Wattle function and territoriality in the South Island saddleback (*Philesturnus carunculatus*)

David Lloyd-Jones

University of Canterbury

2014

Project report submitted in partial fulfilment of the
requirements for the degree B.Sc. (Hons) in the School of Biological Sciences,
University of Canterbury

This thesis is dedicated to the memory of my grandfather,
Ian 'Babu' Foster
(1929 -2014)

As kingfishers catch fire, dragonflies draw flame;
As tumbled over rim in roundy wells
Stones ring; like each tucked string tells, each hung bell's
Bow swung finds tongue to fling out broad its name

- Gerard Manley Hopkins (1844–89)

Abstract

The South Island saddleback (*Philesturnus carunculatus*) is an endangered bird endemic to New Zealand. Both males and females possess wattles, which are colourful fleshy structures that hang from the lower beak. Although a wide range of birds have wattles, the selection pressures and behavioural function of these biological ornaments remain poorly understood. In this study, behavioural observations, morphological measures, and a playback experiment were used to investigate how wattles are used by South Island saddlebacks in their natural habitat. Wattles were found to be monomorphic when body mass was accounted for, and they were observed to engorge in both aggressive and non-aggressive visual displays. In the playback experiment, wattle engorgement in saddlebacks was significantly associated with territorial intrusions in males but not in females, although females were significantly more likely to engorge their wattles and display in the absence of their mate. Larger males with bigger wattles did not have significantly stronger territorial responses. These results provide the first experimental evidence for the functional role that wattle engorgement plays in saddleback signalling behaviour. The markedly similar visual display behaviour between sexes, which is used in both aggressive and non-aggressive contexts, provides insight into possible selection pressures acting in the evolutionary maintenance of wattles.

Table of Contents

Chapter 1 Introduction

Chapter 2 Methods

Chapter 3 Results

Chapter 4 Discussion

List of Figures

Chapter 1. Introduction

1.1 The evolution of ornaments

From the extravagant plumage of male birds-of-paradise (Family Paradisaeidae) to the bright blue feet of the blue-footed booby (*Sula nebouxii*), a diverse range of animals have elaborate, bizarre or beautiful ornaments that initially appear unnecessary or even detrimental to survival (Andersson 1994, Wiley 2006). Charles Darwin (1871) was the first to suggest a coherent evolutionary explanation for ornamental traits after recognizing that his theory of natural selection did not satisfactorily explain their existence. He termed the alternative process 'sexual selection' and described it as selection that "depends on the advantage that certain individuals have over others of the same sex and species solely in respect to reproduction" (Darwin 1871). In sexual selection, individuals with more extravagant traits are better at obtaining mates, and consequently passing on their genes, which in turn leads to selection on those traits (Andersson & Simmons 2006).

Darwin proposed two major mechanisms for how sexually reproducing animals obtain mates. These are: (1) mate choice or intersexual selection, and (2) competition over mates by members of the same sex, which is also known as intrasexual selection (Darwin 1871, Clutton-Brock 2007). Mate choice and intrasexual selection are complex and currently active fields of research (e.g. see reviews in Lyon & Montgomerie 2012, Clutton-Brock & Huchard 2013), yet many of the fundamental principles of sexual selection have changed little over time. The recent growth of molecular genetic techniques has enabled ground-breaking experimentation – especially for understanding, from a bottom-up perspective, the genetic causes of phenotypic patterns of mate choice (Majerus *et al.* 1982, Owens 2006, Jones & Ratterman 2009, Hettyey *et al.* 2010). Sexual selection is no longer considered selection solely on male ornaments, because traits as diverse as behaviour, morphological structures, and reproductive proteins can be all subject to selection pressures imposed through mate choice (Jones & Ratterman 2009). The study of mate choice, which was initially much more controversial than intrasexual selection due to the belief that animals were incapable of choosing, traditionally focused on the female choice of male ornaments despite the fact that females in some species are also ornamented (Anderson & Simmons 2006). This bias is perhaps understandable due to the greater conspicuousness of many male ornaments (Jones & Ratterman 2009), yet such an imbalance in attention by evolutionary biologists does not reflect reality. Mate choice has been shown to occur in both directions, and ornaments in females of some species can be as elaborate as those found in males (Lyon & Montgomerie 2012). It is also becoming increasingly apparent that the selection processes involving female ornamentation are often different to those operating in the female choice of male traits (Kirkpatrick 1982, Kokko *et al.* 2003, Clutton-Brock 2007).

To further add to the complexity of understanding the evolution of ornaments, two additional hypotheses have been proposed: social competition over resources (also known as the 'social selection theory') (West-Eberhard 1983, LeBas 2006, Kraaijeveld *et al.* 2007, Roughgarden 2012), and sexual indistinguishability (Burley 1981, Butcher & Rohwer 1989, Langmore & Bennett 1999). The central mechanism of social selection was originally defined by Mary Jane West-Eberhard (1983) as "differential reproductive success (ultimately, differential gene replication) due to differential success in social competition, whatever the resource at stake." Social selection therefore includes sexual selection as "the subset of social competition in which the resource at stake is mates" (West-Eberhard 1983). In contrast, sexual indistinguishability has been argued to evolve in monogamous, group-living species where the repeated interactions due to sexual competition would at times be disadvantageous. Consequently, the ability to conceal sex may confer a fitness advantage. An important prediction of this hypothesis is that subordinate individuals should conceal their sex more than dominant individuals, because the losers in competitive interactions are more likely to be subordinates (Langmore & Bennett 1999). Both hypotheses have received empirical support, yet have been overlooked by many authors as contributing rather than complete explanations for the evolution of ornaments (Lyon & Montgomerie 2012).

While this view of secondary importance has justifiably persisted for the sexual indistinguishability hypothesis, a growing number of recent studies have shown that the evolution of costly traits in females can be mediated, at least in part, by competition for non-sexual resources (Lyon & Montgomerie 2012, Tobias *et al.* 2012). For example, in the golden-crowned sparrow (*Zonotrichia atricapilla*), ornaments such as the size and colour of the crown patch interact to signal social status. Social status was found to be independent of sex or body size, and therefore influenced access to winter feeding resources (Chaine *et al.* 2011). Increasing evidence of how both sexual (e.g. mates) and non-sexual (e.g. food, territory, cooperation in breeding) resources can be competition-mediated means that the evolution of ornaments in many species, and especially in females, cannot be narrowly attributed to either natural or sexual selection (Lyon & Montgomerie 2012). Therefore, social selection, with sexual selection treated as a specific subset, provides us with a broader framework in which to understand the evolution of ornamentation (Tobias *et al.* 2012, Clutton-Brock & Huchard 2013, West-Eberhard 2014). Considering this framework, Tobias *et al.* (2012) suggest that the most accurate approach would be to partition social selection mechanisms into 'sexual social selection' and 'non-sexual social selection' yet recognise the inelegance of such terms. For this study, I use 'sexual selection' as the definition for the former and 'social selection' for the latter, following Tobias *et al.* (2012). Nevertheless, the theory of social selection is recognised as being inclusive of both processes.

