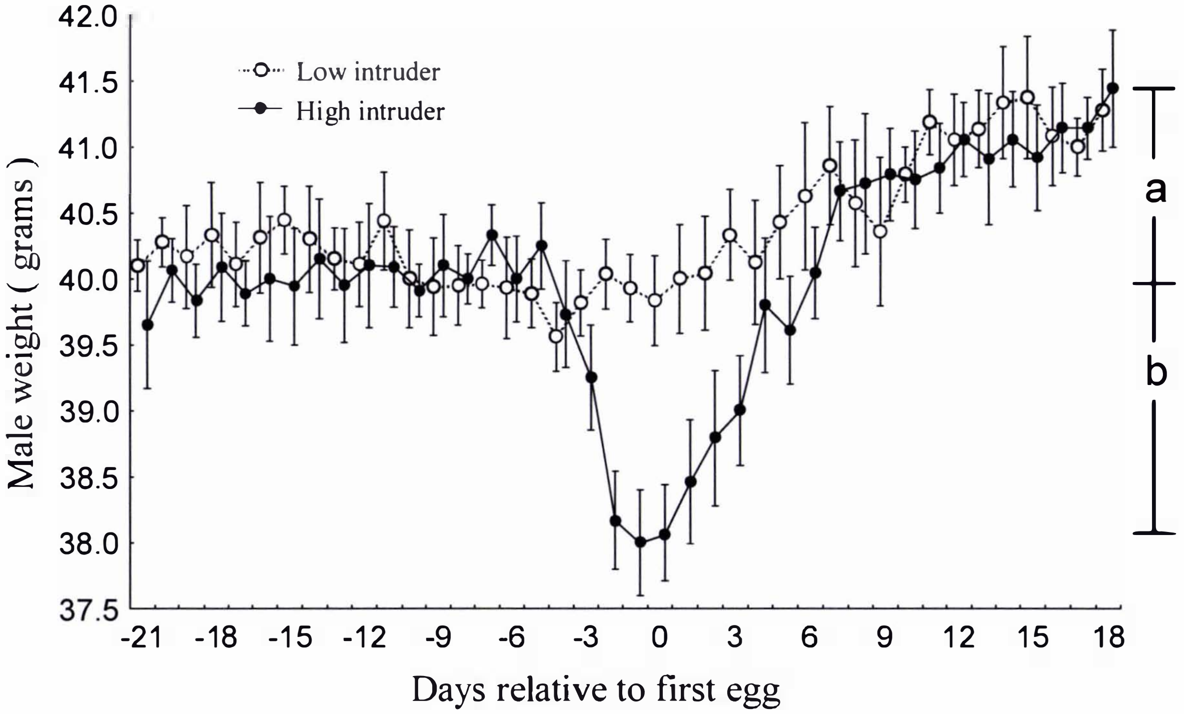

Figure 5. The relationship of male weight in grams (mean ± 1 SE) relative to the laying of the first egg (day 0). Males were divided on the basis of whether extra-pair male intrusion rates during the fertile period were 'low' -○- (< 5 min/hr) or 'high' -●- (> 5 min/hr). The scale to the right of the figure represents the energetic costs as expressed through weight changes of the resident male for (a) territorial and mate guarding duties independent of male intrusion rates and (b) defending the female from male intruders.

The possibility that post-fertile increases in male weight were a function of the males' preparation for chick feeding rather than due to cessation of mate guarding was assessed by comparing breeding male weights to the mean weights of non-partnered males measured during the same period. Non-partnered male weights (40.92 ± 0.34 g, N = 7) were almost identical to the weights of breeding males during their post-fertile period (40.97 ± 0.31 g, N = 28). Because non-partnered males were neither mate guarding nor preparing to feed chicks, the fact that their weight mirrors that of the post-fertile breeding males, suggests that the post-fertile weight increases are more likely due to a reduction in mate guarding. Low numbers of extra-pair male intrusions at some sites is unlikely to be a function of resident male age as 31% of breeding males in the population were one year old and 30 % of the low intruder sites contained first year males as residents. Males were more likely to be at their minimum recorded weight during the female's peak fertile period (day –2 to +1) than expected (81% versus 15%, N = 27, Fisher's exact test $P <$ 0.001). Ten of the 27 males with a weight recorded for day 0 were at their minimum recorded weight on that day.

DISCUSSION

Behavioural Tactics of Mate Guarding

Effective mate guarding generally involves expressing behavioural means of preventing extra-pair fertilisations (EPFs) at times when females are most likely to receive EPFs (Birkhead & Møller 1992). In the majority of bird species, these behavioural tactics manifest as males spending more time in close proximity to the female, males re-establishing contact between the pair should contact be broken, and males responding vigorously to extra-pair male intrusions (Beecher & Beecher 1979; Arvidsson 1992; Komdeur et al. 1999). These behaviours are generally expressed by males during their female's fertile period and have been shown to be effective at reducing the risk of EPFs (Westneat 1994; Wagner et al. 1996; Komdeur et al. 1999; Pilastro et al. 2002).

Stitchbird mate guarding behaviour and its temporal relationship to the female's fertile period follows a pattern similar to that seen in other mate guarding species. This was expected, considering the high paternity risk for the resident male associated with extra-pair forced copulations (Ewen et al. 1999). However in contrast to many other species, stitchbird males were shown in this study to adopt a conditional mate guarding strategy, which is dependent on the stage of fertility and the location of the female, the number of extra-pair male intrusions and forced copulation attempts, and at least one topographical measure. Males generally followed females and maintained close proximity during their fertile period unless they could easily maintain visual contact. In unusual cases, where the combination of a tall canopy and an open understorey existed, males were seen to survey a large proportion of their territory from an elevated position and did not necessarily follow the female. This appears to be a good tactic, as under these conditions the resident male is in an ideal position to identify any intruders and intercept them before they can reach the female.

Previously, mate guarding in the stitchbird has been described as inconsistent (Castro et al. 1996) or involving a trade-off between defending the nest site and guarding the female (Ewen 1998; Ewen et al. in press). I found no such inconsistency or trade-off in this study, as all males engaged in mate guarding would centre the area they defended on the position of the female when she was present. In Ewen's (1998) study, observations of the female within the territory were very low (33%) and may have been related to continual harassment at the nest site due to the heavily male biased population (three males to every female). As was found in my study, when the female is absent or unable to be located by the male, the male adopts a conditional tactic whereby he defends an area that is most likely to contain the female or that the female will return to (*i.e.* around the nest site or where she was last seen). Thus nest site defence under these circumstances should not be viewed as a trade-off, but rather a best-of-a-bad-job tactic contained within a wider strategy to maximise female mate guarding. This conclusion is supported by various other measures including an increasing likelihood for the male to be close to the female and initiate contact during her fertile period, the defended area being mobile and based on the location of the female, and the resident male's significantly increased following of the female to communal sites outside the territory during her fertile period.

While not specifically measured in this study, it is likely that the resident male is effective at limiting extra-pair copulations (EPCs). On all occasions when successful EPCs occurred, the male was temporarily absent from the female. When present, the male was able to interfere and chase any extra-pair male away from the female. An alternative interpretation of the existence of mate guarding under these circumstances is to protect the female from harassment (Gowaty & Buschhaus 1998; Komdeur et al. 1999). This does not appear to be the primary motivation in the stitchbird, as females are also harassed and chased by bellbirds. Bellbirds are smaller than stitchbirds (20 – 33 grams) although they are generally more aggressive (Craig et al. 1982). Females were often observed being chased for up to one minute by bellbirds while the resident male was indifferent to the encounter. This was not the case when extra-pair male stitchbirds chased the female. Whenever this occurred, resident males were extremely responsive to the chase and aggressively attempted to remove that male from the vicinity of the female.

Energetic Costs of Mate Guarding

While males can limit the number of extra-pair copulations in their own nests by engaging in anti-cuckoldry behaviours such as mate guarding (Komdeur et al. 1999), there are energetic costs and other trade-offs associated with this behaviour. Mate guarding has been correlated with reduced opportunities for courtship feeding and copulation (Mougeot et al. 2002), reduced pursuit of extra-pair fertilisations (Chuang-Dobbs et al. 2001) and a reduction in the male's ability to attract secondary females to a territory (Pinxten & Eens 1997). The energetic costs of anti-cuckoldry behaviours are likely due to a trade-off between foraging opportunities and mate guarding and the possible increase in energy expenditure due to increasing male activity (Westneat 1994; Askenmo et al. 1992; Komdeur 2001). These energetic costs have recently been quantified in the Seychelles warbler (*Acrocephalus sechellensis*) and clearly show that males face a trade-off between foraging opportunities and mate guarding (Komdeur 2001). In the Seychelles warbler, males are estimated to lose 13% of their body weight during the intense mate guarding period. This weight loss was recovered after the female laid her egg and the males' subsequent weight gain was correlated to their increased foraging activity (Komdeur 2001).

My study not only supports Komdeur's (2001) findings, but also shows that in the stitchbird there are two factors affecting the relative energetic costs to the resident male. The first is a general cost that is imposed on all males that defend a territorial area. The extent of this is reflected in the males' steady weight gain in the post-fertile period relative to their stable pre-fertile weights. Males gained approximately 2.5% (1 g) in body weight after relinquishing the majority of their territorial and mate guarding duties after the clutch was laid. In cases where territorial intrusion rates were constant during the pre-fertile and fertile periods (*i.e.* none or very low during the fertile period) the increased mate guarding parameters did not significantly affect the male's weight, suggesting that under these conditions foraging opportunities are similar for males in the pre-fertile and fertile periods. This was in contrast to males in territories where extra-pair male intrusions significantly increased during the fertile period. Under these conditions, males appeared to be affected by an additional cost as shown by the resident male losing approximately 5% (2 g) of his body weight over the four days corresponding to increasing extra-pair male intrusions. This energy deficit is likely to be a result of reduced opportunities to feed, increased energy expenditure as a result of chasing extra-pair males from the territory, or a combination of both (Komdeur 2001).

Explanations other than mate guarding are unlikely to account for the differences in male weights between the pre-fertile, fertile and post-fertile periods. The possibility of weights rising or falling as a result of courtship feeding or preparation by the male for incubation, can be discounted as male stitchbirds neither courtship feed nor help during incubation. Males do contribute to chick feeding, albeit at a lower rate than the female (Castro et al. 1996; Ewen & Armstrong 2000). Because of this I considered the possibility that the pre-fertile weights were not low as a result of mate guarding, but instead the post-fertile weights were artificially high due to preparation for chick feeding. When compared to the mean weights of seven non-partnered males, the pre-fertile breeding male weights were low and the post-fertile breeding male weights were almost identical, supporting the idea that pre-fertile weights are low as a result of mate guarding. Another possibility is that breeding males during the pre-fertile period have lost weight to improve their aerial performance to better expel intruders (discussed in Komdeur 2001 and see references therein). This explanation fails to account for the fact that a need for ideal aerodynamics should only apply during the fertile period and should also apply equally to the non-partnered males who did not lose weight, but still attempted extra-pair forced copulations. Seasonal effects can be discounted due to the relative asynchrony of the females' fertile periods.

The fact that male stitchbirds will pay an average cost of 7.5 % (3 g) of their body weight to expel intruders and minimise EPCs suggests that there must be some fitness benefit to the male associated with mate guarding. It is likely that in the stitchbird, as has been found in other species, this benefit is a reduction in EPCs and EPFs (Westneat 1994;

Komdeur et al. 1999; Chuang-Dobbs et al. 2001; Pilastro et al. 2002). If we also consider that the majority of all EPCs are forced, this suggests that forced copulation can successfully inseminate females without their co-operation in this species, an idea that is also leant support from analyses of previous paternity data (Ewen et al. 1999). While the costs of harassment associated with forced copulation have previously focussed on the female (Birkhead & Møller 1992), this study is the first to show that this cost is also significant for the mate guarding male. Thus, as has been recently suggested for future theoretical and empirical treatments of extra-pair paternity in birds (Westneat & Stewart 2003), assessments of reproductive costs associated with forced copulation need to consider their direct impact not only on females, but also on both the resident and the associated extra-pair males.

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CHAPTER VI

A hierarchical model predicts male provisioning of offspring in the stitchbird

A male stitchbird leaves the nest box after feeding the chicks in his primary female's nest

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Chapter reference:
Low, M., Joy, M. K. & Makan, T. A hierarchical model predicts male provisioning of offspring in the stitchbird . Submitted to *Proceedings of the Royal Society of London* B.

Abstract

Males are predicted to trade off parental effort (PE) for current or future mating effort (ME) at times when this is likely to increase their reproductive success. In the stitchbird (*Notiomystis cincta*), a species with male parental care and high levels of extra-pair paternity, we used a cross-validated regression tree analysis to predict the effect on male provisioning visits to the nest of 1. brood size, 2. certainty of paternity 3. additional mating opportunities, 4. female rank (primary or secondary), 5. population density, 6. male age, 7. female age, and 8. food availability. During first clutch attempts, males did not invest in secondary females' broods, nor did they provision nests containing only one chick. Male age, additional mating opportunities and proximity to supplementary food had a minor, but measurable relationship to male provisioning rates in moderately sized broods. Second clutch brood provisioning was also predominantly correlated with female rank and brood size. In the stitchbird, males appear to use a set of 'if-then' hierarchical rules to decide on the level of offspring provisioning. While previous models have focussed on ME / PE trade-offs as static functions, we discuss the possibility that the relative importance of some variables changes as the breeding season progresses.

1. INTRODUCTION

Male contribution to offspring provisioning is often more variable than that provided by the female (Ligon 1999). While both sexes face potential trade-offs between current parental effort and future reproduction (Trivers 1972), males are more likely to be in a position where they can reduce investment in a current brood to take advantage of opportunistic mating possibilities (Magrath & Elgar 1997; Magrath & Komdeur 2003). Selection should favour phenotypic plasticity in reproductive investment, with parental care being seen as a conditional strategy where males seek the best fitness outcomes under given conditions (Badyaev & Hill 2002). This is most commonly interpreted through the examination of an optimal trade-off between parental effort (PE) and mating effort (ME) (Magrath & Komdeur 2003). Predictions of what variables should affect male provisioning rates vary widely, depending on the predictor variable being evaluated and the assumptions of the model (Whittingham & Dunn 2001; Sheldon 2002; Magrath & Komdeur 2003). This is reflected in observational and experimental studies of paternal investment. Males have been shown to adjust their chick provisioning rates to account for clutch size (Komdeur et al. 2002), brood size (Wright et al. 1998), male age (Westneat 1988), additional mating opportunities (Magrath & Elgar 1997), certainty of paternity (Chuang-Dobbs et al. 2001), female rank (Dixon et al.1994), presence of a helper at the nest (Davies et al. 1992), and food availability (Hoi-Leitner et al. 1999). However within these studies, not all predictor variables are significantly correlated with male provisioning (e.g. Chuang-Dobbs et al. (2001) found no effect of additional mating opportunity, and Westneat (1988) and Hoi-Leitner et al. (1999) found no effect of brood size). This suggests that these relationships are complex and are dependent on specific life history traits of different species.

The New Zealand stitchbird (*Notiomystis cincta*) is an excellent model species in which to investigate the influence of a suite of variables on male provisioning behaviour. Males do not incubate but do participate in provisioning the brood, albeit at a lower level than the female (Castro et al. 1996; Ewen & Armstrong 2000). Stitchbirds are predominantly socially monogamous, with males combining nest site defence with the pursuit of extra-pair copulations, the majority of which are forced, at other nest sites (Castro et al. 1996; Low in press). The percentage of extra-pair offspring is high (35 – 46

%), and can be found in the majority (80 – 82 %) of nests (Ewen et al. 1999; Castro et al. in press), with males reported to modify their provisioning of the brood based on paternity levels at their nest site (Ewen & Armstrong 2000). The cue used by the resident male to determine paternity is hypothesised to be the level of attempted and successful forced copulations at the nest site (Ewen & Armstrong 2000). Stitchbirds are an endangered species and are restricted in their distribution to a few islands offshore from the New Zealand mainland. One of these sites, Tiritiri Matangi, contains a closely monitored and intensively managed translocated population in a fragmented landscape. Because of the small population size, it allows many of the variables hypothesised to influence male provisioning behaviour, and not previously assessed in this species, to be evaluated with respect to the entire island population.