A clear emphasis made by Darwin was that the traits favoured by sexual selection are not necessarily advantageous in the struggle for existence, but are simply better for gaining an advantage over other males and passing this on to offspring (West-Eberhard 2014). This concept is important to reiterate, because for many examples of behaviours or ornaments, the distinction between natural selection (where traits are of direct survival fitness value), sexual selection (where traits are of use in obtaining sexual resources), and social selection (where traits are of use in obtaining non-sexual resources), are not clearly defined or are used inconsistently (Lyon & Montgomerie 2012). It is therefore necessary to be explicit about the parameters of the selection processes when discussing the evolution of ornamental traits (West-Eberhard 2014). Lyon & Montgomerie (2012) insightfully suggest that our understanding of social trait evolution may be confused by the current approach, where two different processes (i.e. intrasexual selection and mate choice) are lumped together under 'sexual selection' in theoretical discussion, while different manifestations of the same processes (e.g. choice or competition in both sexual and non-sexual contexts) are considered separately.

Social interactions in both sexual and non-sexual contexts are considered to potentially have a powerful influence on the evolution of ornamental traits (Lyon and Montgomerie 2012). This is thought to be driven through social competition in a wide variety of contexts, including competition over food resources, reproduction, mates, space, social status and even parental care (Tobias & Seddon 2009, Cornwallis & Uller 2010, Griggio *et al.* 2010). Current views on social selection are far from universally held or accepted, especially with regard to how sexual and social selection are related (i.e., should sexual selection be categorically regarded as a subtype of social selection?) (Tobias *et al.* 2012, Clutton-Brock & Huchard 2013).

Yet far from being an obstacle, uncertainty in the literature allows me to discuss the results of this study, where I test the function of an avian ornament, with a wider perspective than would have been previously applied. Social selection is currently being recognized as playing a bigger role than previously suggested in the evolution of ornaments, particularly in the evolution of female ornaments (Tobias *et al.* 2011, Clutton-Brock & Huchard 2013).

1.2 Ornaments as signals of fitness

The question of why animals select mates with particular traits has long intrigued biologists and has prompted a wide range of ultimate explanations for mate choice (Andersson 1994, Andersson & Simmons 2006, Jones & Ratterman 2009). In mate choice theory, the reason for female choosiness of male ornaments has been explained in four major ways: (1) through Fisherian self-reinforcing selection (Fisher 1958), (2) as signals of fitness (Hamilton 1964, Zahavi 1975), (3) as selection for species recognition, and (4) through direct phenotypic benefits for females (Fisher 1958). Three alternative hypotheses for the evolution of sexually dimorphic ornamentation have been largely refuted as insufficient in explaining the maintenance and evolution of ornaments (Andersson & Simmons 2006, Kraaijeveld *et al.* 2007). These are: pleiotropic gene effects (Lande 1980, Endler & McLellan 1988), ecological sex differences (Selander 1966, Shine 1989) and unprofitability as prey (Baker & Parker 1979). Many of these supported theories are not mutually exclusive. Consequently, they are often not open to strong inference testing (Platt 1964). This has led to difficulties in disentangling the relative strength and interactions of the various mechanisms (Andersson 1994, Andersson & Simmons 2006).

Most studies testing mate choice have focused on the 'good genes' hypothesis where ornaments are proposed to be honest indicators of an individual's fitness (Møller & Alatalo 1999). Zahavi (1975) first proposed the handicap hypothesis by which individuals display their fitness through survival despite the energetic and survival handicaps imposed by ornaments (e.g. the extra-long tails found in some bird species). Following this, Hamilton and Zuk (1982), in their seminal paper, proposed an alternative hypothesis whereby ornaments enable males to advertise their health, vigour and low parasite load to potential mates. This is also known as the 'parasite-mediated sexual selection' hypothesis. These non-mutually exclusive concepts were later combined into the 'immunocompetence handicap' hypothesis (also known as the 'bright male' hypothesis). 'Bright males' with high immunity against parasites can maintain their ornaments and successfully display them despite survival and immunological handicaps (Folstad & Karter 1992, Wedekind & Folstad 1994, Roberts *et al.* 2004). Under this hypothesis, diseased individuals are not able to grow, display and maintain high quality ornaments (Wedekind & Folstad 1994, Roberts *et al.* 2004, Andersson & Simmons 2006). Consequently, individuals that select mates with the largest or brightest trait have a means to ensure their offspring inherit high quality genes and higher levels of fitness (Rosen & Tarvin 2006).

Due to the conspicuous nature of many vocal and visual avian ornaments, and the suitability of birds for a wide variety of research, a large number of studies have investigated avian ornamentation (Amundsen 2000). Yet, despite extensive research, a number of major questions regarding ornamentation remain (Badyaev & Hill 2003). These are largely centred on variation in ornamentation with respect to phylogeny, habitat and life histories (Friedman *et al.* 2009, *Price et al.* 2009). For example, the way in which many bird traits are used in signalling is poorly understood. The selection pressures acting on some sexually or socially selected ornaments – such as wattles – are also untested and speculative (Amundsen & Pärn 2006, Smith *et al.* 2009, Potti *et al.* 2013). Consequently, birds remain an ideal (although by no means exclusive) study system for investigating ornamentation due to: (1) the diverse range of species to study, (2) the high degree of variation in types of ornamentation across species, (3) their suitability for field and lab experimentation, and (4) their similar visual sensory perception to humans (see Clutton-Brock & Sheldon 2010, Tobias *et al.* 2012).

1.3 Sexual differences in ornamentation in birds

A number of factors, in addition to sexual or social selection processes, are likely to influence the presence and degree of sexual dimorphism in birds (Badyaev & Hill 2000, Figuerola & Green 2000, Dunn *et al.* 2001). The mating system, degree of territoriality, and overall life history strategy have been shown to influence the degree of sexual dimorphism in plumage, ornaments, body mass, wing length and tail length (Amundsen *et al.* 1997, Harper 1999, Potti *et al.* 2013). In general, polygynous or lekking species tend to be more sexually dimorphic than those with monogamous mating systems (Trail 1990, Dunn *et al.* 2001, Bennett & Owens 2002). However, as showy ornamentation in birds is more frequently observed in males (Amundsen 2000), relatively few studies have investigated whether the selection processes acting on female ornaments are similar to those acting on male ornaments (Rosvall 2011, Tobias *et al.* 2012, Potti *et al.* 2013).

Female ornamentation in birds is far from rare, with conspicuous crests, beaks or plumage often observed in both sexes (e.g. auks, puffins and cormorants) (Jones & Hunter 1998, Childress & Bennun 2002, Doutrelant *et al.* 2013). Ornamental plumage that is the same in both sexes (monomorphic plumage) is found in a variety of bird taxa (e.g. toucans, parrots, parakeets, hummingbirds and tanagers) (Cunningham & Birkhead 1998, Amundsen & Pärn 2006). Lack of sexual differences are also occasionally seen in vocal behaviours (monomorphic vocal 'ornaments') where both sexes have similar song repertoires (Seddon 2005, Tobias & Seddon 2009). Monomorphism (where the female is ornamented in the same way as the male) has traditionally been explained as either the result of genetic correlation or through direct selection of ornaments in both directions (Rice 1984, Lande & Arnold 1985, Kraaijeveld *et al.* 2007).

In genetic correlation, conspicuous female ornaments are thought to evolve as a genetically correlated response to selection on males (Darwin 1871, Lande 1980). This is because most of the genome is shared by both sexes, and therefore females can inherit the genetic basis for ornamentation without their ornaments being subject to direct selection (Clutton-Brock 2007). Females lacking ornaments (or with highly reduced ornaments) under this hypothesis are suggested to have evolved drab plumage for crypsis. This is due to the counter-acting natural selection pressure of predation on nesting females (Martin & Badyaev 1996). If ornaments are indeed genetically correlated, selection pressure is still possible. Theoretically, sexual or social selection pressure can still act on female trait expression to either reinforce or diminish the selection strength (Amundsen 2000). In addition, because ornaments are costly to maintain (Møller 1991, Walther & Clayton 2005), a selective advantage is required to explain their persistence over time – even if they are initially present as a result of genetic correlation (Price & Birch 1996). Evidence showing that the transition between dimorphism and monomorphism has evolved numerous times suggests that the genetic correlation hypothesis is best considered a process of 'preadaptation' which is later acted on through either mate choice or competition (Price & Birch 1996, Omland 1997, Price 1998, Badyaev & Hill 2003, Amundsen & Pärn 2006).

Although not mutually exclusive, direct selection is the alternative to the genetic correlation hypothesis when explaining the evolution of female ornamentation (Amundsen 2000). Direct selection can arise through both mate choice (where individuals select breeding partners based on ornamental traits), and through intrasexual contest competitions when resources are limited (West-Eberhard 1983, Langmore 1998, Owens 2006, Clutton-Brock 2007). If females compete for limited resources, then ornaments that confer status in competitive interactions can lead to selection for those ornaments directly (Johnsen *et al.* 1996). This can also occur indirectly through selection by male mate choice (Amundsen *et al.* 1997, Lyon & Montgomerie 2012). This hypothesis has received considerable empirical support (Burley 1981, Trail 1990, Bleiweiss 1992, Whittingham *et al.* 1996). However, because of overlap in the genetic constraints in sexual and social selection, there remains a need to understand how the various mechanisms interact to shape ornamentation in both sexes (West-Eberhard 2003, Amundsen & Pärn 2006, Clutton-Brock & Huchard 2013). For example, it can be hard to determine if: (1) an ornament is simply sexually selected during courtship (such as via mate choice) (Andersson & Simmons 2006), (2) or is selected through social competition (by using the ornament to gain social dominance and thus resources and then a mate) (Tobias *et al.* 2012), or (3) selection processes are a combination of both processes (e.g. mutual mate selection operating based on both the quality of the ornament and non-sexual resources possessed by the individual) (e.g., Tobias *et al.* 2011).

Monomorphic ornamentation in birds may be associated with aggressive social displays (over territories or other resources), especially where both sexes are involved either together or in alternation (West-Eberhard 1983). If having similar ornaments is equally advantageous to both members of a pair in social interactions, then social selection of this kind may play a key role in favouring the elaboration and maintenance of monomorphic ornamentation. Tobias *et al.* (2011) suggest that monomorphic ornamentation via social selection never gained widespread acceptance because of the impression that sexual selection theory can account for the same patterns; however, this view now appears to be quickly changing (Hooper & Miller 2008, Rubenstein & Lovette 2009, Botero & Rubenstein 2012, Lyon & Montgomerie 2012, Clutton-Brock & Huchard 2013).

In their constructive review, Kraaijeveld *et al.* (2007) suggest that social selection is particularly relevant to the study of mutual ornamentation because competition over non-sexual resources is likely to be more balanced between the sexes than with sexual competition. In other words, when both sexes of a species experience the same selection pressure (such as when they both compete for food resources), the ornamental traits are under similar selective pressures and thus more likely to be monomorphic. Yet, as discussed above, the distinction between sexual and social selection can be quite unclear. Consequently, many cases of social selection in the past may have been interpreted as simply sexual selection, without an in-depth investigation of the way ornaments are used in competition over non-sexual resources (Kraaijeveld *et al.* 2007). The evolution of ornamentation via social selection has received support from several taxa (e.g. starlings, parrots and hummingbirds); however, relative to studies which narrowly focus on sexual selection, empirical research on social selection is limited (LeBas 2006, Rubenstein & Lovette 2009).

Overall, there is growing evidence supporting the observation that monomorphic ornamentation, territorial defence behaviour and social competition are linked (Seddon & Tobias 2006, Tobias *et al.* 2011). South Island saddleback (*Philesturnus carunculatus*) (Māori: tīeke), an endemic New Zealand passerine, are monomorphically ornamented and both sexes are involved in territory defence and social conflict (Hooson & Jamieson 2003, Higgins *et al.* 2006). Since these are all indicators of a social selection system (West-Eberhard 1983, Higgins et al. 2006, Hale & Briskie 2007), this presented an ideal system for experimentally testing the role of wattle ornamentation and territoriality in both sexes.

1.4 Evolution and function of bird wattles

Wattles are a colourful ornament which many bird species use in visual signalling (Wiley 2006). These thin, fleshy structures hang loosely from the lower beak and have the capacity to become engorged with blood, thus enlarging and becoming brighter and more prominent (Buchholz 1997; Stettenheim 2000). In ring-necked pheasants (*Phasianus colchicus*), wattles are important in male courtship (Johnsgard 1999), and their size in other species has been shown to be positively correlated with circulating testosterone levels (Briganti et al. 1999; Papeschi et al. 2000), viability (measured as the ability to evade predators) (Papeschi & Dessi-Fulgheri 2003; Baratti et al. 2010), and early hormonal and nutritional conditions (Ohlsson et al. 2002; Bonisoli-Alquati et al. 2011).

Phylogenetic analyses of fleshy trait evolution demonstrate that wattles may have evolved multiple times in the Galliformes (the order including junglefowl, turkeys, pheasants and partridges), although the ability of the wattles to engorge has apparently only evolved in the order once (Kimball & Braun 2008). The evolution of wattles does not appear to have been investigated in any other avian lineage. If wattles are indeed honest signals of good genes then they must be both costly to produce and maintain, and they must discriminate between high and low quality individuals (Zahavi 1975, Grafen 1990). Since Hamilton and Zuk's famous paper (1982), genes related to ornament development are considered likely to be related to disease resistance (Bernatchez & Landry 2003, Mays Jr & Hill 2004, Neff & Pitcher 2005, Milinski 2006). Supporting this is the finding that wattle size in the males of some birds can reflect androgen levels, and therefore be honest signals that vary in colour according to testosterone plasma levels (Folstad & Karter 1992, Owens & Short 1995, Briganti *et al.* 1999; Papeschi *et al.* 2000, Kimball & Braun 2008). Hale (2007) found that wattle size reflects the level of immune function in both sexes of South Island saddleback, which suggests that females may play a greater role in offspring fitness than has previously been appreciated in sexual selection theory.

The behavioural signalling function of wattles is poorly understood despite a large number of bird species possessing wattles in some form. This has led to wattles being referred to as an "enigmatic ornament" (Smith *et al.* 2009). A number of birds perform elaborate displays in which the wattles feature prominently among a number of signals. However, in some junglefowl (*Gallus gallus*) displays, female preferences often depend on display movement and a specific subset of the ornaments presented (Rowe 1999, Smith *et al.* 2009). This has led to the concept that ornaments (such as wattles) may not be directly selected for, but rather have an ancillary function where they enhance signal efficacy or modify information content (Morton 1977; Guilford & Dawkins 1991). Smith *et al.* (2009) found that wattles do not function strongly in female choice in the junglefowl, but they increased the conspicuousness of the "tidbitting" signal (a food-related display), thus suggesting that they are maintained to enhance signal efficacy. Past studies exploring the signalling function of wattles have almost exclusively focused on Galliformes. Therefore, it is unclear if wattles in other taxa function similarly in signalling behaviour (Kimball & Braun 2008, Smith *et al.* 2009).