In this study we evaluate the relationship between male stitchbird provisioning rates and the following eight variables; 1. brood size, 2. certainty of paternity, 3. additional mating opportunities, 4. female rank, 5. population density, 6. male age, 7. female age, and 8. food availability by using a cross-validated regression tree analysis. Regression trees are a relatively new approach to modelling complex ecological data and have many advantages over the standard statistical techniques previously used for examining similar relationships (see De'Ath & Fabricius 2000 for review). This allowed us to include in the model both normal and non-normally distributed categorical and continuous variables that did not necessarily share a linear relationship with the dependent variable. Because of these limited constraints on the data, as well as the potential for highlighting high-order interactions and the ability to cross-validate our results, we were able to robustly model multivariate relationships with our dependent variable (offspring provisioning by the male).

2. METHODS

(a) Study population

The birds in this study were observed during three breeding seasons between September 2000 and January 2003 and comprise a closed population on Tiritiri Matangi Island (36°36'S, 174°53'E), located off the northeast coast of New Zealand's North Island. Stitchbirds were translocated to the island in 1995 as part of the ongoing management of the species by the New Zealand Department of Conservation. All birds on the island are uniquely colour banded with their ages and social parentage known. Stitchbirds on Tiritiri Matangi Island breed during the spring and summer (September to February) and will successfully raise either one or two broods of between one and five chicks. Chicks remain in the nest for approximately 30 days after hatching. While most of the males in this population were socially monogamous, a minority were polygynous with usually two but occasionally three females nesting in their territories. In polygynous territories females can usually be ranked as either primary or secondary, with the primary female being physically dominant to the secondary female and occupying a more central position within the territory. Males generally associate with the primary female and only spend the majority of their time with the secondary female during her fertile period when they instigate mate guarding.

The population on Tiritiri Matangi is small (27 – 35 breeding females in each year) allowing all breeding attempts to be comprehensively monitored. Supplementary food in the form of a 20 % (by mass) sugar solution was fed from up to nine feeding stations which were provided year round and used by all birds on the island. Because the stitchbird is a cavity nesting species and the island is mostly comprised of young regenerating forest, artificial nest boxes were provided and used by all birds. These were situated approximately 1.5 m off the ground with a hinged lid and allowed easy monitoring of nesting.

(b) Certainty of paternity observations

Stitchbird pairs were located and identified during September and October, to coincide with male territorial calling and female nest site selection. An attempt was made to monitor each bird's territory for a continuous 30 to 60 minute period every day, from the onset of nest building until chick hatching. In order to measure perceived threats to paternity, all stitchbirds other than the residents entering the territory had their identity and the time of entry and exit recorded. If more than one intruder was present, then the times of each male were summed giving total male intruder times of more than 60 minutes per observation hour in some territories. All attempted and successful forced extra-pair copulations directed towards the resident female were also recorded. An attempted forced copulation was defined as the female emitting a specific high-pitched alarm call and attempting to flee from one or more pursuing males (Castro et al. 1996).

The majority of these chases ended with the resident male chasing away the extra-pair males involved. Extra-pair males however, were occasionally successful with the female being caught, brought to the ground and being subjected to a face-to-face forced copulation.

(c) Provisioning observations

Nests were monitored daily from the completion of nest building to accurately determine the date of first egg lay, the onset of incubation and the date of chick hatching. Chick numbers were also counted in every nest each day during the provisioning observation period. An average of 10 provisioning observations (range 6 – 15) were undertaken between day 5 and 20 after the chicks hatched. Nests often failed prior to this time and thus provisioning data were not collected for many nests. Nests that failed before more than five observations had been recorded were excluded from the analyses. Only one observation per nest occurred on any given day with observations lasting for exactly 30 minutes and beginning from the time of arrival of the observer. Observers sat 10 m away from the nest box, with a clear line of sight to the entrance hole and recorded the time of entry and exit of both males and females during the observation period. This did not appear to affect the birds' behaviour in any way as stitchbirds are easily approachable and have been habituated to being closely monitored on this island. If a bird was on the nest at either the beginning or end of an observation session, this was counted as a half visit. For each nesting attempt, a mean value was generated for male brood visits per hour and this was also converted to visits per chick per hour. We assumed that brood visitation rates served as a reasonable indicator of total food mass being delivered by the male, based on the observation that visitation rates were correlated with decreasing male body weights (M Low unpublished data; see also Stoehr et al. 2001).

(d) Analyses

(i) Variable selection

Eight variables with the potential to influence male provisioning were derived for the analyses. Brood size was calculated by taking a mean value of the chick numbers recorded during observations at that site (range 1-5), and thus was a continuous rather than a categorical variable. This was necessary as chick mortality could change the numbers of chicks in the nest from one observation to the next. Female rank was divided into either primary or secondary females, with the status of each female determined through observations of polygynous male behaviour and interactions between the two females (range 1-2). Female partners of monogamous males were always classed as primary females. Additional mating opportunity was calculated as the total number of days during the chick provisioning observation period (day 5-20 after hatching) that other females in the population were fertile. If more than one female was fertile on any given day, then the numbers were summed for that day (range 0-137). Certainty of paternity was evaluated as the sum of the mean attempted forced copulations per hour during the female's fertile period and the number of successful extra-pair copulations for that site (range 0-7.1). Local population density was calculated by summing the total number of nest sites within a 115 m radius of the provisioned nest site (range 0-10). The figure of 115 m was chosen as it was the mean distance nest boxes were located from supplementary feeding stations, and thus it was thought to be representative of the local area that birds would regularly travel outside their territory. Male and female age was recorded in years (range 1-7), with the data accessed from banding records. Food availability was recorded as the distance in metres from the nest box to the nearest supplementary feeding station (range 28-360). Distances to supplementary feeding stations and other nest boxes were calculated from digitised maps using GPS mapping software (OziExplorer 2000).

(ii) Regression tree analysis

We performed a regression tree analysis to examine the relationship between male provisioning of offspring (measured in visits per brood per hour) relative to the eight explanatory variables as defined above for both first and second clutches. Regression trees are constructed by continuously dividing data into mutually exclusive groups by comparing every possible binary split in every variable and choosing the division that minimises heterogeneity of the resulting two groups. This process is then repeated on the next grouping level. To determine the optimal tree size, we used a leave-one-out cross-validation procedure (jack-knifing) and chose the model that best predicted the excluded data. This method involved excluding one observation, reconstructing the model and then predicting the response of the excluded observation. This was repeated for the entire dataset, with a correlation coefficient derived from comparing predictions to observations for each tree size. All regression tree analyses and their cross-validation were conducted using computer macros written in the MatLab® programming language.

We also evaluated the full 'unpruned' first and second clutch regression tree and noted which explanatory variables were used for the basis of each data division. For each division, the relationship (+ or -) between the explanatory variables highlighted by the analysis and the dependent variable (male visits / brood / hour) was recorded. Because divisions made at lower levels of the tree are based on a dwindling dataset and are more prone to be influenced by "noise" in the data, we weighted each decision by giving a score that was calculated by counting how many divisions occurred from that point of the tree onwards (with the final division having a score of one). This meant that divisions based on larger sample sizes were accorded greater predictive value.

(iii) Additional analyses

For discussions of PE / ME trade-offs, we defined parental effort as mean male feeding visits to his brood per hour during the observation period of 5 – 20 days post hatching. Mating effort was defined as activity by the male, either mate guarding or attempted extra-pair copulation, that was likely to increase his chances of paternity at a particular site. For trade-offs with PE, this necessarily was at a site other than the female he was investing PE and was occurring during the same period as was observed for offspring provisioning. For post-hoc comparisons, parametric statistics were used when data were normally distributed and variances were not significantly heterogeneous. In comparing brood size with male visits per brood and male visits per chick in figure 4, least squares means, rather than raw values of male visitation were used. Each male is represented only once per analysis except in the regression tree analyses when a male has a secondary female, where he is represented twice. Means are displayed with standard errors unless otherwise indicated. All analyses other than regression trees were undertaken using the Statistica software package (StatSoft 1997).

3. RESULTS

Provisioning data for first clutch broods used in this analysis were collected from 51 sites (11 in year 1, 23 in year 2 and 17 in year 3) during 521 observation periods. For second clutch broods these data were collected from 23 sites (4 in year 1 and 19 in year 2) during 225 observation periods. The possibility that offspring provisioning by a male towards clutches of his primary and secondary female were not independent, was solved for first clutches with the regression tree dividing these off at the first division (Figure 1). For second clutches, the original analysis incorporating both primary and secondary females did not initially split the dataset based on female rank and thus secondary females were split off manually and the regression tree analysis rerun on the remaining primary female dataset (Figure 2).

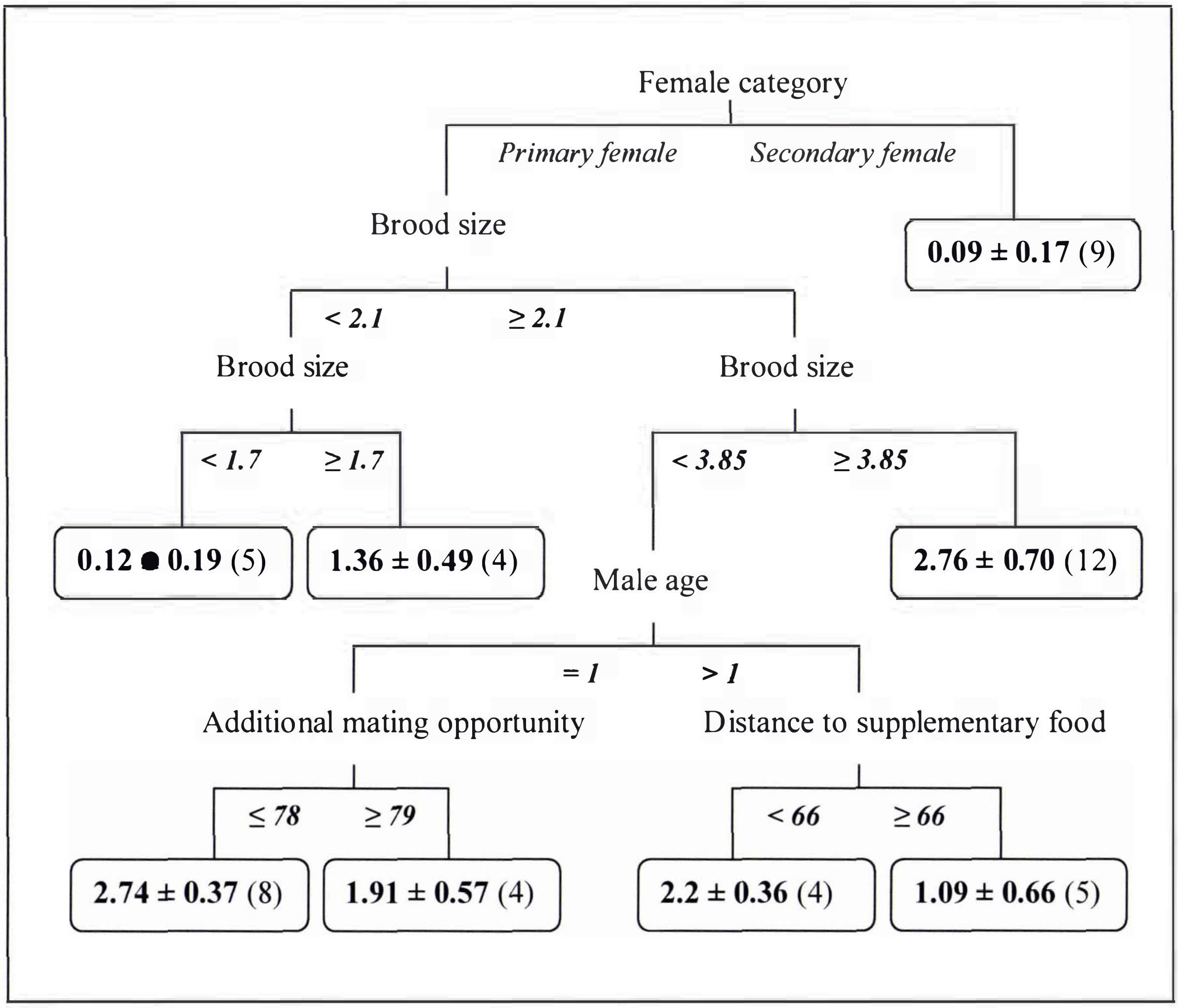

Figure 1. Regression tree generated from first clutch data ($n = 51$) showing relationships between five explanatory variables and male paternal investment as measured in visits per brood per hour. Mean male visitation rates ± SD are given at each terminal node with sample sizes in parentheses. This tree was pruned from a 39 level tree to the six level tree presented here based on correlation coefficients generated from a leave-one-out cross-validation procedure (see Figure 3a, b).

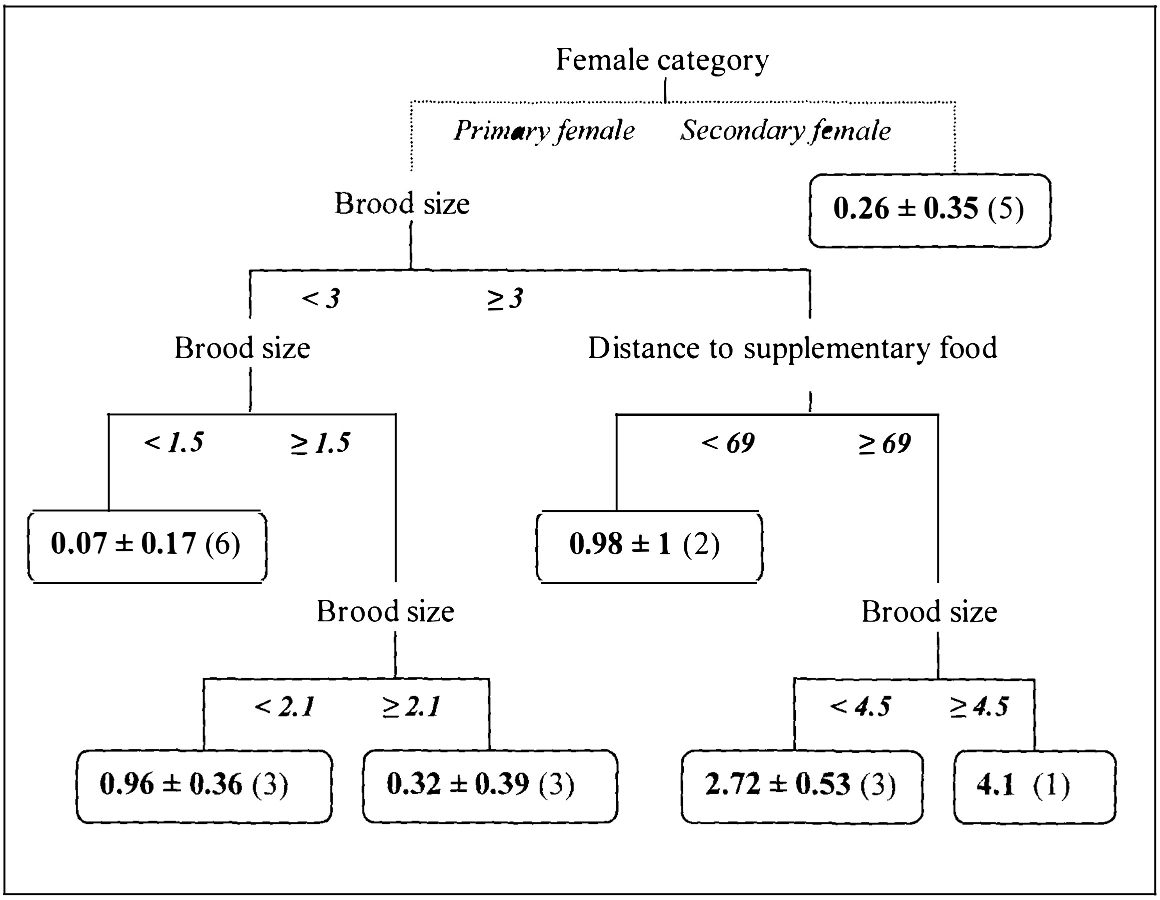

Figure 2. Regression tree generated from second clutch data (n = 18) after secondary females were manually split from the dataset (dotted lines). The tree was pruned to five levels out of a possible 13 based on cross-validation (Figure 5) and shows the relationship between two explanatory variables and male visits per brood per hour. Mean male visitation rates ± SD are given at each terminal node with sample sizes in parentheses.