1.5 Ornamentation in the South Island saddleback

The South Island saddleback is an endangered forest bird endemic to the South Island of New Zealand (Holdaway *et al.* 2001, Higgins *et al.* 2006, Parker *et al.* 2013). Along with the North Island saddleback (*P. rufusater*, Gmelin), South Island kokako (*Callaeas cinerea*, Gmelin), North Island kokako (*C. wilsoni*, Gmelin) and extinct huia (*Heteralocha acutirostris*, Gould) it forms the New Zealand wattlebird family (Callaeidae), all of which are characterised by conspicuous wattles which vary in size, shape and colour (Higgins *et al.* 2006).

Saddlebacks ('saddlebacks' hereafter refers to 'South Island saddlebacks' unless otherwise stated) are a medium-sized passerine (c. 26 cm long) and both sexes have the same glossy-black plumage, chestnut-coloured saddle on the back, and orange-red wattles (whose colour changes when engorged with blood) (Lovegrove 1980, Higgins *et al.* 2006). First year birds (also known as 'jackbirds') have chocolate-brown plumage, grow full-sized wattles and occasionally breed. This life history trait is an example of delayed plumage maturation (Hawkins *et al.* 2012), and while the reasons for it are not fully understood, they are likely to be part of a life history strategy which maximises reproductive fitness by reducing intra- or intersexual conflict between mature breeding birds and young birds, especially in high population densities (Studd & Robertson 1985, Hawkins *et al.* 2012). In the context of other saddleback life history traits, delayed plumage maturation provides a possible indicator of the strength of social competition in the species. Saddlebacks are also cavity-nesters and form lifetime pair-bonds (Pierre 2001, Hooson & Jamieson 2003, Higgins *et al.* 2006). Finally, they are relatively long-lived for medium-sized passerines, and can live up to 21 years (Lindstedt & Calder 1976, Higgins *et al.* 2006).

Observations on how the closely related North Island saddlebacks use their wattles, and the circumstances under which they engorge, have been made during other behavioural studies (Jenkins 1978), but have never been tested experimentally. Wattle engorgement in North Island saddlebacks has been observed to occur in several contexts: 1) between a pair and opponents during territorial disputes, 2) between birds of a bonded pair as pair-reinforcement, 3) by a male near a nest when calling a female off to be fed, and 4) very occasionally towards human observers (Lovegrove 1980, Jenkins & Veitch 1991, Higgins *et al.* 2006). The specific interactions under which wattle engorgement occurs have only been anecdotally investigated in the North Island saddleback, and never in the South Island saddleback, which is assumed to be similar (Blackburn 1964, Jenkins 1978, Lovegrove 1980, Jenkins & Veitch 1991).

Ornamentation in the South Island saddleback extends beyond the wattles. The chestnut saddle, black plumage, loud sexually-dimorphic song and tail-length can be also considered ornaments (Amundsen *et al.* 1997, Gil & Gahr 2002, Fleishman *et al.* 2006). How these ornaments are used varies with context. Distant interactions between saddlebacks in forested environments are almost exclusively vocal. Both male and female saddlebacks have powerful sound projection and a high number of harmonics (Ludwig & Jamieson 2007), which are hypothesized to have arisen through selection pressures for accurate signal transmission in a habitat with numerous sound-transmission obstructions and a high level of sound degradation (Azar et al. 2013; Parker et al. 2013). In contrast, close interactions between individuals also involve visual signalling displays. Furthermore, because many signalling behaviours are inherently multimodal, engaging multiple receiver sensory systems simultaneously, the interactions between the visual and vocal signals are likely to influence a signal's function and efficacy (Wiley 2006; Smith & Evans 2013). Consequently, it is possible that wattles in the South Island saddleback, like in junglefowl, are maintained to enhance signal efficacy. Understanding the contexts under which a signal change occurs (i.e., wattle engorgement) is the first step to testing whether wattles function as part of a complex multimodal signal, or are either signal enhancers, redundant secondary signals or "unreliable signals" that are produced because they are energetically cheap (Møller & Pomiankowski 1993).

1.6 Study objectives

In this study I use field observations, morphological measures, and a vocal playback experiment to investigate some of the behavioural conditions under which South Island saddleback engorge and display their wattles. My objective was to test the conditions under which wattles are used in territorial interactions, and then relate them to selection pressures on the ornament in both sexes. Using morphological measures of individual birds, the visual signalling behaviour of individuals is linked to their morphology (mass, wattle length and wattle size) to test whether wattles fit a sexually-selected model of fitness. To contrast this, I use a vocal playback experiment to test behavioural responses by saddlebacks towards intruding males, and subsequently explore whether evidence exists for a socially selected pressure on wattles in the species. Overarching the specific questions of this study is the aim of better understanding how the presence of wattles in saddlebacks can be related to their life history as a whole. To my knowledge, this is the first experiment specifically testing wattle function in a passerine bird in a natural setting. The results are divided into three sections: the first deals with behavioural observations made regarding wattle use under natural conditions, the second presents correlations found between morphological measures and sex, and the third section reports the results of the playback experiment. The thesis concludes with a general discussion, where I draw together the main findings and place them in the context of visual signalling theory, and social and sexual selection.

Chapter 2. Methods

2.1 Study species

South Island saddlebacks are long-lived for a passerine (up to 21 years), nest in cavities, and form long-term pair bonds (Lovegrove 1980, Higgins *et al.* 2006). The vocal differences and smaller body and wattles size of females are the only obvious differences between the sexes (Taylor & Jamieson 2007). Although the size differences are relatively small and unreliable for sexing, vocal differences can be used to distinguish males from females (Parker *et al.* 2013). In contrast to the similar-looking adults, first year juveniles (referred to as 'jackbirds') are easily identified by their rich brown plumage covering their entire body and also lack the chestnut-coloured saddle patch on the back (Pierre 1999).

Both North Island and South Island saddlebacks were widespread and abundant prior to the arrival of humans to New Zealand (Hooson & Jamieson 2003). However, following the introduction of predatory mammals, the North Island saddleback population quickly declined to ~500 individuals while the South Island saddleback became confined to Big South Cape Island (939 ha) and two adjacent islets, Pukeweka (2 ha) and Solomon (25 ha), situated south-west of Stewart Island. When rats wiped out this last population in the early 1960's, the remaining 36 South Island saddlebacks were translocated to two rat free islands (Hooson & Jamieson 2004, Hale 2007). These populations on Jacky Lee (30 ha) and North islands (8 ha) off the east coast of Stewart Island flourished and were later used to re-establish populations on a number of islands around the South Island of New Zealand (Michel *et al.* 2008).

The South Island saddleback population on Motuara Island was used in this study. Motuara Island was made mammalian predator-free in 1991 when kiore (*Rattus exulans*) were eradicated (Cash & Gaze 2000). Twenty six South Island saddleback were translocated onto the island in March 1994 from Jacky Lee and North Island islands, near Stewart Island (Pierre 1999). In 2002, saddlebacks on Motuara Island suffered a population crash, declining from over 100 to less than 50 individuals within a period of 1–2 months, as a result of a disease outbreak (Hale 2008). The population has since recovered and was estimated at 130 individuals in 2007 (Hale & Briskie 2009). At the conclusion of data collection (January 2014) I estimated the population to be between 180 and 200 adults; in the more accessible parts of the island 59 adult saddlebacks were captured, and many additional unbanded individuals were also observed and counted.

2.2 Study site ecology

Small and heavily-vegetated (59 ha, maximum elevation 128 m), Motuara Island (-41°05.5' S; 174°16.5' E), lies at the entrance to Queen Charlotte Sound, in the Marlborough Sounds (Fig. 2.1). Following Māori and non-Māori occupation, the island's habitat was drastically modified (Walls 1984, Michel *et al.* 2008). In 1926, Motuara Island was declared a nature reserve, and since then a mosaic of vegetation has vigorously regenerated (Cash & Gaze 2000). A tall (3–13 m) canopy of kanuka (*Kunzea ericoides*) dominates the inland vegetation, and across the island there is a dense understorey of five-finger (*Pseudopanax arboreus*), mapau (*Myrsine australis*), kōhūhū (*Pittosporum tenuifolium*), shiny karamu (*Coprosma lucida*), karamu (*C. robusta*) and twiggy coprosma (*C. rhamnoides*) (Cash & Gaze 2000, Walls 1984). The vegetation fringing the shore is primarily a scrub of kōhūhū (*Pittosporum tenuifolium*), ngaio (*Myoporum laetum*), taupata (*Coprosma repens*), akiraho (*Olearia paniculata*) above a dense fringe of flax (*Phormium cookianum*). Patches of remnant vegetation are found on the island, mostly in steep gullies, including large stands of kohekohe (*Dysoxylum spectabile*) and on the moister eastern side of the island, titoki (*Alectryon excelsus*), tawa (*Beilschmiedia tawa*), milk tree (*Streblus banksii*), hīnau (*Elaeocarpus dentatus*), and makomako (*Aristotelia serrata*).

Saddlebacks on Motuara Island range throughout all habitat types but tend to remain low in the canopy or on the ground. They have been observed foraging up to 4 m above ground, mostly on five-finger (*Pseudopanax arboreus*). South Island saddleback males spend more time feeding on the ground than the North Island saddleback (Pierre 2000, Pierre 2001). My observations during the behavioural observation periods, searching for nests, netting birds and playback experiments matched these findings. However, an exception to their generally terrestrial behaviour is that of males singing from perches in the canopy.

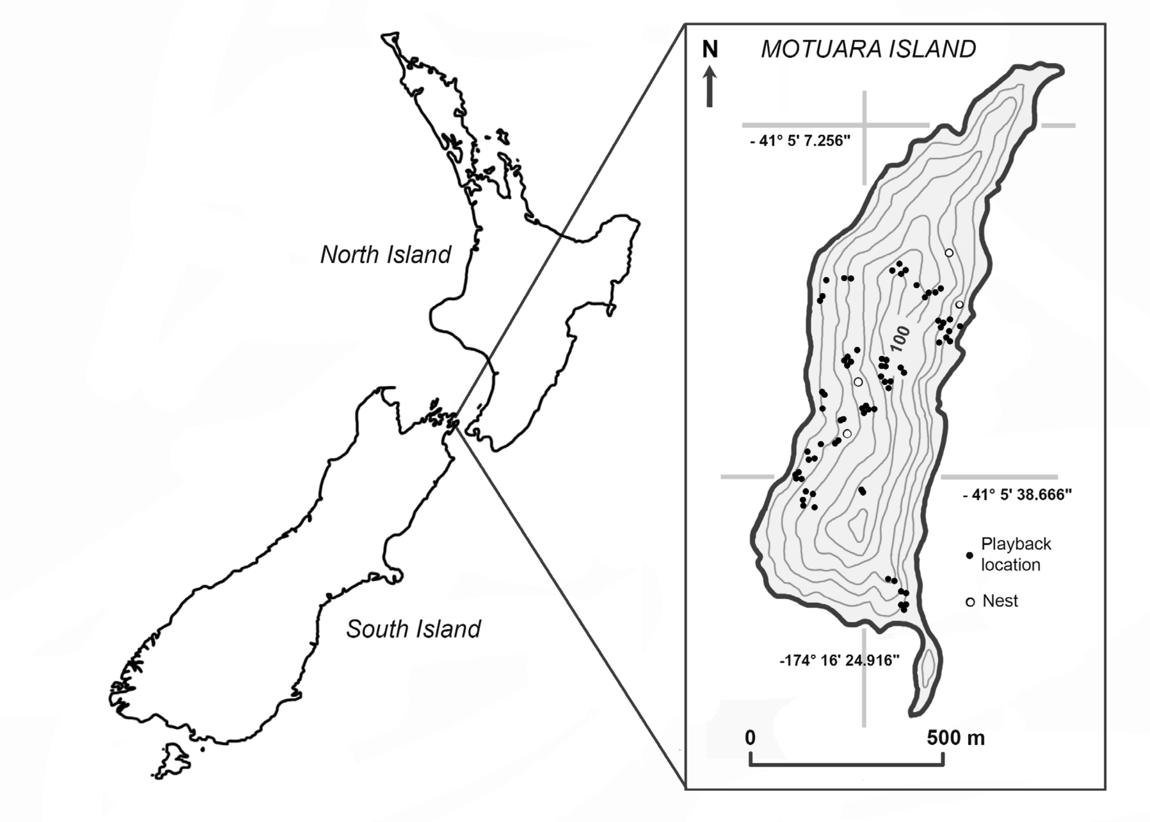

Fig. 2.1. Map of Motuara Island within Queen Charlotte Sound (South Island, New Zealand). Experimental playback locations (closed circles) and active nests (open circles; 2013-2014 breeding season) are marked.

2.3 Morphological measures

Between 12 December 2014 and 14 January 2014, I caught 59 adult saddlebacks using mist-nets (standard design: 2.7 m high × 12 m long; 30 mm mesh) and banded each individual with a unique colour band combination to allow for individual identification. Jamieson *et al.* (2005) have previously shown that the capture and handling of saddlebacks during pre-nesting and breeding does not affect timing of egg-laying or reproductive success. Seventeen of the saddlebacks that were netted had previously been banded. Age was calculated for 4 individuals using their original banding date. Mist netting was conducted using a vocal lure of a female 'quiet song' (Higgins *et al.* 2006). This was recorded on Motuara Island on 25 November 2013 (see section 2.4 for recording specifics), and was completely different from any male song played back in the playback experiment. Quiet songs in North Island saddleback are described as 'soft, melodious, flute-like and audible only at close range' (Lovegrove & O'Callaghan 1982).

South Island saddleback vocalisations are noted to be similar to those of North Island saddleback (Hooson & Jamieson 2003), and are highly effective for attracting nearby saddlebacks. Mist nets were opened for a maximum of 2 hours at a time and were monitored continuously from a distance. Because saddlebacks rarely leave their territories (Pierre 2000), netting was conducted at 38 different locations on the island. Multiple individuals of the same sex were often netted if the net was set up on a territorial boundary.