Male visits per chick did not significantly differ for first (0.43 ± 0.05) versus second clutches (0.38 ± 0.07) (t = 0.57, d.f. = 72, p = 0.56). There were significantly more female fertile days in the population during first clutch chick provisioning (63 ± 6 days) than second clutches (35 ± 8 days) (t = 2.58, d.f. = 72, p = 0.01).

(a) Predictors of male provisioning

(i) First clutches

Using cross-validation we determined that the appropriate tree size to best predict novel data consisted of the first six tree levels out of a possible 39 (Figure 3a, b).

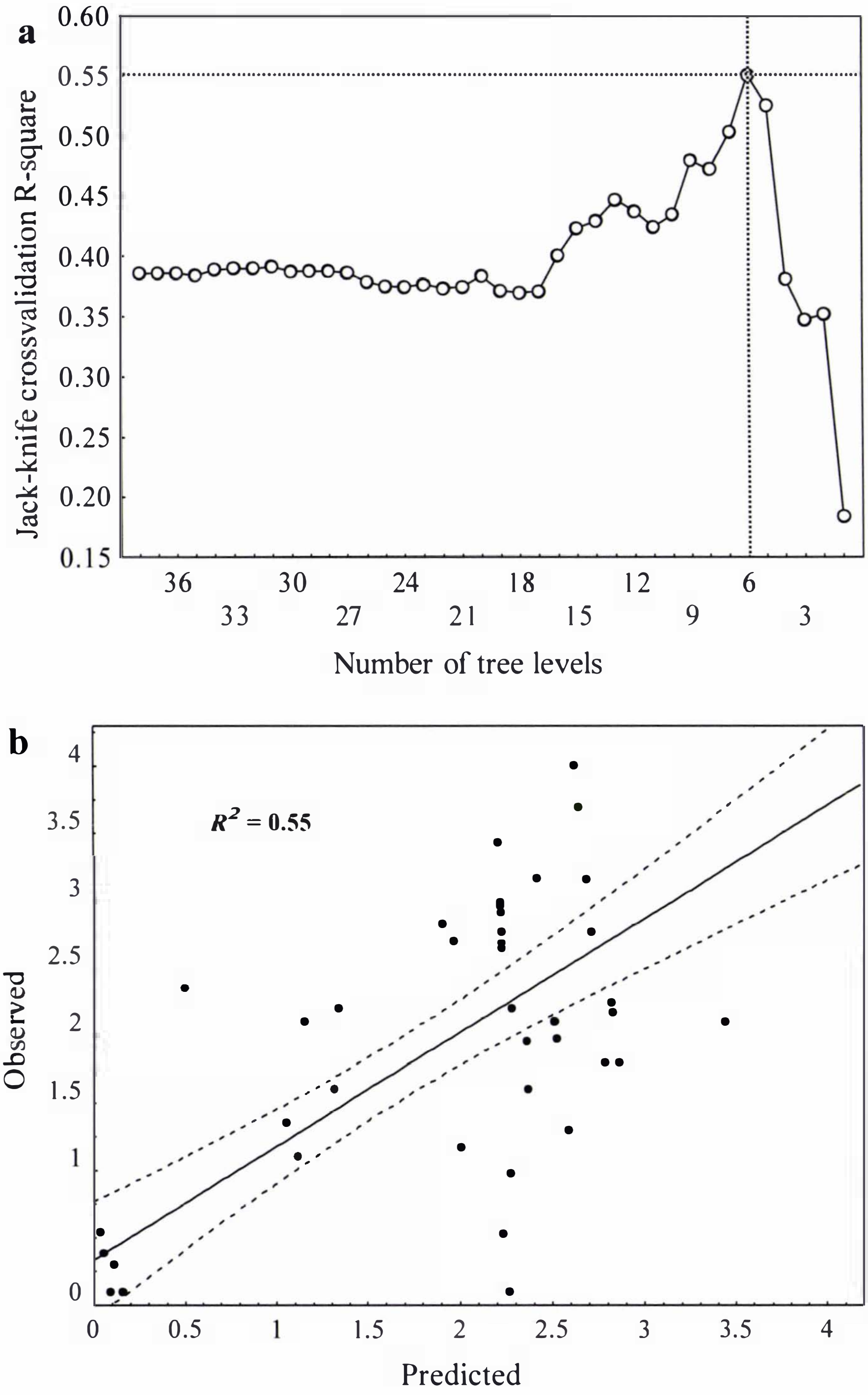

Figure 3. Leave-one-out (jack-knife) cross-validation of first clutch regression tree analysis. Maximum prediction capability of the (**a**) first clutch regression tree is at 6 tree levels with predicted versus observed outputs from the model peaking at $R^2 = 0.55$. The relationship of observed against predicted (y=0.23+0.84x) is plotted (**b**) for the first clutch tree with 95% confidence intervals.

At this pruning level, regression tree analysis grouped the data relative to male visitation rate into 8 categories (Figure 1). Female rank (primary or secondary) and brood size were the two strongest predictors of male provisioning for first clutch nests. In nests of primary females, based on the variable 'brood size', regression tree analysis grouped the data into 4 categories (< 1.7, 1.7 – 2.1, 2.1 – 3.85, > 3.85), with the values from these categories being positively correlated with mean male feeding rates per hour (0.12, 1.36, 2.09, 2.76 respectively). In general, males did not visit broods of only one chick, but proportionally increased their investment from two to five chicks to maintain a similar level of investment per chick for this brood size range (range 0.51 - 0.63 visits per chick per hour) (Figure 4a). Within the modal brood size category of 2.1 to 3.85 (*n* = 21), male age, additional mating opportunities and distance to supplementary food all explained additional variation in male chick provisioning (Figure 1).

When the relationship between the dependent variable and explanatory variables used more than once to divide the data (brood size, additional mating opportunities, distance to feeder, and certainty of paternity) was examined in the 39 level unpruned tree, only brood size and additional mating opportunities consistently predicted male investment in offspring in the expected direction (Table 1).

Explanatory variable	Relationship to dependent variable at each tree division **+ve : –ve**		Predicted relationship
	First clutch	Second clutch	
Brood size	12 : 1 (97 : 1)	5 : 2 (28 : 6)	positive
Additional mating op.	0 : 5 (0 : 24)	0 : 0 (0 :0)	negative
Certainty of paternity	2 : 4 (12 : 10)	0 : 1 (0 : 2)	positive
Distance to feeder	8 : 8 (18 : 25)	3 : 2 (8 : 3)	negative

Table 1. The relationship between the dependent variable (male visits / brood / hour) and explanatory variables used to repeatedly divide the data within the full 39 level first clutch and the 13 level second clutch regression tree analyses. The ratio of values not contained within parentheses show the actual numbers of divisions based on that variable in the analysis, and the proportion that were positively or negatively correlated with the dependent variable at that division. Weighted values (in parentheses) take into account the level at which the data were divided in the tree, with a greater weighting being placed on higher-level (and hence more influential) decisions. The predicted relationship between the dependent and explanatory variable is listed in the far right column.

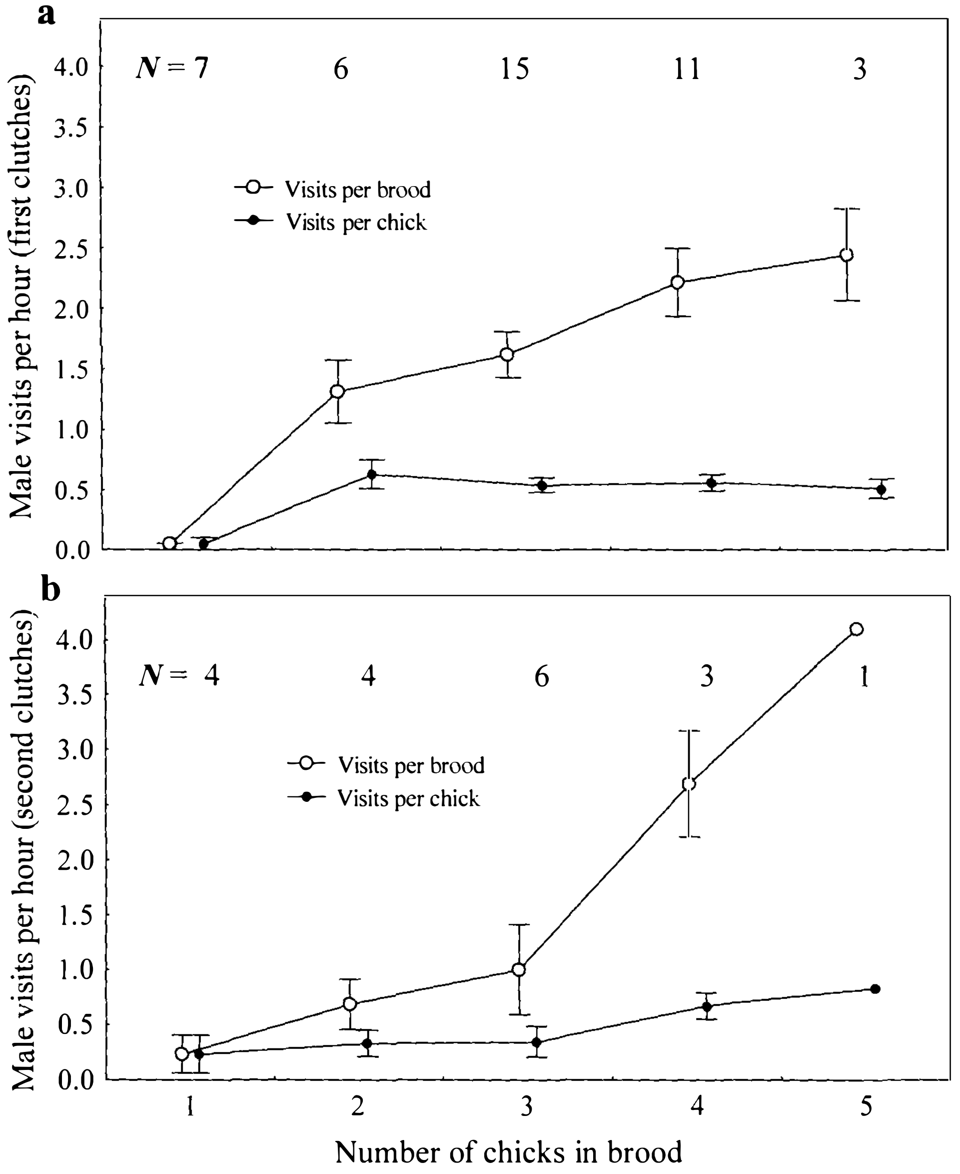

Figure 4. Male provisioning visits of both per brood and per chick per hour (mean ± 1 SE) for **(a)** first clutches and **(b)** second clutches relative to increasing brood size. Values presented are least squares means with the number in each sample displayed towards the top of each figure.

(ii) Second clutches

Cross-validation of the second clutch (*n* = 18) regression tree, determined the appropriate tree size to contain 8 levels (out of a possible 13) (line "1" in Figure 5). We further pruned this to 5 levels based on the cross-validation output showing that this would reduce the model's R^2 by only 0.025 (line "2" in Figure 5). This was done because these three pruned levels were making divisions based on only two or three data-points and were unlikely to be robust in their predictive capability outside of this dataset. Despite the relatively poor cross-validation R^2 for the model (a likely consequence of a small dataset), brood size still appears to be a major factor in predicting male investment in offspring (Figure 2), with female rank also influencing male offspring investment decisions (primary female 1.03 ± 0.03 (*n* = 18) visits/brood/hour versus secondary female 0.25 ± 0.15 (*n* = 5) visits/brood/hour). Second clutch data (*n* = 23) was also run through the first clutch regression tree model, with the predicted to observed comparison producing an R^2 = 0.35, placing it almost midway between the cross-validated outputs of the first clutch tree (R^2 = 0.55) and the second clutch tree (R^2 = 0.21).

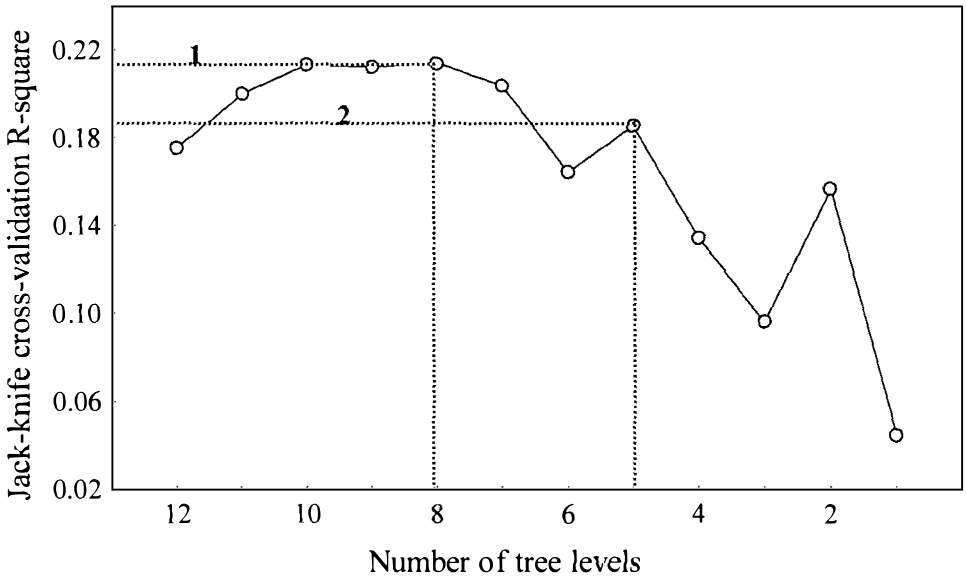

Figure 5. Leave-one-out (jack-knife) cross-validation of the second clutch regression tree analysis. For second clutches, the cross-validation showed that the best predictive model incorporated *eight levels* '**1**', but this was further pruned back to five based on evaluation of division sample sizes in the terminal nodes '**2**' (see text for further discussion).

While males did increase their brood feeding rates as the brood size increased, second clutches differed from first clutches in the relative change in visits per chick per hour (Figure 4b). Males maintained a moderate level of investment in brood sizes ranging from 1 to 3, with this disproportionately increasing for clutch sizes greater than this.