Captured individuals were placed in a clean paper bag and weighed to ± 0.1 g using digital scales. Individuals were then fitted with a D-sized, numbered aluminium metal band (issued by the Department of Conservation), and 2 or 3 PVC colour bands in a unique colour combination. Wing length (maximum unflattened chord) was measured with a stopped ruler to the nearest ± 1 mm. Tarsus length (proximal end of the tarsometatarsus to the middle of the midtarsal articulation), bill length (exposed culmen) and bill width (at the start of the wattles) were measured with digital slide callipers to ± 0.1 mm. A single measurement each of the two wattles was made to ± 0.01 mm with slide callipers. These were reset to zero between measurements. Wattle measurements were averaged to give the average wattle length for an individual. An important point here is that all wattle measurements were made of flaccid wattles, under the assumption that a linear relationship exists between flaccid and engorged wattles (Buchholz 1997). All bird handling and morphological measurements were carried out by me to avoid any errors associated with multiple measurers.

Any outliers due to measurement error or highly aberrant wattles (difference between left and right wattles exceeded 5 mm; average difference was 0.06 ± 0.23 mm) were excluded from the final results (3 out of 59 birds). Digital measurements of beak length, wattle length and wattle area were made by taking high quality digital photographs of the head from either side and from the front (e.g., Rosen & Tarvin 2006). Photographs were taken by holding the birds in a natural position against a white background, using a Nikon D3200 digital camera (Nikon Corporation, Tokyo, Japan), with manual focus and a flash. Bill length (from tip to nares), wattle length and wattle area (Fig. 2.3) were measured in a TIFF-formatted file of the photograph using the outline and area measure tools in ImageJ (Rasband, W.S., ImageJ, U.S. National Institutes of Health, Bethesda, USA, 1997-2014). Wattle area and beak length were measured as the number of pixels within the selected outline (see Bonisoli-Alquati *et al.* 2011 for similar methodology).

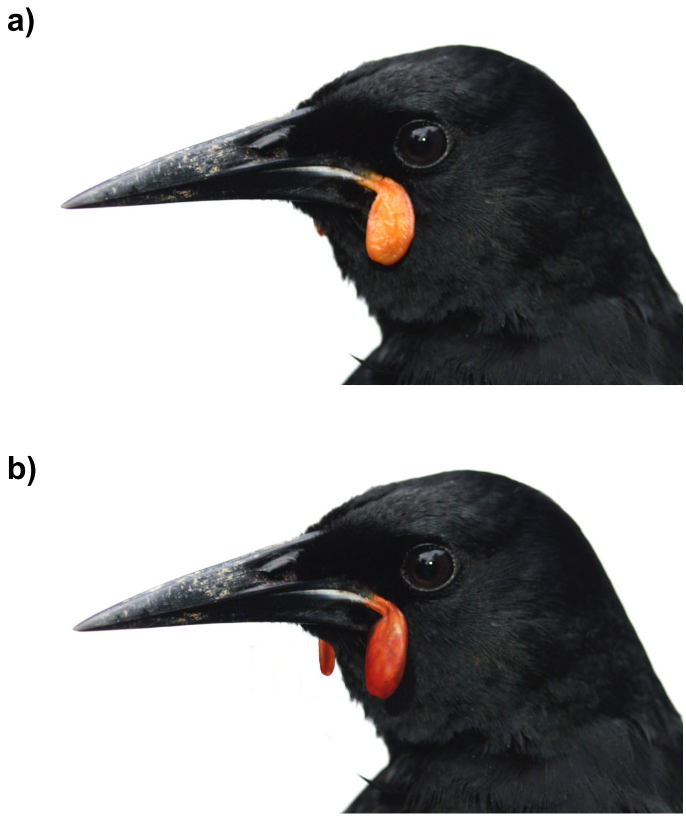

Fig. 2.2. Shape, angle and colour change between unengorged (**a**) and engorged wattles (**b**). Wattle engorgement is digitally illustrated.

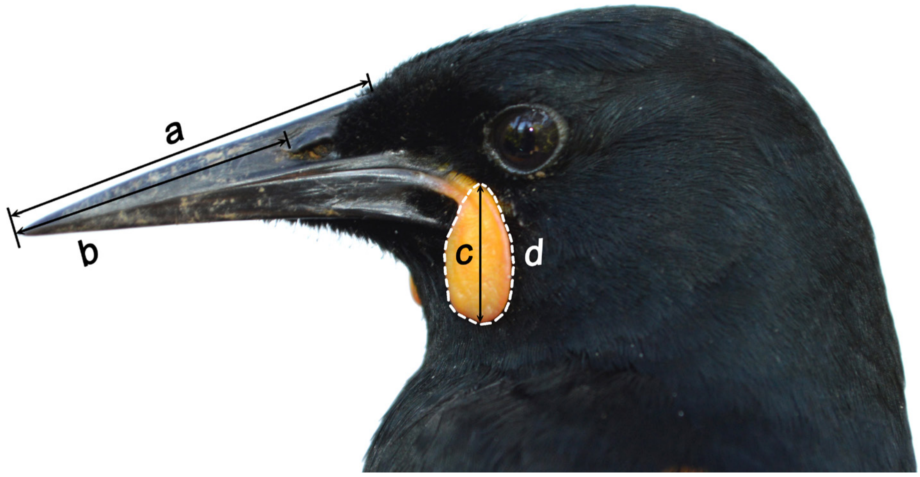

Fig. 2.3. Positioning for culmen measurement (**a**), beak tip to nares measurement (**b**), wattle length (**c**) and wattle area (**d**) digital measurements. Wattle area was measured up to the natural apex of the flaccid oval wattle shape when viewed from directly side-on.

Due to variation in image size caused by changes in distance between the bird and camera during photography, the raw measured values were not used in calculation. Instead, they were used to calculate relative size and this was compared between individuals. Averages of four replicate digital measures were used to minimise measurement error (see Rosen & Tarvin 2006). Only photos with the bird's beak and wattles directly side on and in focus were used. Although beak length along the culmen (Fig. 2.3.a) was the physical measurement taken with the bird in hand, it was difficult to measure digitally, as the notch where the beak joins to the skull is not exposed in a side-on photograph. Consequently, for the relative measurements, the beak was measured from the beak tip to the start of the nares, since both points are clearly visible in a side-on photograph. It is likely that ornaments such as wattles may be viewed by other individual saddlebacks relative to the size of owner of the ornament rather than using absolute size judgements (Gallistel & Gelman 2000). In other words, a wattle of the same size on a smaller bodied bird might be viewed by a mate or competitor as bigger than that on a larger bodied bird. Consequently, I tested the relationship between the relative size (of wattle length and area to beak length) against body mass. Relative size was calculated as:

Relative length = wattle length/beak length from tip to nares [1]
Relative area = wattle area/beak length from tip to nares [2]

Accurate sexing is a key component of any study with South Island saddleback because of their monomorphic plumage, so several techniques were used to sex individuals. Firstly, after capture, the birds were inspected for a brood patch (a patch of bare skin on the abdomen where feathers are shed during nesting season to aid incubation). In saddleback, females exclusively brood the eggs so this is one reliable indicator of sex (Hooson & Jamieson 2004). All individuals were also inspected for a cloacal protuberance, the presence of which is a reliable method to determine males during the breeding season (Beaman & Madge 1998). Secondly, most netted individuals vocalized near the net prior to capture, and due to their highly sexually dimorphic calls (Lovegrove 1980, Higgins *et al.* 2006) it was possible, in most cases, to note the sex and keep track of the individual prior to capture. Taylor and Jaimeson (2007) found that a combination of tarsus length and body mass could be used to classify birds with 90% accuracy. These measurements were used to sex individuals that could not be sexed using the previous methods. When the sex of individuals was plotted against body mass and tarsus length (Fig. 2.4) there was a clear separation of points supporting the sex determination selection.