(b) Mating effort (ME) and parental effort (PE) trade-offs

Because first clutch male PE was negatively correlated with additional mating opportunities (Figure 1, Table 1), we tested whether reduced PE translated into an increase in ME as determined by extra-pair sightings during this time. Males were significantly more likely to be observed as an extra-pair intruder within another bird's territory during the 15 days of incubation when he has no direct PE, compared to the 15 days of chick provisioning observations (5.8 ± 0.67 versus 2.8 ± 0.57 intrusions per 15 days, Paired *t*-test: $t = 3.63$, d.f. = 35, $p < 0.001$). However the changing proportion of fertile females in the population during those periods makes this comparison difficult to interpret. If the number of sightings for each male is divided by the number of fertile female days for that period, then incubation intrusion percentages (7.3 ± 1 %) are almost identical to chick feeding intrusion percentages (7.9 ± 2 %, $t = 0.19$, d.f. = 35, $p = 0.85$). There was also no significant correlation between male visitation rates at the nest and sightings of these individual males in other territories during the chick-feeding period (Pearson product-moment correlation: $r = 0.07$, $p = 0.66$).

Where overlaps occurred between the chick feeding period of a primary female and the fertile period of a secondary female, individual males were observed trading-off PE for ME at these times (Figure 6). While these males invested a large amount of ME in both of their females, they generally only invested PE in one of the broods. For seven polygynous males with chick provisioning data for both their primary and secondary females' broods, they invested significantly more in the primary female (0.54 ± 0.12 visits/chick/hour) than the secondary female (0.02 ± 0.01 visits/chick/hour, Paired *t*-test: $t = 4.18$, d.f. = 6, $p = 0.005$) (see also Figure 1). This larger investment in the primary female's brood was not significantly different from the population of monogamous males (0.57 ± 0.06 visits/chick/hour, $t = 0.28$, d.f. = 28, $p = 0.78$). While brood size was slightly larger in the nests of primary compared to secondary females (3.34 ± 0.16 versus 3.01 ± 0.38 chicks respectively), this difference was not significant and is unlikely to explain why males did not invest in the clutches of secondary females (Paired *t*-test: $t = 0.69$, d.f.

= 6, p = 0.513). Of the nine secondary females from first clutches with chick feeding data, only two received any help from the male, and these had the two largest brood sizes of this group (brood size = 4). However even this level of help was almost an order of magnitude less than a primary female with an equivalent brood size (secondary versus primary: 0.36 ± 0.07 versus 2.82 ± 0.21. t = 4.7, d.f. = 11, $p < 0.001$)

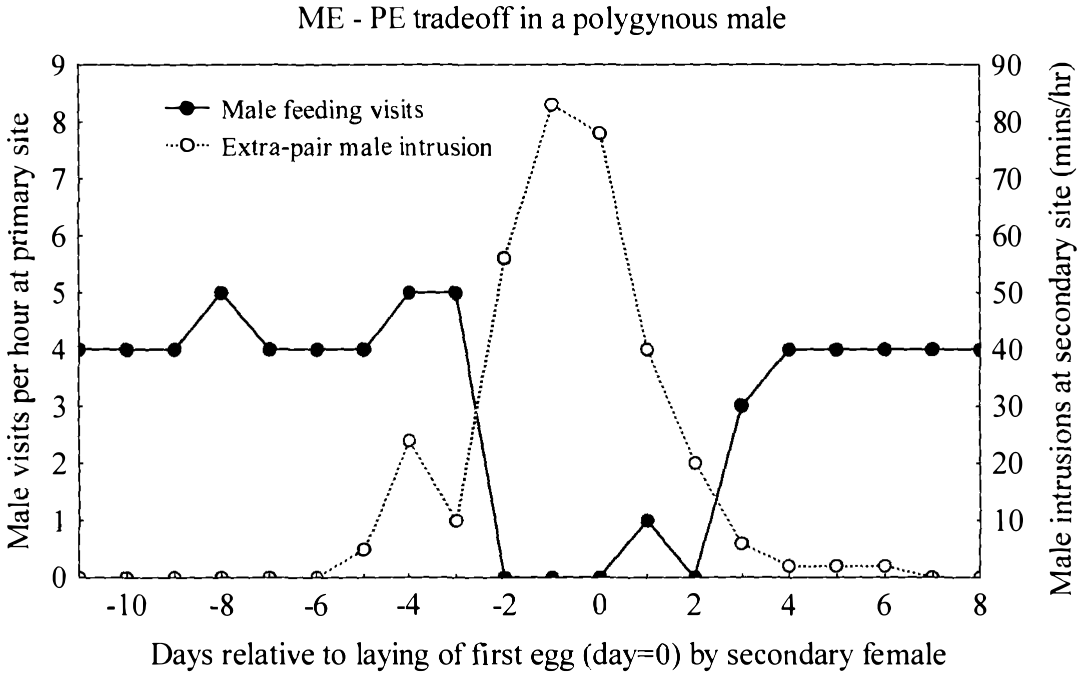

Figure 6. One male's trade-off between the parental effort of feeding chicks of his primary female (site 01/by/rm) and the mating effort of mate guarding his secondary female during her peak fertile period 88 m away (site 01/bm/gg). The male only reduces his chick-feeding rate between day –2 and +2 (first egg = day 0), which reflects not only the secondary female's peak fertile period but also an escalation in extra-pair male activity around the secondary female.

4. DISCUSSION

(a) Predictors of male provisioning in first clutch broods

By modelling male offspring provisioning using regression tree analysis, our study suggests that male stitchbirds use a hierarchical set of decision rules (a 'decision tree') when determining the level of paternal investment for each brood. The first distinction made by males is not 'how much to invest' but rather 'in which female's brood should I invest?' In dunnocks (*Prunella modularis*), males will feed a brood provided they have mated with that female during her egg-laying period (Davies et al. 1992). In stitchbirds, males gain mating access to many extra-pair females through force (Castro et al. 1996; M Low unpublished data), but in this population no extra-pair males were observed feeding chicks. Males preferentially feed the broods of their primary female, with the secondary female generally receiving no help in rearing his offspring. This has been described in other species, where polygynous males direct their nest-feeding effort solely to their primary female's nest (Dixon et al. 1994).

For monogamous males and the primary female of polygynous males, the number of chicks in the brood was the most important determinant of male provisioning. In these clutches, males make a second distinction regarding which females' broods should receive paternal help. Males did not contribute to the feeding of broods containing only one chick, however they usually contributed help towards rearing broods ranging from two to five chicks. In these larger clutches males then use a number of factors in deciding the level of investment the brood will receive, with some factors being more influential than others.

Brood size remained the most important predictor of male provisioning in these larger clutches, with males increasing their visitation rate relative to the size of the brood in a linear relationship, thus maintaining a similar level of investment per chick for brood sizes from two to five (Figure 4). Many studies have examined the relationship between brood size and paternal investment, with some finding an effect (Smith et al. 1988; Moreno et al. 1995) and others finding none (Hoi-Leitner et al. 1999; Komdeur et al. 2002). One way of controlling for the effect of brood size has been to convert male investment per brood into investment per chick. Because our results show a non-linear relationship between male provisioning per chick and brood sizes ranging from one to five, this suggests that converting investment into 'per chick' will not necessarily control for the confounding effect of brood size in all species. As has also been reported in a tropical fish species (*Abudefduf sexfasciatus*) (Manica 2002), males with a small brood disproportionately increase their chance of switching from PE to ME.

A male reducing investment in his offspring only makes sense if the benefits to the male outweigh the costs to his fitness of reduced offspring care. In our study we found evidence that males were trading PE for ME as they visited the nest less when the numbers of fertile females in the population was high. This pattern was similar to that found in the fairy martin (*Hirundo ariel*) (Magrath & Elgar 1997). However, data on sightings of males at extra-pair sites during these times are difficult to reconcile with a straightforward interpretation of the results in this way. This may be because males were not always going to other territories, and instead were congregating at communal sites where fertile females would come to feed. Male sightings at these feeding stations were not systematically recorded during this study, however it has been shown that high rates of forced copulation attempts occur in these areas (Low in press; see also Castro et al. 1996).

While certainty of paternity has been the only variable previously identified as being correlated with male feeding rates in stitchbirds (Ewen & Armstrong 2000), and appears to be the variable generating the most research interest (Davies et al. 1992; Dixon et al. 1994; Ewen & Armstrong 2000; Chuang-Dobbs et al. 2001; Sheldon 2002), in our study it was not selected as an explanatory variable in either of the 'pruned' regression trees. This was despite us using the same behavioural cues that Ewen & Armstrong (2000) used in their analysis. In the 'full' tree analyses where all divisions were examined, certainty of paternity was a poor predictor of male provisioning. While distance to supplementary food also featured in the pruned regression tree, its low level ranking and its generally poor predictive ability in the full tree analysis, suggests that if the relationship is real, its effect is relatively weak. Male age only featured in one tree division, also suggesting that any effect on male provisioning attributed to this variable is relatively weak.

From these analyses it appears that male stitchbirds follow an ordered series of rules of varying importance. Males first make the distinction between primary and secondary females, and then distinguish between broods of one chick and those containing two or more. They generally only invest in these larger broods of primary females and modify their visitation rate based primarily on brood size. These rates are then affected to a lesser degree by other variables that possibly include (in order of importance) additional mating opportunities in the general population, male age and access to supplementary food.

(b) Changing predictors for second clutch broods

In previous studies on male provisioning, the possibility that differences exist between the paternal investment of first and second clutches is generally not considered (but see Dixon et al. 1994). This is understandable for species with only a single clutch per year (e.g. *Ficedula hypoleuca* Moreno et al. 1995; *Sturnus vulgaris* Komdeur et al. 2002), however many studies only examine the first or an unspecified clutch in double-brooding species (Smith et al. 1988; Westneat 1988; Magrath & Elgar 1997), or pool the data from both first and second clutches for analysis (Ewen & Armstrong 2000). Because second clutches occur toward the end of the breeding season, seasonal influences may become more important (Davies et al. 1992), with some social factors becoming less so. While a number of studies have not found a relationship between male provisioning and seasonality or clutch number (Davies et al. 1992; Dixon et al. 1994; Chuang-Dobbs et al. 2001), these have only compared the absolute provisioning rates of males and have not assessed the possibility that the variables influencing male provisioning may vary as the season progresses. This has been found on a much shorter time-scale, with fairy martins trading PE for ME at times of the day when their copulation attempts are most likely to be successful (Magrath & Elgar 1997). Similarly, males may be more likely to trade-off PE for ME early in the season, but for later clutches this opportunity may be lacking, or PE may be traded for something else, such as body condition. Therefore overall feeding rates remain steady, but the impact of particular variables (such as those associated with mating effort) may vary and therefore be less useful as predictors at different stages of the breeding season. In the stitchbird, fledging rates from second clutches are significantly lower than from first clutches (Castro et al. 2003), as are additional mating opportunities. This indicates that the optimal ME / PE trade-off may change as the breeding season progresses.

Evidence for this possibility is circumstantial from this study. Overall male-feeding rates of second clutch nests did not significantly differ from first clutches, however the relative importance of explanatory variables changed between clutches. Brood size and female rank remained the most influential factors affecting male provisioning rates, with predictions derived from these variables changing relative to clutches earlier in the season. Also, while brood size, certainty of paternity and distance to supplementary food were used to make data divisions in both first and second clutch regression trees, additional mating opportunity was never used in the second clutch tree, while having an excellent record of predicting male provisioning in first clutches. The significant reduction in additional mating opportunities towards the end of the breeding season may explain why males were more likely to feed broods containing a single chick in second clutch nests. This suggests that towards the end of the breeding season, the payoff to males for trading PE for ME is lower than at the beginning. While these findings may be an artifact of the smaller second clutch sample size, it still highlights an important consideration. Not only are male decision rules hierarchical in that certain variables override consideration of other variables, and are complex in that they trade-off one variable against another, but that they are also dynamic, with the relative weights of each variable potentially changing as the breeding season progresses.

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"I mean, when you look at natural beauty you look at a beautiful pastoral scene. If you look closely, what you will see is pretty horrible. If you really could look closely, you would see violence and chaos and murder and cannibalism. But when you look at the broad picture, a Constable painting, it looks quite beautiful."

Woody Allen 1993

Thesis Discussion – Syn*thesis*

Chaos at the electronic scales

When collecting weight data at the main supplementary feeding station, sometimes up to ten birds would arrive in quick succession. Weighing individuals under these circumstances was something of a challenge.

Stitchbirds on Tiritiri Matangi Island behaved as predicted by a conditional strategy model where males primarily attracted nesting females to their breeding territories, and pursued extra-pair copulations (predominately forced) with fertile females as an additional insemination tactic. Evidence supporting this model comes from the fact that all males attempted to attract a female(s) to a defended area, with males only exclusively pursuing forced extra-pair copulations if they failed to attract a female to their territory. Males primarily invested mating effort in their own female at times when she was fertile (as expressed by within-pair copulations and mate guarding) and in fertile extra-pair females outside of this time (as expressed by the male's absence from his own territory and his forced copulation attempts at extra-pair sites).

Two alternative hypotheses to this interpretation of male behaviour, the CODE hypothesis (Gowaty & Buschhaus 1998) and the resistance-as-a-ploy hypothesis (Westneat et al. 1990), failed to account for the patterns of forced copulation seen in this species (Chapter 1). The CODE hypothesis makes a number of novel predictions regarding the outcomes and temporal patterns of forced copulation in species such as the stitchbird. However, my data did not support these predictions (Table 1), suggesting that the CODE hypothesis does not explain patterns of forced copulation in the stitchbird. The fact that a game theoretic examination of the CODE hypothesis shows that under certain conditions as imposed by Gowaty & Buschhaus (1998) the strategy is not evolutionarily stable, suggests that it might generally fail to predict patterns of forced copulation in other species (Chapter 2). The resistance-as-a-ploy hypothesis, predicts that females should gain additional matings from higher ranked males as a result of their resistance behaviour. This assumption was not met and thus the resistance-as-a-ploy hypothesis was also not supported by this study.

The possibility that communal supplementary food stations altered the birds' "natural" behaviour and biased the results of this study requires a comparative study between this population and a population without food. However, male-male and male-female chases have been reported in the "natural" Little Barrier Island population (Angehr 1984; J Crispy pers. comm.). Regardless of the presence of supplementary food, stitchbirds do leave their territories to feed at natural communal feeding areas, these being the clumped resources of flowering trees and shrubs often outside their preferred nesting areas (Castro et al. 1996; pers. obs.).

CODE hypothesis prediction	Observed stitchbird behaviour	Support for CODE?
Forced copulation is directed at both fertile and non-fertile females, particularly prior to the breeding season.	Forced copulation almost exclusively directed at fertile females.	No
Males direct forced copulation at unmated or unguarded females, often in view of other females	Males direct forced copulations at fertile females primarily within the female's own territory, usually with the resident male in attendance	No
Forced copulation correlates with modifications of female behaviour to favour social monogamy in ecological rather than evolutionary time	Females pair up in monogamous or polygynous consorts prior to the expression of forced copulation behaviour	No
Fertilisation success from forced copulation is absent	Previous work shows that forced copulation is well correlated with extra-pair paternity	No
The behaviour of females changes after a forced copulation attempt that prevents them from mating with preferred males	Females generally resist all extra-pair matings and preferentially mate with the resident male	No
Female's vulnerability to forced copulation varies so that females in more open habitat are more vulnerable	Females in preferred higher density habitat face more opportunistic forced copulation from neighbours	No
Female behaviour is altered by the removal of aggressive males from the area	Females will become more cryptic around their fertile period, with this possibly increasing with extra-pair males in the local area	Yes
When males are aggressive to only one or a few females in the population, the behaviour of many females changes	All females receive harassment primarily within their own territories	No
Extra-pair paternity is negatively correlated with forced copulation	Extra-pair paternity is positively correlated with forced copulation	No

Table 1. CODE hypothesis predictions against observations of stitchbird behaviour. The CODE hypothesis only predicts one observation, an observation that is also consistent with direct insemination theories of forced copulation.