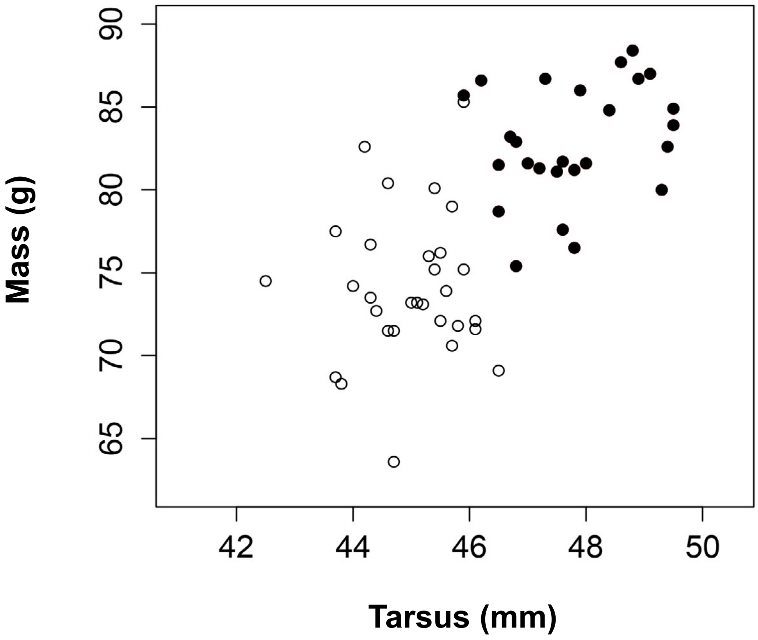

Fig. 2.4. Relationship between tarsus length and body mass of male (closed circles) and female (open circles) South Island saddlebacks. Differences in tarsus and body size were used to sex individuals that could not be sexed using other methods.

2.4 Sound recording

South Island saddleback vocalisations were recorded opportunistically over the entire period spent at the study site (November 2013 - January 2014); however, this was more systematic between late November and mid-December 2013 when approximately 2 hours (falling between 0530 - 0940 hrs) every morning were spent recording. The study period was timed to coincide with the breeding season when males are most vocal (Higgins *et al.* 2006). Male territorial song is loud, often broadcast from a high perch, and repetitive. The start of the male dawn chorus shifted from 0515 hrs on 20 November to 0615 hrs on 25 January 2014. All North Island saddleback produce male rhythmical song (Jenkins 1978, Jenkins & Veitch 1991, Parker *et al.* 2010), and South Island male vocalisations are very similar (Parker *et al.* 2013). However, Ludwig & Jamieson (2007) suggested that in the South Island saddleback males, unlike the North Island males, this song is not stereotypical. This was based solely on recordings from the South Island saddleback population on Ulva Island. I found that saddleback song on Moutara Island fits the definition of male rhythmical song, thus I use the term to describe male song given in territorial encounters and during counter singing, despite uncertainty over whether it properly fits the technical definition of stereotypical song (Ludwig & Jamieson 2007).

Audio recordings were made with a ME66 highly directional microphone (Sennheiser, Wademark-Wennebostel, Germany) with a frequency response of 40 – 22,100 Hz ± 2.5 dB. The microphone was fitted with a Rycote windshield (Rycote Microphone Windshields Ltd, U.K.), and recordings were stored on a Sony PCM D50 portable solid-state digital recorder (Sony Inc., Japan) with a 96 kHz sampling rate as 48-bit WAV files. Recordings were analysed and visualised using the sound analysis programme Raven Pro v1.4 (Cornell Lab of Ornithology, Ithaca).

2.5 Behavioural observations

To confirm the natural contexts for wattle engorgement and displaying behaviour, I specifically followed focal individuals for a total of 14 h on pair territories, and noted all visual signalling behaviour. This was conducted by moving into a territory, and using resident pair vocalisations to locate the pair. Unlike Pierre (2001), I did not deliberately create a disturbance to locate individuals. Individuals or pairs were followed for 0.5-2 hours (mean = 44 ± 21 min). All active focal watches were conducted between 21 November and 20 December 2013, although opportunistic focal watches were made after this. Where possible, all conspecific behavioural interactions with the focal individuals were visually recorded using the same camera as used for photographing wattles (see section 2.3). All evidence of breeding events, including nest-building, chick provisioning and nest brooding was also collected (*n* = 4 active nests).

During observations, wattle engorgements, intra- or extra pair displaying and the identity of individuals was noted. Focal periods were not long or consistent enough to calculate rates of engorgement per unit of time, however they fulfilled the purpose of confirming that wattle engorgement occurs in South Island saddlebacks, similar to that described in North Island saddleback (see Blackburn 1964, Jenkins 1978, Lovegrove 1980). It should be noted that changes in wattles during displays are based on my qualitative observations as it was not possible to measure changes in colour quantitatively (e.g. with spectrophotometer) while birds were engaged in behavioural displays. It is possible that aspects of wattle change may be invisible to humans (i.e, in ultraviolet), so I only report what is visible to human vison. Supporting this approach, recent research suggests that in most situations, human vision provides a valid proxy for avian perception (Seddon *et al.* 2010).

One particular aspect of saddleback display behaviour is important to note. When North Island saddleback males approach each other in conflict (Blackburn 1964) they fly or bound towards each other and, once visual contact has been made, the males face each other at a distance of ≤ 1-2 metres and commence a 'bow-fan-warble' display (Higgins *et al.* 2006). South Island saddleback are thought to behave similarly. When performing this display the bird perches on a branch or fallen log and leans the whole body forward, with the beak pointing towards the ground (Fig. 2.6). The tail is fanned out and raised up, and the chestnut 'saddle' plumage is made prominent (Blackburn 1964, Lovegrove 1980). North Island saddlebacks have been reported to puff out their abdominal plumage and stretch out their necks during displays as they engorge their wattles (Lovegrove 1980). Wattle engorgement in bow-fan-warbles are anecdotally observed to occur: (1) between a pair and between opponents during intense territorial disputes along or near territorial boundaries; (2) between birds of a pair as a form of pair-reinforcement; (3) by male near nest when calling female off to be fed, or after feeding nestlings; and (4) rarely by a single bird towards heterospecific intruders or human observers (Higgins *et al.* 2006). All these contextual observations are from North Island saddleback, thus making behavioural observations on South Island saddleback necessary to confirm the presence of wattle engorgement in bow-fan-warble displays in the same contexts.

2.6 Playback Experiment

2.6.1 Playback procedure

Male and female saddlebacks are easily approachable in their natural habitat for observation and experimentation because they evolved in the absence of mammalian predators (Pierre 2001, Hale & Briskie 2007). Their tame behaviour around researchers makes them an ideal (and rare) study species in which to investigate visual signalling and wattle function. With previous work indicating that wattles are used by both males and females in response to the intrusion of unfamiliar males, I used a vocal playback experimental design. Playback experiments are common in studies of avian communication, and techniques for managing pseudoreplication are well developed (Kroodsma 1989, Kroodsma *et al.* 2001, Vehrencamp 2001).

Playbacks were conducted with 2 observers quietly moving into a mapped saddleback territory and noting whether the resident male had engorged or unengorged wattles, whether he was singing, and any other behaviours that were taking place.