In bird species such as the stitchbird, where males lack an intromittent organ (phallus), it has been suggested that insemination is only possible with female cooperation (Fitch & Shugart 1984; Weatherhead & McRae 1990; Gowaty & Buschhaus 1998 but see Birkhead et al. 1985). If this were the case, it would leave unexplained the huge male investment in forced copulation attempts, and the female investment in avoiding these attempts. To investigate the possible mechanisms by which males may successfully overcome female resistance in a species lacking a classic intromittent organ, I measured the seasonal changes in both the male's and female's cloacal protuberance (CP). Not only did they show a significant seasonal change in size, as is witnessed in other species (Wolfson 1952; Briskie & Montgomerie 1997), but also a significant change in the angular position of the male's CP (Chapter 3). This allows the male to achieve successful cloacal contact (and presumably sperm transfer) during face-to-face forced copulation. Previous studies of CP function have found little support for Wolfson's (1952) copulation efficiency hypothesis (Birkhead et al. 1993). However, copulation efficiency has traditionally been assessed in relation to cloacal contact time and the potential advantage of a more forward pointing CP has not been adequately considered. The fact that bellbirds (*Anthornis melanura)* also show significant seasonal changes in their CP position indicates that a wider survey of avian species with varying sizes of breeding CPs is now required. Findings arising from further study into other species' CP angles may aid theory development associated with fields such as sperm competition, forced copulation, and the evolutionary loss of the avian intromittent organ.

Because most forced copulation attempts are not successful in stitchbirds or other species (*e.g.* Birkhead et al. 1985; Chapter 1) in order to maximise forced copulation success males need to specifically target females that offer the highest likelihood of fertilisation success. The mechanism by which male birds may assess female fertility has been suggested to come from cues directly from the female (flight behaviour, nest building, egg-laying, or female solicitation) or indirectly from the resident male (within pair copulation, mate guarding intensity, or song rate or quality) (Birkhead et al. 1987; Komdeur et al. 1999). However, it has not generally been appreciated that correlational studies looking at relationships between female fertility and 'indirect' fertility cues are confounded with the direct cue the resident male must be using. This has lead to hypotheses aiming to explain why the resident male broadcasts fertility information (Møller 1991) when in fact his behavioural changes may simply be a result of increasing extra-pair activity due to a single 'direct' cue available to all males in the population. Because of this problem I concentrated on comparing 'direct' fertility cues with extra-pair male activity (Chapter 4). I demonstrated that female weight is strongly correlated with both female fertility and observed patterns of extra-pair male behaviour and thus is the most likely candidate for fertility assessment in this species. In order to elucidate the exact 'cue' associated with this (*e.g.* changes in female flight performance) an experimental approach similar to Jones (1986) is required. The need for experimental testing also applies to evaluating my hypothesis that females may be 'hiding' their fertility by burying eggs within the lining of their nests (Chapter 4).

Male stitchbirds show intense mate guarding, as was predicted by their life history traits (Komdeur 2001). I found that this mate guarding is condition dependent, with the male actively following the female when her presence is known, and changing to a site defence centred on her last known location or nest box when she is absent during her fertile period (Chapter 5). This explains the results of Ewen (1998), who studied the Tiritiri Matangi stitchbird population at a time when it was highly male biased population and had poor female attendance at the nest site, and concluded that male stitchbirds guarded the nest site rather than the female.

The costs associated with forced copulation have often focussed on the female (McKinney et al. 1983; Smuts & Smuts 1993; Olsson 1995). However, in this study I was able to demonstrate that the resident male also suffers a significant cost. As was found in Komdeur (2001), males appeared to trade off foraging for mate guarding and in the pre-fertile period were 2.5% lighter than when they had relinquished their mate guarding duties. By separating males into two groups depending on the level of extra-pair male intrusions their territory received, I show that extra-pair male intruders impose an additional cost as measured by an average 5% loss of body weight by the resident male (Chapter 5). Future theoretical and empirical treatment of reproductive costs associated with forced copulation need to consider the direct impact of male forced copulation behaviours on other males, rather than only focussing on the female.

One cost of forced copulation to females is that of reduced resident male provisioning of offspring because of a perceived or real loss of paternity. Of all the potential factors affecting male provisioning, certainty of paternity has been the variable generating the most research interest (Davies et al. 1992; Dixon et al. 1994; Chuang-Dobbs et al. 2001; Sheldon 2002). In the stitchbird however, despite previous work showing a significant positive correlation between certainty of paternity and male provisioning (Ewen & Armstrong 2000), I show that it has little or no effect when compared to female rank, brood size and additional mating opportunities. Males follow a set of rules as predicted by a hierarchical model, with them making 'if-then' decisions based on female rank and brood size, with offspring provisioning rates being further modified relative to other factors such as additional mating opportunities (Chapter 6). The possibility, as suggested by this study, that the impact of particular explanatory variables is dynamic relative to the time of season, means that in future studies of parental investment, second clutches need to be considered independently of first clutches with the relative impact of time of season on explanatory variables compared.

While investigations into the reason for the ubiquity of forced copulation has generally focussed on evolutionary (ultimate) explanations in non-humans, sociological interpretations have focussed on proximate motivations in humans. While the two perspectives (proximate and ultimate) are complementary and together generally provide a broader understanding of the causes of biological phenomena (Alcock 2001), in the case of forced copulation, an unnecessary clash of these two perspectives has been the cause of most of the disagreements between sociologists and sociobiologists. The point of contention has been the 'uniqueness' of human forced copulation, which is usually referred to as rape. Following a common scientific practice, scientists began applying the label "rape" to non-human forced copulation in the 1970s but due to criticism this practice ceased in the early 1980s. This criticism of non-human rape was multifaceted, and focussed on the different definitions of rape / forced copulation in humans as compared to non-humans. Unfortunately, rather than arguing that human rape is somehow special and immune from biological interpretations, sociologists and sociobiologists were arguing at different levels of interpretation. These different levels (proximate and ultimate) stress different factors as important in their definitions and hypotheses and thus cannot be meaningfully compared. Thus much of the criticism of applying an evolutionary approach to understanding rape / forced copulation relied on reiterating sociological (proximate) assumptions regarding the nature of rape, rather than comparing evolutionary (ultimate) hypotheses to available data (Appendices 1 & 2).

The stitchbirds on Tiritiri Matangi Island are an excellent model population for evaluating factors important in understanding patterns of forced copulation despite the experimental limitations imposed by working with an endangered species. The birds are easily accessible, easily observed and monitored, individually identifiable, with population records extending back to 1995. Behaviourally, face-to-face forced copulation in the stitchbird is obvious and easily distinguishable from other behaviours, with females alerting observers to their occurrence by their specific resistance behaviours. With the ongoing expansion of the population, resulting in birds being forced into lower quality habitats and higher population densities, and with this producing a larger male bias in the operational sex ratio, future monitoring of this population provides a rare opportunity for studying the influence of these changing factors relative to the expression of forced copulation.

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"[I]f scientific observations reveal rape in nature, must we not face up to this reality?"

Anne Fausto-Sterling (1992) page 162.

APPENDIX 1

Can non-human animals rape?

Forced copulation (rape) in the stitchbird

Forced copulation in this species occurs in a face-to-face position, with the female lying on her back and the male lying face down on top of her. In this photo the male is using his beak, claws, wings and tail to prevent the female from moving under him.

Appendix reference:
Low, M. Can non-human animals rape? Formatted for *Animal Behaviour*.

Abstract

The term “rape” has not generally been applied to non-human animals since the early 1980s due to extensive criticism of the term at that time. Most of this criticism focussed on the inappropriateness of using an emotionally laden term within an objective scientific discipline, and/or the negative implications of hypothesising that rape is part of an adaptive mating strategy. In this paper I suggest that these criticisms resulted in inappropriate constraints on the definition of rape, and that the defining elements of rape in humans and forced copulation in non-humans are the same. My conclusion is not that we should change our current terminology, but rather we need to be aware of the reasons for why “rape” is not used to refer to non-human behaviour. This will allow us to better evaluate theories on rape and sexual coercion that take advantage of a cross-species comparative approach.

Introduction

In 1975, the social scientist Susan Brownmiller wrote that:

> No zoologist, as far as I know, has ever observed that animals rape in their natural habitat...Zoologists for the most part have been reticent on the subject of rape. It has not been, for them, an important scientific question. [page 3]

However, zoologists had begun studying rape in a range of animal species at that time (Parker 1974; Barash 1977; Abele & Gilchrist 1977; McKinney et al. 1978; Mineau & Cooke 1979). This research interest was associated with the development of 'sociobiology' (Wilson 1975), a branch of biology devoted to understanding the evolution of social behaviour in a wide range of species including humans. Sociobiological research on rape did not attract significant criticism until Thornhill (1980) published his study on rape in scorpionflies (*Panorpa* sp.) and formulated a "general rape hypothesis" that included reference to humans. Zoologists studying rape in animals were consequently accused of being anthropomorphic, sensationalistic, having dubious ulterior motives and questionable politics, and being against the goals of science because of their investigations and analyses (Estep & Bruce 1981; Gowaty 1982; 1984; Hilton 1982; see Segerstråle 2000 for review). The term "rape" was quickly dropped in the non-human literature, and replaced by "forced copulation" (McKinney et al. 1983; Afton 1985).

It is possible that calling a non-human behaviour rape may colour our perception of that behaviour (Gowaty 1982; Hilton 1982). However, by denying human rape and non-human forced copulation are equivalent (if this is the case), we also risk colouring our perception of the two behavioural groups and may fail to take advantage of what a comparative approach may bring in uncovering causal factors in rape (Thornhill & Palmer 2000). While "forced copulation" is an adequate term and any attempt to now replace it with "rape" is probably unrealistic and unwarranted, it is still worth examining whether rape is unique to humans by definition (Palmer 1989). The reason for this is that past criticisms failed to disentangle two separate questions, 1) Is rape a behaviour unique to humans, and 2) Is it appropriate to use this term in non-humans where the behaviour occurs? Much criticism has focussed on the second question, and where the first question was addressed, critics have not separated definitions of rape from hypotheses about why rape occurs (see Gowaty 1982, Hilton 1982, Fausto-Sterling 1992). Thus two decades on, it is still not obvious whether it is scientifically sound to think about rape in non-humans, even if it is not acceptable (rightly or wrongly) to refer to it as such in the biological literature.

The aim of this paper is to elaborate and compare the generally accepted definition of rape in humans with that of forced copulation in non-humans. I also examine several influential criticisms regarding whether or not it is scientifically sound to refer to such behaviours in non-humans as rape. This exercise is important, for if the word "rape" as a label for particular non-human behaviours is deemed to be unacceptable, it is necessary to know exactly why this is the case. An erroneous belief in this regard may lead to resistance in comparing behaviours across species, possibly hampering theory development and resulting in premature dismissal of rape theories that warrant consideration.

Defining rape in humans

Rape is a commonly used term regarding particular human behaviours, and it is likely that most people understand its general meaning. Sociobiologists have been criticised for applying a definition of rape to non-humans that is inconsistent with how it is commonly understood (Gowaty 1982), without the two definitions being explicitly compared. Legal and textbook definitions of rape have three general features in common. Firstly, rape is a sexual encounter. Secondly, the rapist uses force or a threat of force to achieve sexual access. Finally, the victim actively resists unless her will has been overcome chemically (*e.g.* the drug 'rhohypnol') or resistance is likely to result in serious physical harm (Brownmiller 1975; Fausto-Sterling 1992; Thornhill & Palmer 2000). Despite the relative conformity of these definitions, there is a range of opinion in society as to what constitutes rape, and this is constantly evolving. At one extreme, only forced vaginal penetration by the penis with evidence of ejaculation counts as rape, and at the other, unwanted dirty jokes at work or touching constitute rape if a woman indicates by word or by deed that such actions impinge on her personal space (Bourque 1989).

Despite this diversity of opinion regarding what constitutes rape, its key features were identified in the only large-scale study where variables within descriptive scenarios were altered to assess what information influences a person's decision in judging whether something should be regarded as rape (Bourque 1989). Two hundred and fifty-one people were interviewed regarding 8000 scenarios in which variables relating to victim characteristics, offender characteristics, relationship between the victim and offender and the circumstances of the sexual encounter were altered. From an analysis of these data, it was found that in combination with a sexual context, people generally rely on only two pieces of information in determining whether rape had occurred; physical force from the assailant, and physical resistance from the victim. Seventy-six percent of people used the variables of force and resistance either alone or in combination to determine if rape had occurred. Another twelve percent decided that most, if not all, the examples were rape and did not necessarily require obvious force or resistance (although they were more certain if those factors were present), and the remaining twelve percent used force and resistance in judging if a rape occurred in combination with other information such as the marital status of the victim, the assailant's race and the location of the assault. Thus, for the majority of people to determine if an act constitutes rape, the same three pieces of information as identified from textbook and legal definitions are used; a forced sexual assault that is resisted by the victim.

Describing rape and forced copulation in animals

Parker (1974) discusses the necessary considerations for an act to be judged as rape in the fruit fly (*Drosophila melanogaster*). Here the behaviour in question is not described, but the notion of active female rejection or resistance is deemed crucial in differentiating rape from female 'coyness'. In a study of rape in mallards (*Anas platyrhynchos*), Barash (1977) saw forced copulation and rape as synonyms and specifically introduced the notion of force (on the part of the male) and "obvious resistance" (on the part of the female) in defining rape. Importantly, Barash (1977) also distinguished the behaviour from 'normal' copulations, something that can help determine the underlying motivations of both assailant and victim.

During this time, rape was also defined in a much broader sense by Burger (1976) in a study on laughing gulls (*Larus atricilla*). Here rape was defined as "when a non-mate mounts and tries to copulate with a female." In this study, no differentiation was made between forced and non-forced extra-pair copulations. The broad definition and the lack of description of the behavioural sequence in the paper make it difficult to say whether the behaviour has any similarity to rape as it is commonly understood. Birkhead (1979) used a similar definition in the magpie (*Pica pica*) when he stated that, "It is interesting that the fertile female did not resist the 'raping' male, and that the raping male's partner did not interfere." In both cases, rape appears to have been used as a seemingly inappropriate euphemism for extra-pair copulation.

This broader definition of rape was soon abandoned in favour of usage incorporating notions of force and resistance. Since 1980, rape or forced copulation has been described for many species including insects (Arnqvist 1989), arachnids (Schneider & Lubin 1998), crustaceans (Liu & Li 2000), fish (Farr 1980), amphibians (Halliday 1983), reptiles (Olsson 1995), passerines (Westneat 1987), waterfowl (Sorenson 1994), and various mammal species including dogs (Pal et al. 1999), sheep (Lovari & Ale 2001), dolphins (Connor et al. 1992) and primates (Mitani 1985). The common elements of the behaviours described in these studies are identical to those identified for defining rape in humans. The male uses force to achieve sexual contact with the female while she is overtly resisting the encounter. We also consider that rape has occurred in humans even when behavioural resistance is not obvious due to the threat of physical harm leading to passive consent of the victim (Thornhill & Palmer 2000). This form of sexual coercion has also been described in mammals (Smut & Smuts 1993) and its evolutionary stability modelled for non-human animals (Clutton-Brock & Parker 1995).

Where there's a way, there's a will

Fausto-Sterling (1992) objects to "rape" being used as a label for any non-human behaviour and justifies this position by attempting to highlight a significant bridge between humans and non-humans in how the behaviour is defined. Fausto-Sterling argues that

> [Rape is]...the crime of having sexual intercourse *with a woman* against her will. The definition contains two parts: rape is something done to a woman (although in common use we also recognize male-male rape), and it involves her conscious state of mind. For it to be called rape it must be against her will. When scientists apply the word to fruit flies, bedbugs, ducks, or monkeys, the common definition expands to include all living things and the idea of will drops out. Yet the "instinct" of a female bedbug to avoid forced intercourse certainly holds nothing in common with the set of emotions experienced by a woman who has been raped [page 160].

Here Fausto-Sterling uses a general dictionary definition of rape to exclude anything 'non-woman'. This fails to acknowledge how word usage evolves and how terminology comes to be legitimately used, to varying degrees, outside of its original context (e.g. 'male-male rape' as mentioned in the passage above). Even 'rape' in its modern usage evolved from its original meaning of, "The act of taking anything by force" (Oxford English Dictionary 1989). Fausto-Sterling insists that for a claim of rape to be legitimate, there must exist a conscious decision on the part of the victim to resist the rape. However this criterion is not applied when judging cases of 'date rape' in people, where a drug may have been used to remove any inhibitions or conscious decision-making processes from a woman.

Supposing we decide that it is necessary to incorporate a notion of 'will' into our definition, does this now exclude most (all?) animals from being potential perpetrators or victims of rape simply because they are not consciously aware of the reason for their behaviour? Fausto-Sterling's claim that the idea of will "drops out" when we extend the rape umbrella to cover other living things is simply false. Despite the likelihood that the female bedbug (or duck or monkey) does not consciously deliberate or understand the reason behind its actions, this does not mean that no reason for the behaviour exists. The rationale or 'will' of an animal to do or avoid something does not have to be located within the animal's immediate cognitive state, but rather it can reside within its genotype. This is what Dennett (1983) calls a free-floating rationale. For a ground nesting bird adopting a distraction display, the rationale (or will) to deceive the predator does not have to be consciously decided, but may simply be a hard-wired instinct with the bird not 'knowing' what it is doing (Dennett 1983). Whether the bird produces a rational choice through conscious deliberation or blind genetic programming is irrelevant. Behaviour mediated by conscious choice in humans can be similar to evolved behaviour patterns in non-humans mediated through other means (Gowaty 1992). The logic and outcome of the bird's display is still deception, despite the underlying processes differing from how humans may deceive each other.

Fausto-Sterling's final attempt to dismiss the notion of rape in non-humans is to compare the instinct of a bedbug to the emotional trauma of a woman. She is careful not to make the comparison between an orang-utan and a woman, as the emotional divide may not appear so clear-cut. To argue that the instinct of a bedbug needs to be as sophisticated as the emotional trauma a woman suffers before it can be called rape, is no different from claiming that animals do not 'play' because they simply fail to enjoy themselves as much as humans do. While most women suffer terribly from rape, this is a *consequence* of the act and thus we should not insist on their suffering before we consider that they were raped. To divide behaviours across the animal kingdom (or between humans and other animals) based solely on whether you consciously 'decide' to do something, or you are driven to it by 'instinct', limits useful comparisons across species for nothing more than to satisfy a pre-Darwinian, anthropocentric view of the biosphere.

Drawing the line

One obvious strategy in dividing those organisms that can rape from those that cannot is to draw a line between humans and non-humans. Currently this is the 'official' position, whether to avoid anthropomorphism (Hilton 1982), or because rape can only occur in the presence of human cognitive and emotional abilities (Fausto-Sterling 1992). For scientists whose only justification for not using the term is perceived anthropomorphism, their position still fails to define exactly to what they are referring and whether non-humans are capable of behaving in such a way, under a different label. It is difficult to evaluate how valid this position is, as it is often unclear in these cases whether human rape is being separated from non-human forced copulation based on some measurable quality, or simply to avoid an argument about the use of language. The division of animals from humans based on the belief that forced copulation requires a human level of cognition and emotion for it to become rape (Fausto-Sterling 1992), implies that any human lacking these necessary requirements, such as people in comas, mentally impaired individuals and babies, cannot be raped (Pinker 2002). This suggests that a simple division based on specific human mental attributes is suspect, if its straightforward application would deny legal rights to certain groups of people.

As with many conceptual categories, there exists a grey area where it is difficult to decide whether things do or do not qualify for membership. Thus it is not surprising that because varying levels of sexual coercion occur within mating systems, it is difficult to decide which behaviours should be called rape. Dennett (1995) explains that we should expect evolution to produce a series of:

> [E]lements that manifestly lack the properties [of in our example, rape] to elements that manifestly have them. There will have to be isthmuses of dubious or controversial or just plain unclassifiable intermediates...Darwin has taught us not to look for essences, for dividing lines between *genuine* function or genuine intentionality and mere *on-its-way-to-being* function or intentionality.

This means that we should be wary of approaches that advocate finding the 'essential properties' of rape. We should not expect there to be a single correct way to divide behaviours, with everything on one side definitely having the property and everything on the other obviously lacking it. Because there is no 'rape essence' that can be distilled and measured, in our quest to define rape we need to change our thinking from one of finding the boundary to one of choosing the boundary (Pinker 2002).

To better understand why we should expect any boundary to have a degree of arbitrariness, it is useful to examine specific borderline cases and to ask why one behaviour should be labelled rape while another is not (see below). These examples illustrate two general points that need to be remembered when discussing and defining rape. Firstly, various proximate and ultimate motivations may underlie the rationale behind the behavioural manifestation of rape in different species. Secondly, a particular reason for why animals might rape (*e.g.* bypassing female mate choice), may be achieved in a number of ways, some of which will not be easily recognisable from a male force - female resistance model. This means that behaviourally similar but functionally divergent behaviours could conceivably be labelled as rape, while other functionally similar behaviours may require a different behavioural label.

(i) Lack of consent

While lack of female consent is commonly associated with rape, it does not necessarily mean active resistance. In a number of species, males achieve sexual access by timing their copulatory attempts at times when females cannot resist. In the stoat (*Mustela erminea*) males enter the nest soon after the kits are born and impregnate the young females, before they have been weaned (King 1990). In the fruit fly males will seek out virginal females emerging from fruit and copulate with them while they are immobile and waiting for their exoskeletons to harden (Markow 2000). In a number of spider species, males will mate with females during moult when their exoskeletons are soft and they cannot resist (Schneider & Lubin 1998 and references therein). In cases such as these where the male does not need to use force because the female is unable to resist, should it be described as rape?

(ii) Motivation

In some species it has been suggested that female struggle and behavioural resistance may be a tactic to improve the genetic quality of offspring by physically 'testing' the male, or inciting male-male competition (Cox & Le Boeuf 1977). Under these conditions it is thought inappropriate that the behaviour should be labelled rape, as the female is receiving some benefit (Estep & Bruce 1981). If ultimate motivations have precedence over proximate ones as this position suggests, can we now claim that rape would now cease to exist in human society if it could be conclusively shown that women "benefited" from rape, because the genetic fitness of their offspring was generally higher than that from consensual sex?

(iii) Location of fertilisation

In livebearing fish species such as the guppy (*Poecilia reticulata*), males have a highly developed anal fin that acts as a phallus (gonopodium) for depositing semen directly into the reproductive tract of the female. Rape in these species is characterised by the male sneaking up behind the female, then quickly forcing the gonopodium into the genital pore of the female and depositing semen. The female actively avoids males attempting this tactic (Farr 1980). The externally fertilised European wrasse (*Symphodus* sp.) also shows elements of male force (satellite males will rush in and dump sperm in the resident male's territory) and female resistance (females will avoid sites with satellite males around it) (van den Berghe et al. 1989). If we accept that fish with a gonopodium can rape, should this be extended to fish species where external fertilisation occurs?

(iv) Crossing the species boundary

Sub-adult male orang-utans engage in aggressive and forceful sexual acts with females that bear a close resemblance to human rape (Mitani 1985). However, the recipients of this behaviour are not only female orang-utans. Male orang-utans will grab human females and drag them up into the trees to have sex with them despite the women actively resisting (Jahme 2000). People working with orang-utans view this behaviour as rape, with women suffering emotional trauma as a result of these encounters (Jahme 2000). If non-humans cannot rape, do we find ourselves in the bizarre situation of the women being raped by the orang-utan, but the orang-utan not raping the women?

Definitions and hypotheses

When discussions have turned to comparing human and non-human rape definitions, a tendency to adopt narrow functional definitions has been responsible for a large amount of the disagreement between sociobiologists and their critics regarding whether animals can rape (Thornhill 1980, Fausto-Sterling 1992). Rape has generally been defined in one of two ways. The first is a description of the act in terms of the animal's overt behaviour, such as; "Rape may be defined as forced copulation... [with] the female showing obvious resistance" (Barash 1977). The second type of description is functionally oriented and linked to hypotheses about the nature of rape, such as; "...male fitness must be enhanced by rape" (Thornhill 1980) and "Rape is a conscious form of intimidation by which *all men* keep *all women* in a state of fear" (Brownmiller 1975). While both types of descriptions have functional elements (Hinde 1970), as the behavioural sequences of force and resistance may vary, only the second type of description attributes a functional motive to the action. These two ways of describing rape, either descriptively or functionally, are sometimes confused as being rival definitions. However, the behaviourally descriptive perspective broadly defines the behaviour while at the same time encompasses the functional description, which is a hypothesis to explain why the behaviour occurs in particular cases.

The general criticism of the sociobiological use of rape was partly based on a confusion of these two levels of rape description. Thornhill (1980) presented a "general rape hypothesis" based on his work with scorpionflies, and was accused of having redefined rape to require an enhancement in the fitness of the rapist where in common usage no such requirement is made (Estep & Bruce 1981, Gowaty 1982, Fausto-Sterling 1992). Sociobiologists were seen as adding a level of obfuscation to discussions on the nature of rape as the sociobiological definition was now to be added to social, psychological, legal and ideological meanings (Gowaty 1982). It is not generally appreciated that the criticisms and concerns that pushed rape out of common biological usage were predominantly based on a misreading of Thornhill's (1980) text. Thornhill introduces his paper with, "The adaptive significance of heterosexual rape is difficult to demonstrate because (1) female coyness is difficult to distinguish from apparent rape, and (2) male fitness must be enhanced by rape" (Thornhill 1980). The paper provides a behavioural description of rape in the scorpionfly and a hypothesis regarding the adaptive function of rape in this species and a generalisation to other species. Thornhill's hypothesis that rape is an adaptive male reproductive tactic should not be confused with the behavioural definition of rape he provided for the scorpionfly. Unfortunately Thornhill was not careful enough in keeping these points separate in his discussion on rape in other species and so the critics mistook a new sociobiological hypothesis for the existence of rape to be that of a new definition. Thornhill's (1980) general rape hypothesis is exactly what it claims to be. The possibility that scorpionflies (and other species) can rape was lost to the side issue of whether an adaptive hypothesis for rape was correct.

When defining rape it is important not to create a circular justification by defining it in reference to a hypothesis and then using the predictions of this hypothesis to dictate the necessary elements of the definition. A behavioural description of rape incorporating the necessary elements of force and resistance would appear to be the most appropriate level at which to define rape. This means that sociobiologists need to make it clear that in discussions of function they are defining a subset of the group of all rapists and that adaptive hypotheses are not generalised to be the definition of rape. This applies equally to their critics, who want adaptive elements of the definition removed but want to include human cognitive states and motivations which are things often needed to justify their own interpretations of why rape occurs in human society (Brownmiller 1975; Fausto-Sterling 1992). Hypotheses regarding the cause of the phenomenon need to be kept separate from the description of the act itself.

Can the human definition of rape be applied to animals?

If we accept that male force and female resistance in a sexual context are enough to judge that an act constitutes rape, it is difficult to argue that non-humans, in principle, cannot rape. While under some circumstances there may be disagreement as to whether a particular sexual act involves male force and female resistance (Estep & Bruce 1981), in many cases it is obvious. Even when females do not overtly resist through obvious behavioural means, passive non-consent can be identified by observable behaviour and its context (see Palmer 1989 for examples). When a sub-adult male orang-utan chases and catches a female, overpowers her despite her cries, slaps her and then holds her struggling body down so he can copulate with her (Mitani 1985), it is unclear as to why this should not be seen as rape. The motivations of the assailant and the victim in encounters such as this become clearer when co-operative matings are also described to allow comparison. Because behavioural manifestations of male force and female resistance may be species specific, it is essential that these two factors be individually assessed relative to that species.

A working definition such as; 'the use of force by a male to achieve sexual contact with a female who, to the best of her ability, is showing species typical resistance behaviours that reduce the likelihood of successful copulation' incorporates all the necessary elements previously defined for both rape in humans and forced copulation in non-humans. Any definition of rape or forced copulation such as this should be flexible and could be expanded to incorporate circumstances where males use threats and females do not openly resist sexual encounters because of a fear of retribution (Palmer 1989; Smuts & Smuts 1993), or when same sex rape occurs (Abele & Gilchrist 1977). Other behaviours previously included as examples of rape, such as sneaky external fertilisation in fish (Thornhill 1980) are questionable, in the same way that it is questionable calling a substitution of semen in a human sperm bank, rape. The fact that both rape and forced copulation can be similarly defined suggests that there is no *a priori* reason for generally asserting that rape in humans differs from forced copulation in non-humans in any fundamental way other than the expected species typical differences. Acknowledging this more openly may lead to a greater consideration of currently controversial theories regarding causal factors of human rape (Thornhill & Palmer 2000).

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"Great is the power of steady misrepresentation"

Charles Darwin as quoted by Rose and Rose (2000).

APPENDIX 2

Ten misunderstandings of forced copulation / rape in non-human animals

Female stitchbird after being subjected to a forced copulation

Female M/RO is on her back and has been forced head first into the leaf litter during a face-to-face forced copulation. Her tail, abdomen and both legs are visible.

Appendix reference:

Low, M. Ten misunderstandings of forced copulation / rape in non-human animals. Formatted for *Evolution and Human Behaviour*.

Abstract

The idea that non-humans engage in behaviour that can be referred to as "rape" has attracted significant criticism. This has had the effect of forcing a change in terminology (animals now engage in "forced copulation") as well as questioning the validity that rape is part of a male's reproductive strategy. I propose that much of this criticism is based on a number of misunderstandings and in this paper I present and discuss ten of these; 1) rape is an anthropomorphic term, 2) insemination from rape should be equal to that from consensual sex, 3) sons of rapists should be more likely to rape, 4) male-centred perspectives distort the non-human literature, 5) adaptive strategies always yield adaptive behaviour, 6) birds lacking intromittent organs cannot rape, 7) females are the ultimate arbiters of sperm competition, 8) testosterone 'causes' rape, 9) rape is pathological, and 10) by discussing biological factors that influence rape, this will lead to the justification of human behaviour. The fact that the majority of misunderstandings either limit human and non-human comparisons or downplay the idea that rape is often about sex and reproduction, suggests ideology from the social sciences may be behind resistance to scientific investigations of this topic. Many of these misunderstandings have gone unnoticed or have been ignored, with one consequence being that this has possibly contributed to the delayed scientific questioning of traditional rape theories.

Introduction

The idea that rape in humans may be examined using an evolutionarily informed theory of human behaviour is receiving increased attention and analysis (reviewed in Thornhill & Palmer 2000). While this field is controversial and has generated significant criticism, much of this criticism is based on a number of misunderstandings (Palmer 1989; Jones 1999; Thornhill & Palmer 2000; Pinker 2002). The fact that similar objections exist towards rape research in non-humans has attracted less attention, despite many of these criticisms being based on similar misunderstandings and having had a significant impact on the field.

The most obvious influence of works critical of the non-human field of rape research occurred in the early 1980's when it was argued that the term "rape" should be abandoned and replaced with an operational descriptive term (Estep & Bruce 1981; Gowaty 1982; Hilton 1982). Because of these critiques, "rape" was replaced in the literature almost overnight by euphemisms such as forced copulation, resisted mating, forced mating, forced insemination, coercive mating, forced intercourse, aggressive mating and sexual coercion (Figure 1). The arguments used to secure this change were generally uncritically accepted (McKinney & Stolen 1982; Power 1984; for an exception see Stuart 1983) and were based on numerous misunderstandings or a reliance on controversial analyses (see below). It has since been suggested that this change in terminology has caused unnecessary confusion and limited cross-species comparative analyses, a potentially important source of information about the causes of human rape (Thornhill & Palmer 2000). Despite this change in terminology, criticism of the field of non-human rape research has continued, with much of this being directed at the idea that rape is primarily about sex and reproduction (Fausto-Sterling 1992; Gowaty & Buschhaus 1998).

In this paper I discuss ten intuitively appealing misunderstandings that have been the core of criticism of rape and forced copulation in non-humans over the past 25 years. While some of these misunderstandings are outright errors, a number are controversial arguments that require clarification or are an overzealous application of a currently established theory. The general lack of an adequate definition of rape in non-humans underlies a number of these misunderstandings and has been examined in detail elsewhere (see Appendix 1). Despite my discussing a number of the misunderstandings that lead to the word "rape" being removed from the non-human literature, I am not advocating a return to using this terminology. My reasoning is that even if no logical or scientific grounds exist for not using a term like "rape", the term is perceived as being so encumbered with emotional and semantic baggage that it prevents some people from seeing the term for how its application is intended. Thus despite my using the term "rape" to refer to both human rape and non-human "forced copulation" in this article, I am not advocating that this approach necessarily be adopted.

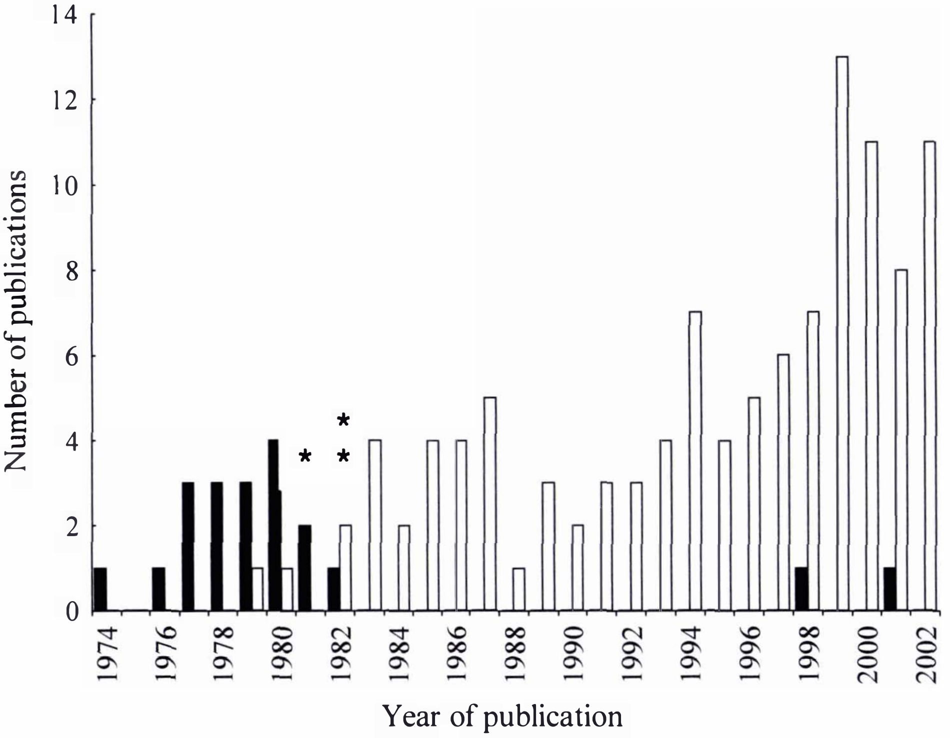

Figure 1. The number of journal publications in the years between 1974 and 2002 that use either "rape" (black bars) or one of its various euphemisms *e.g.* "forced copulation" – see text for full list, (white bars) as a label for non-human sexually coercive behaviour. The three asterisks represent when Estep & Bruce (1981), Gowaty (1982) and Hilton (1982) published their critiques on the use of 'rape' terminology. Papers were sourced through the ISI Web of Science and by working backwards from 1980 using reference lists.

Misunderstanding # 1: "Rape" is anthropomorphic

It is commonly acknowledged that anthropomorphism is to be avoided when discussing animal behaviour. When Hilton (1982) states that, "…it is important that such titles [rape] fairly reflect the behaviors involved with no hint of anthropomorphism", he is clearly implying that anthropomorphism is some form of mistake. While critics of 'rape' terminology in non-humans commonly accuse its proponents of anthropomorphism (Estep & Bruce 1981, Gowaty 1982, Tang-Martinez 1997), it is never made clear exactly what is meant by this and what type of mistake the critics believe is being committed. Yet unless the meaning and implications of anthropomorphism are made explicit, it is difficult to know whether the criticism is fair when applied to rape. Fisher (1991) has shown that the common charge of anthropomorphism in the field of animal behaviour is neither well defined nor clearly fallacious, and Stuart (1983) defends the use of so-called anthropomorphic terminology, because it can be, "quite appropriate, very descriptive and highly informative."

The Oxford English dictionary (1989) defines anthropomorphism as the "ascription of a human attribute or personality to anything impersonal or irrational". This notion of a human attribute being applied to an animal can be taken to mean one of two things. Firstly, labelling the application of any human characteristic to other animals as being anthropomorphic. This would include all things originally derived from a human perspective; from anatomy, physiology, behaviour and psychology. So to describe an animal as being 'thirsty', 'sleeping', 'playing', 'seeing', feeling 'pain' or even describing light sensitive organs in insects, as their 'eyes' would mean one was being anthropomorphic. This is obviously not what is meant when people level the charge of anthropomorphism, as it would make the claim ubiquitous. The second interpretation of anthropomorphism is that it only applies when a uniquely human characteristic is ascribed to another species. It is likely that humans have many unique features that set them apart from other animals, but it is not necessarily obvious what these are and which animals may share features with humans (for example, some people think that elephants can show grief, but it is unlikely that anyone thinks a spider can). Fisher (1991) argues that the rhetorical effect of claiming someone has committed anthropomorphism is one of a blatant logical mistake. This logical mistake is a form of category mistake, meaning that an entity of one type has been mistakenly treated as the entity of another. Other species are obviously not human, but it does not follow that comparing other species to humans is making a category mistake. All animals share many anatomical, physiological and behavioural attributes and it becomes an empirical question as to which of these are similar enough to those found in humans to be given a human label. Thus before a claim of anthropomorphism can be made, it must be shown that the character or behaviour in question is unique to humans and does not occur in animals in any form. It cannot be determined *a priori* that rape is anthropomorphic until this has been specifically demonstrated. This would require an exploration of the definition of rape as it is applied to humans and animals, with the critical factors needed in the definition compared between the two. Because of this, it becomes a scientific question as to whether particular behaviours in animals qualify as satisfying the requirements of a descriptive definition of rape, and any claims of anthropomorphism become irrelevant.

Misunderstanding # 2: If rape is adaptive, insemination rates should equal those for consensual sex

In 1998, Gowaty and Buschhaus developed their "CODE hypothesis" to explain the evolution of rape in birds. This theory draws on Brownmiller's (1975) feminist analysis that rape is about power rather than sex, and applies it to non-humans. Gowaty and Buschhaus (1998) contrast the CODE hypothesis predictions against the standard sociobiological model (the "immediate fertilisation enhancement hypothesis") and find that the CODE hypothesis better predicts fertilisation outcomes for rape in birds. However, this favourable comparison is only possible because of the "predictions" attributed to the sociobiological model. Gowaty and Buschhaus state that one prediction from the standard sociobiological explanation for rape is,

> Fertilization success from aggressive copulation [rape / forced copulation] is as frequent as from copulations with preferred partners in which females do not resist.

Because in most cases of rape in non-human species this is not the case, Gowaty and Buschhaus conclude that there must be an explanation other than sex and immediate reproductive advantage. Unfortunately, Gowaty and Buschhaus have only considered a mixed strategy prediction where payoffs to all behavioural alternatives are equal (Maynard-Smith 1982). For most, if not all, species that exhibit rape behaviour, rape operates as a behavioural tactic within a conditional strategy (Gross 1996). Therefore it is to be expected that fitness payoffs from rape should be lower than consensual sex, and in many cases may be close to zero. This method of dismissing the importance of rape as a reproductive tactic has also been applied to human sociobiology. Brownmiller and Mehrhof (1992) state that, "In terms of successful reproductive strategy, the hit or miss ejaculations of a single-strike rapist are a form of Russian roulette compared to ongoing consensual mating." In such cases, so long as the benefits of attempting rape as a condition-dependent tactic outweigh any costs, it could be selected for as part of an adaptive conditional reproductive strategy.

Misunderstanding # 3: Sons of rapists should be more likely to rape

Fausto-Sterling (1992) states that Thornhill's (1980) work on rape in scorpionflies (*Panorpa* sp.) is "poorly scientific" and in order to make his theory "minimally tenable" he needs to show that male offspring from females who were raped, are more likely to rape when compared to male offspring from consensual sex. Here Fausto-Sterling is confusing the heritability of a behaviour (rape) with the heritability of a strategic rule (under certain circumstances males should attempt rape). Because Thornhill (1980) clearly demonstrates that rape in scorpionflies is condition-dependent and thus is most likely a tactic contained within a conditional strategy, the population is expected to be genetically monomorphic for that trait (Gross 1996). This means that all else being equal, the offspring of scorpionfly rapists will be no more likely to rape than any other member of the population. Fausto-Sterling's prediction will only hold for situations where rape is a separate strategy within a genetically polymorphic population where a mixed strategy (Maynard-Smith 1982) or alternative strategies (Gross 1996) exist. These situations are thought to be extremely rare, if they exist at all (Gross 1996).

Misunderstanding # 4: 'Male-centred perspectives' distort non-human rape research

A large body of research in non-humans shows that rape (or as it is usually referred, "forced copulation") is a widespread biological phenomenon, and from this exists the potential for a comparative approach to better understand rape in humans (reviewed in Thornhill & Palmer 2000). In an attempt to discredit this approach, Polaschek et al. (1997) dismiss the non-human literature as irrelevant with the claim that,

> ...the animal literature is seriously flawed in that both what is observed and the interpretation made are paradigmatically driven and typically reflect a male-centred view.

This claim is remarkable, not only in its blanket dismissal of hundreds of observations and studies, but also in that the two citations listed as supporting this assertion, do not make this claim (Gowaty 1992a,b). Instead, Gowaty (1992a,b) makes the reasonable suggestion that cultural practices may influence scientific hypothesis generation and that a feminist informed evolutionary biologist might view interactions and social behaviour in novel ways. However, as unsupported as the claim of Polaschek et al. (1997) may be, it appears to be derived from the consistent assertion by some feminists that biology emphasises 'typically male' behaviours such as aggression, dominance, conflict and the mating success of male animals, and thus does not accurately reflect the 'true' nature of animals. From this comes the accusation that the study of animal social behaviour is 'sexist' (Rosser 1982; and see Holmes & Hitchcock 1997 for review).

Contrary to this 'male-paradigm' view of science, an analysis of animal behaviour research shows very little difference in the subjects investigated by men and women. Female and male biologists were equally likely to study agonistic interactions, sexual selection (and equally likely in this field to study male conflict and female choice), male-male and female-female dominance behaviours, and social behaviours associated with parental care and conflict. Men and women were also just as likely to study the behaviour of males, females or juveniles in their study species (Holmes & Hitchcock 1997). While it may still be true that a 'female perspective' exists and women may be predisposed to interpreting behaviour differently to men (Gowaty 1997b), there is absolutely no evidence that behavioural biology is seriously flawed, or that it represents any 'male-centred' viewpoint.

Misunderstanding # 5: Adaptive rape strategies must always yield adaptive behaviour

Gowaty (1982) attempts to refute Thornhill's (1980) hypothesis that rape is part of an adaptive strategy whereby males attempt rape to increase the number of their offspring when she asks;

> Is it rape when a virgin is forced to intercourse?' Similarly, is it rape when a post-menopausal woman is forced to intercourse? ...[I]n the sociobiological sense of Thornhill [1980], neither of these would be rape,

> because in the first example the virgin could be impregnated and her genetic fitness thereby increased, and because in the second example the fitness of the male who forces a post-menopausal female to copulate would not be increased.

Here it does not matter whether Thornhill (1980) is correct in narrowing his definition of rape to being an evolved behaviour subject to fitness payoff constraints. Gowaty is asking us to believe that an adaptive behavioural strategy must *always* yield adaptive behaviour. An adaptive behavioural strategy does not necessarily produce adaptive behaviour with positive payoffs every time it is implemented (imagine an animal drinking from a poisoned water source, can we now say that drinking is not adaptive?). Gowaty's argument about the virgin and the post-menopausal female can be seen as a form of naïve falsification (Lakatos 1970). It is still rape even if you believe that Thornhill is correct in describing rape in terms of fitness outcomes, as the general strategy over time is what is evaluated for fitness payoffs, not some positive function attached to every expression of a behaviour from within that strategy.

A similar form of naïve falsification is used by Rose and Rose (2000) against the notion that rape is an evolved phenomenon in humans, when they state that:

> They [Thornhill & Palmer 2000] claim that rape is an evolutionary strategy...Thus their definition of rape is restricted to the forced penile penetration of fertile woman. So victims of forced anal or oral sex or same-sex rape, as well as raped pre-pubescent girls or post-menopausal women, have, according to the authors, not been raped at all.

Claiming that rape is an evolved strategy does not lead to the definition that Rose and Rose (2000) claim (that rape is restricted to forced penile penetration), nor that sexual assaults that do not result in the production of offspring are not rape (and Thornhill & Palmer (2000) do not claim this). No evolutionary biologist would deny that normal sexual behaviour and sexual drive are products of evolution, and yet that does not lead to the conclusion that because consensual sex in our society includes all of the above variations, sex is not an evolved behavioural means for producing offspring. To effectively criticise the hypothesis that rape is an adaptive sexual strategy, it needs to be demonstrated that the general patterns of behaviour expected from an evolutionary perspective do not occur, rather than pointing to a singular exception (Jones 1999; Alcock 2001).

Misunderstanding # 6: Birds lacking intromittent organs cannot inseminate through rape

Mating in birds usually consists of the male standing on the female's back and the two birds bringing their cloacae together for sperm transfer. Because of the mutual behaviours involved, it has been assumed that unless the female actively presents her cloaca, sperm transfer cannot occur (Fitch & Shugart 1984). This idea that males are unable to successfully force copulations on females if they lack an intromittent organ is cited to discount rape as a viable male reproductive tactic (Weatherhead & McRae 1990; Gowaty & Buschhaus 1998). Using this platform, Gowaty & Buschhaus (1998) speculate that rape in birds is not about sex at all, and invoke Brownmiller's (1975) feminist rape analysis in humans to explain why rape (or as they call it "aggressive copulation") occurs in birds. However, in the original study (Fitch & Shugart 1984), the authors are modelling avian 'mixed reproductive strategies' and provide no evidence to support their assumption that males cannot successfully inseminate. Fitch & Shugart (1984) state that, "It is unlikely that EPC [extra-pair copulation] has been successful through forced copulation in most avian species…[and] may require female cooperation for successful transfer of sperm and fertilization of ova." This is used to justify their modelling assumption that "…males are unable to force fertilization with females." Thus the paper provides no evidence that forced copulation is impossible in passerines, only that the authors believe it *unlikely* and that it *may* require female co-operation. It is important to recognise an opinion that sperm transfer is unlikely is not that same as providing evidence that it does not occur.

While it appears true that in some species females can effectively prevent insemination from rape either through behavioural means (Wagner 1991; Hunter & Jones 1999) or through cryptic female choice (Burley et al. 1996), there is a growing body of evidence that suggests forced copulation is a viable and widespread male reproductive tactic (Birkhead et al. 1985; Emlen & Wrege 1986; Westneat 1987; Hatchwell 1988; Adkins-Regan 1995; Birks 1999; Ewen et al. 1999). In these studies, males do occasionally achieve cloacal contact during forced copulation despite female resistance (Japanese quail *Coturnix japonica* 5% of all successful matings (Adkins-Regan 1995), guillemot *Uria aalge* 6% of all forced copulation attempts (Hatchwell 1988), zebra finch *Taeniopygia guttata* 80% of successful EPCs were forced (Burley et al. 1994)). Fertilisation from successful forced copulation in birds lacking intromittent organs has both been demonstrated experimentally - where fertilisation success was the same as for solicited copulations (Adkins-Regan 1995), and inferred from strong correlations between forced EPCs and extra-pair paternity (Ewen et al. 1999). The selective advantage to males adopting forced copulation has been calculated to be approximately 2.5 % in the guillemot (Birkhead et al. 1985; Hatchwell 1988). These figures suggest that while forced copulation in many birds may be a poor reproductive option when compared to consensual copulation, it is effective enough to be selected for as a tactic within a conditional male reproductive strategy.

Misunderstanding # 7: Females are the ultimate arbiters of sperm competition

The idea that females will always win conflicts arising from sperm competition has been used to reject the idea that rape has evolved through achieving additional inseminations (Gowaty & Buschhaus 1998). There is evidence demonstrating that females have a variety of mechanisms at their disposal to manipulate and select against undesirable sperm (Birkhead & Møller 1993). However, focusing only on female mechanisms neglects the 'male perspective' crucial in understanding the evolution of mating systems. Gowaty and Buschhaus (1998) state that:

> [E]ven if males of a species without an intromittent organ forcefully inseminated a female, she has built-in counter-mechanisms that she may use to decrease the likelihood that forced insemination results in fertilization... Thus, altogether it seems unlikely that forced inseminations would often be successful at fertilization in any birds... It is these options for successful post-insemination resistance that render the Immediate Fertilization Hypothesis for forced copulation in birds truly suspect.

The authors are ignoring the fact that rape may incur costs to females without these females being able to evolve effective counter-adaptations. Evolutionary arms races between the sexes (Dawkins 1989), or sexual dialectic theory (Gowaty 1997a), assumes that for every fitness gain one sex makes at the expense of the other, a counter selection pressure will operate tending to counteract it. However, in evolutionary arms races there can be winners and losers (Dawkins 1989). For rape, females may be more likely to lose the arms race, as the value of winning for females will generally be smaller than for males. This is due to the benefit to the female of being able to choose her mate being generally less than the benefit, to males, of additional matings (Clutton-Brock & Parker 1995). This suggests that for a female, there may be an effective means to prevent a rapist's sperm from inseminating her, but the necessary physiological or anatomical adjustments incur a greater cost than the costs of rape. In these cases it is expected that female cryptic choice will be less than one hundred percent effective. As long as the male can achieve some positive payoff, however small, there will be some positive selection for rape.

Gowaty and Buschhaus (1998) claim that rape in birds is unlikely to be a direct male reproductive tactic by claiming that, "Selection could act easily on females to use these powerful [cloacal] muscles to rid themselves of unwanted inseminates", and thus "fertilization after forced insemination should be especially unlikely." However, in an experimental evaluation of the likelihood of forced copulation in Japanese quail to achieve fertilisation, Adkins-Regan (1995) found that forced inseminations had the same fertilisation success as other inseminations despite the male lacking an intromittent organ. Japanese quail can also void sperm after insemination, but this only affected insemination rates in one out of three experimental trials (Adkins-Regan 1995). In the mallard (*Anas platyrhynchos*) females do not consistently select or utilise the same type of sperm as is predicted by post-copulatory mate choice, despite being subject to high levels of extra-pair forced copulations (Cunningham & Cheng 1999). This lack of cryptic female choice in some species despite them suffering a relatively high rape likelihood compares well with humans where fertilisation rates from rape are at least as high as from consensual sex (Gottschall & Gottschall 2003).

Because of the conflicting forces acting on both the male and female, one should not interpret Eberhard (1985 p.107) too literally when he states that, "Females, because fertilization takes place within their bodies, generally have the last say in reproduction and can exercise... 'cryptic female choice'". Simply because females can have the last say, does not mean that they will have the last say. Just as a cuckoo's host has the last say in the reproduction of the cuckoo, it does not mean that cuckoos never successfully get other birds to raise their chicks.

Misunderstanding # 8: "Testosterone made me do it"

Davis (2001) proposes that forced copulation in the mallard arose as an evolutionary epiphenomenon because high male testosterone was selected to promote mate-guarding behaviour. This hypothesis is presented as an alternative 'ultimate' hypothesis to forced copulation as a secondary male reproductive tactic (McKinney et al. 1983) and to the CODE hypothesis (Gowaty & Buschhaus 1998). Davis' (2001) hypothesis is currently a focus of debate in human evolutionary biology (Thornhill & Palmer 2000). It needs to be stressed that forced copulation arising as some sort of by-product of high testosterone is not the same as claiming that testosterone levels mediate the prevalence of forced copulation behaviour (Davis 2002). In the latter, testosterone mediation of rape simply describes one proximate mechanism causally affecting expression of the behaviour, and not the selective forces that acted to produce rape in the animal's evolutionary past. In such cases, claiming that testosterone causes rape makes about as much sense as claiming that poverty in human society causes rape.

For the testosterone epiphenomenon theory to be considered as a serious rival ultimate hypothesis, several factors need to be demonstrated and considered. The first is that the singular effect of increasing testosterone levels will cause an animal to rape. This is not as simple as it might first appear, as effects of testosterone on behaviour are often difficult to predict (Sapolsky 1997). In many species rape does not appear to be just an over exuberance of normal sexual behaviour, but it involves a complicated and sometimes unique, set of specialised behaviours (Thornhill 1980; Castro et al. 1996). Thus it is unclear whether rape, as is described in most species, would spontaneously arise simply as a result of increasing testosterone levels.

The second and most important criterion to be satisfied to show support for this hypothesis, is that for it to be an epiphenomenon (and thus an ultimate explanation) in any meaningful sense, it must be shown that rape arose as a by-product to mate guarding and that natural selection has not since acted to specifically adapt rape to any purpose. If natural selection has acted upon rape and 'fine tuned' it to have a positive effect on fitness, it fails to be an epiphenomenon and becomes an adaptation for increasing male reproductive success by subverting female mate choice. If this is the case it is indistinguishable from the already established ultimate hypothesis of McKinney et al. (1983). It would be a mistake to argue that it is somehow different because it did not arise from direct selection pressure, but rather came into existence by accident (as an epiphenomenon) and from there was adapted to be part of a reproductive strategy. All adaptations (whether structural, physiological or behavioural) at some point in evolutionary history developed from predecessor structures that had either some other function or no function at all (Dennett 1995). The seemingly adaptive behavioural switching between mate guarding and pursuing extra-pair copulations (Arvidsson 1992; Komdeur et al. 1999), and the precision with which males can assess female fertility and preferentially focus forced copulation attempts on these females (Beecher & Beecher 1979; Westneat 1987; Low in press) suggests that rape in many species has been adapted to a reproductive function.

Misunderstanding # 9: Rape is pathological or a laboratory artifact

Fausto-Sterling (1992) examined two studies of non-human rape and called into question their conclusions regarding rape being an adaptive reproductive strategy. Thornhill's (1980) work on scorpionflies is dismissed because it took place in a laboratory and thus rape may just be laboratory artifact. Barash's (1977) study on rape in mallards is brought into question, citing that the study birds were in an artificial environment and stressed, and this lead to "pathological" rape behaviour. What is surprising about these dismissals is that Fausto-Sterling finds it more plausible to believe that a complex set of specific condition-dependent behaviours that are finely attuned to bringing a male in sexual contact with a female, often at exactly the right time to maximise his chances of fertilisation are due to a sudden, and relatively minor change in environmental situation rather than as a result of selection for a reproductive strategy over thousands of generations. Fausto-Sterling's claim that, "...for if it [rape] is but a laboratory artifact, it loses all interest [if studying adaptive mating strategies]." assumes that changes in behaviour due to changing environmental circumstances cannot be adaptive. Rather than it losing all interest, it would generate testable (and interesting) hypotheses as to the environmental cues required in 'natural' populations to induce the condition-dependent rape behaviour. As it turns out, this is a moot point as scorpionflies have conclusively been shown to rape under 'natural' conditions (Thornhill 1981; 1987) and mallard rape is anything but 'pathological'; ubiquitously occurring in natural mallard breeding populations and in at least 38 other duck species (McKinney et al. 1983; McKinney & Evarts 1998).

Misunderstanding # 10: Because of non-human rape research, human rapists could be acquitted by claiming that their impulses are 'natural'

This common charge that sociobiology endorses naïve genetic determinism, and that this will lead to people committing the 'naturalistic fallacy' has been discussed and rebutted in detail elsewhere (Dawkins 1982; Dennett 1995; Waage & Gowaty 1997; Jones 1999; Segerstråle 2000; Thornhill and Palmer 2000; Alcock 2001; Pinker 2002) and the reader is referred to these sources for a more in depth analysis of these issues. I mention them here not to discuss the general problems with the critics' position, but to illustrate that the criticisms levelled at sociobiologists apply equally to those levelling the criticisms.

Fausto-Sterling (1992) begins her discussion of sociobiology and rape with the following passage:

> "Imagine a look into the future. The headlines leap off the front pages of newspapers across the country. ADMITTED RAPIST FREED AS JURY BUYS BIOLOGICAL DEFENSE! Admitted rapist Joe Smith was released today after a jury – in a landmark decision – bought the defense that sexual assault is biologically natural, and that some men – including Smith – have especially strong urges to rape. Since courts have not established procedures for confining "involuntary rapists" Smith was freed."

Fausto-Sterling uses this scenario to warn of the dangers of claiming that rape occurs in non-humans and that it is 'natural' in any sense of the word. She specifically targets the work of Barash (1977) on mallards and Thornhill (1980) on scorpionflies and quotes from them in the hypothetical legal defence of the rapist. Unfortunately Fausto-Sterling does not extend her critical eye beyond her target to see if the same argument could equally apply to her own colleagues. Consider the following:

> Imagine a look into the future. The headlines leap off the front pages of newspapers across the country. ADMITTED RAPIST FREED AS JURY BUYS CULTURAL DEFENSE! Admitted rapist Joe Smith was released today after a jury – in a landmark decision – bought the defense that sexual assault is promoted by exposure to legally acquired pornography, and that some men – including Smith – have especially strong urges to rape after exposure to pornography. Since courts have not established procedures for confining "involuntary rapists" Smith was freed.

Feminism has emphasised the cultural causal factors driving behaviours such as rape in human society, while at the same time discrediting the search for causal factors derived from biology (Brownmiller 1975; Baron & Straus 1984; Tang-Martinez 1997). This approach ignores the fact that genetic causes and environmental causes are in principle no different from each other (Dawkins 1982). While it is not illogical to be concerned that the public may commit the 'Naturalistic Fallacy' when processing evolutionary theories (Jones 1999), it is inconsistent to believe that this misunderstanding cannot apply equally to cultural factors. Promoting one set of causal variables while at the same time ignoring the other, only reinforces the false 'nature / nurture' dichotomy that plagues understanding of the causes of behaviour (Ridley 2003).

A possible origin of misunderstanding

When examined in context, almost all of the misunderstandings listed above contribute to limiting comparisons between humans and non-humans, or calling into question the idea that rape in humans or forced copulation in non-humans is about sex. This suggests that there is some resistance to biologists' findings that rape or forced copulation in non-humans is ultimately about sex and reproduction because of its possible application to analyses of human rape. In Brownmiller's (1975) seminal rape analysis, she states that no animal has been observed to rape in the wild. Brownmiller did not raise this point to argue that animals could not, in principle, rape, but rather that it was thought not to occur. From this came the idea that rape must be cultural in its origin, as this is the major difference between animals and humans. This has been the foundation of feminist analyses of rape in human culture, with the assertion that rape is about power and not sex (Brownmiller 1975; Whatley 1986).

One factor common to many of the misunderstandings discussed above, is that they are perpetuated by self-labelled feminists and feminist scientists (Gowaty 1982; 1992a,b; 1997a,b; Rosser 1982; Brownmiller 1975; Brownmiller & Mehrhof 1992; Fausto-Sterling 1992; Tang-Martinez 1997; Gowaty & Buschhaus 1998; Rose & Rose 2000). This suggests that much of the non-human forced copulation / rape research may be perceived by some to be in conflict with feminist ideology. One reason why this might be the case is that if it were accepted that some behaviours equivalent to rape in humans occur in non-humans, and that the ultimate motivation of these behaviours is sexual, this would suggest that current evolutionary hypotheses regarding the sexual motivation of human rape (Jones 1999; Thornhill & Palmer 2000) would require serious consideration

Critics of sociobiology have, in the past, been quick to point to possible social consequences of sociobiological reasoning (reviewed in Segerstråle 2000) while simultaneously failing to consider the impact that a blanket denial of biological theories will have on the study, understanding and control of rape in human society. Feminism can retain many of its core beliefs while still embracing a biological analysis of rape in all species (Pinker 2002). One possible way for this to be achieved would be if feminism was clearly identified as an ideology, and an emphasis was placed on the clear distinction between ideology (how the world ought to be) and theory (how the world is) (Craig Palmer, personal communication). Another way for feminism to embrace biological explanations would be for it to acknowledge that its theories are based on the proximate motivations of human behaviour, and thus are a complementary explanation to evolutionary analyses and are not necessarily in conflict (as is often believed). Unfortunately until this integration of explanatory levels is achieved, biological theories of rape will continue to be dismissed. Thus in the meantime, while care needs to be exercised when undertaking cross species comparisons, non-human rape researchers (working under euphemisms such as "forced copulation") need to question a number of the default assumptions behind criticisms of the comparative approach.

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Massey University
COLLEGE OF SCIENCES

INSTITUTE OF NATURAL RESOURCES
Te Kura Mātauranga o ngā Taonga ā
Papatuanuku
Ecology
Private Bag 11 222
Palmerston North
New Zealand
T 64 6 356 9099
F 64 6 350 5623
www.massey.ac.nz

Ph.D. CANDIDATE DOCTORAL EXAMINATION APPLICATION

Candidate's Name: **Low, Matthew Richard**

Academic Unit: **Institute of Natural Resources (Ecology)**

Provisional registration date 24.05.1999: Thesis submission deadline 24.04.2004

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Statement regarding the nature and extent of any assistance received during the doctoral research:

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Candidate Matthew R. Low

Massey University
COLLEGE OF SCIENCES

INSTITUTE OF NATURAL RESOURCES
Te Kura Mātauranga o ngā Taonga ā Papatuanuku
Ecology
Private Bag 11 222
Palmerston North
New Zealand
T 64 6 356 9099
F 64 6 350 5623
www.massey.ac.nz

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Thesis title: "The behavioural ecology of forced copulation in the New Zealand stitchbird (hihi)"

Statement regarding doctoral thesis:

This statement confirms that the candidate has pursued the Doctoral Course in accordance with the University's Doctoral regulations.

Supervisor Ed O. Minot

Massey University
COLLEGE OF SCIENCES

INSTITUTE OF NATURAL RESOURCES
Te Kura Mātauranga o ngā Taonga ā Papatuanuku
Ecology
Private Bag 11 222
Palmerston North
New Zealand
T 64 6 356 9099
F 64 6 350 5623
www.massey.ac.nz

Ph.D. CANDIDATE DOCTORAL EXAMINATION APPLICATION

Candidate's Name: **Low, Matthew Richard**

Academic Unit: **Institute of Natural Resources (Ecology)**

Provisional registration date 24.05.1999: Thesis submission deadline 24.04.2004

Thesis title: "The behavioural ecology of forced copulation in the New Zealand stitchbird (hihi)"

Statement regarding the thesis:

1. Reference to work other than that of the candidate has been appropriately acknowledged.
2. Research practice, ethical and genetic technology policies have been complied with as appropriate.
3. The thesis does not exceed 100,000 words (excluding appendices).

Supervisor Ed O. Minot

Candidate Matthew R. Low