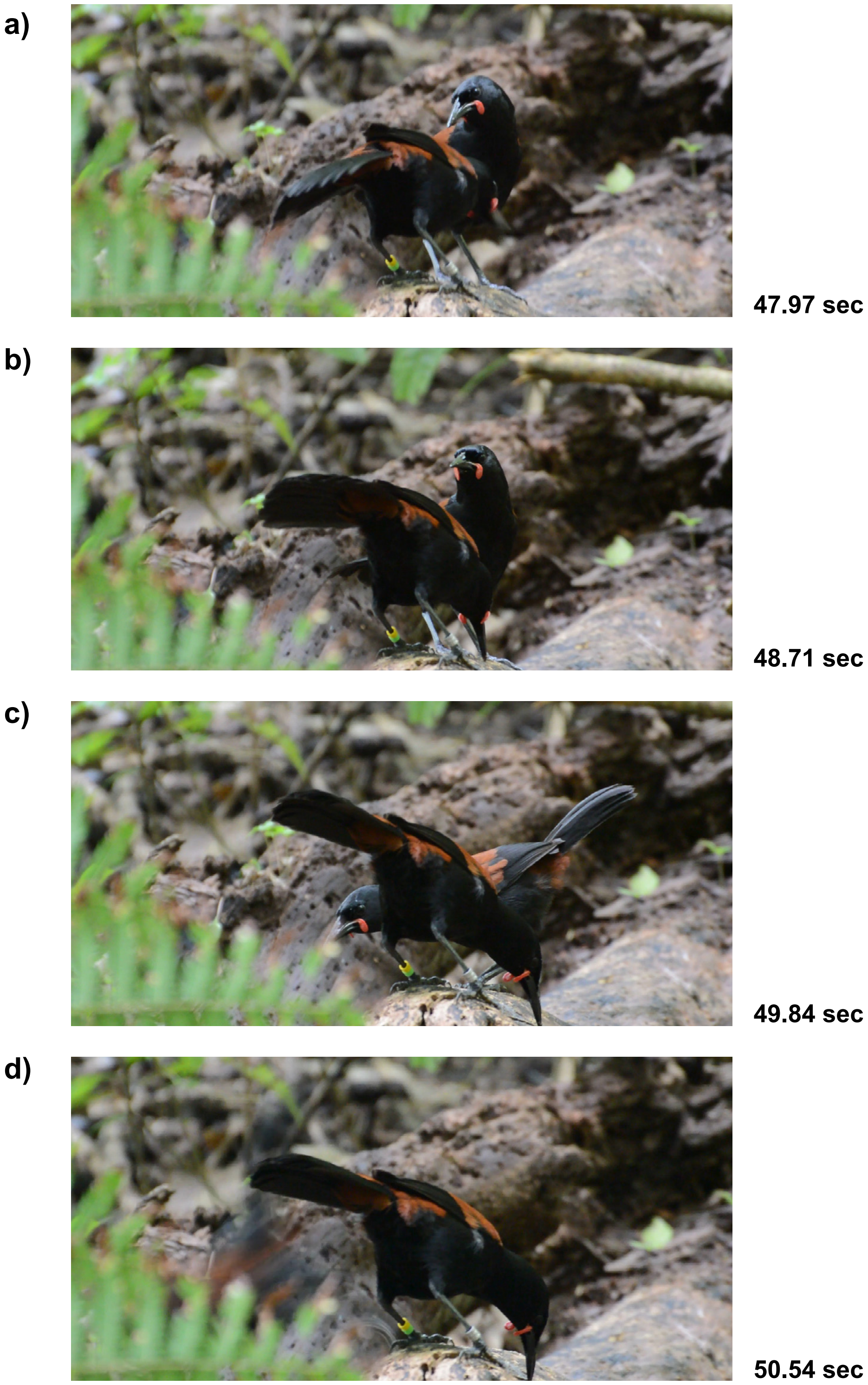

Fig. 2.5. Still frames from a video showing an example of a fast bow-fan-warble display between a South Island saddleback pair. The male (colour-bands: yellow, light-green/metal) is the only one with engorged wattles in this brief interaction, and this interaction is representative of non-aggressive pair-bond displays.

Weather conditions were noted, and maximum and minimum sound level measured with a handheld sound meter to determine if ambient noises had an effect on playback signal efficacy. If the resident male was engaged in any territorial behaviours (e.g., territorial conflicts or conspecific displays) prior to the start of the playback, then the trial was not conducted. For each trial, one 5-minute bout of male rhythmical (territorial) song was played in the territory using a black Y-Storm RYGHT audio speaker (RYGHT Electronics, Paris), attached to a 3 m telescopic aluminium pole. The pole height enabled broadcast from a height similar to that which natural territorial song would be given (pers. obs.).

To avoid pseudoreplication I played back 6 audio tracks recorded from 5 different males. The playback track for each territory was randomised between the 6 tracks and the control. If an audio track was a song from a neighbour or from a territory within 500 m it was not used. Control tests consisted of moving into a territory, locating the resident male, setting up the speaker, positioning the two observers in the same way as during playback but not broadcasting a track. The playback tracks were selected as the best quality matching song recorded from a wide spread of locations. They were amplified by 50% using Audacity software (http://audacity.sourceforge.net/) to enable playback at a similar power level as saddleback song (53-57 dB). For a level of temporal consistency, each playback track was 1 minute and 50 seconds in duration and looped for the total broadcast length of 5 minutes. Songs of species other than saddlebacks (e.g bellbirds or South Island robins) were edited out of the playback track using Raven Pro v1.4.

Territories were identified prior to playback by: (1) mapping nests (*n* = 4) and their attending adults, (2) by following individuals during focal watch periods, and (3) by mapping the locations of singing males. All playbacks were conducted from a central point within the territories of known individuals. In total 11 territories were mapped to a high resolution (and used for the repeat trials). For the territories that were less resolved, an estimated middle-point was selected based on available observations. Saddleback territories on Motuara Island were not areas of exclusive use, and birds attended water points beyond territorial boundaries (Pierre 2000). During the 2013-2014 breeding season, after determining territories, I never observed banded adults more than 50 m outside their territories. All playback trials were conducted a minimum of 7 days after mist-netting in the area.

2.6.2 Behavioural responses to playback

During the broadcast of a playback track or control, any individuals that responded to the speaker were identified and the behavioural responses of: (1) wattle engorgement and bow-fan-warble displays; (2) speaker approach of < 2 m, and (3) counter singing were recorded. In 81% of trials (48/59) photographs and/or videos were taken of engorged wattles to supplement direct observations through binoculars. Where possible vocal responses were also recorded. In all trials there were 2 observers at a distance of > 8 m from the speaker, often partially concealed by vegetation. Observer movement throughout the playback period was restricted to one or two slow steps to gain better observations. Trials (discounting control trials) were repeated twice for 12 males and 5 females, and of these, 8 males and 2 females were tested a third time. Repeated testing of the same individuals was carried out in order to determine the wattle engorgement consistency. Repeat playback broadcasts in the same territory were never conducted on the same day. North Island saddleback males have been shown to share song types with their neighbours (Jenkins 1987), and in South Island saddlebacks this so-called 'syllable sharing' has also been found (Ludwig & Jamieson 2007). In a small area such as Motuara Island it is unlikely that there is absolutely no overlap of song repertoire from birds on one side of the island with those on the other. However, my experimental design attempts to use song stimuli that may be unfamiliar in some of the more subtle vocal features. These include syllables patterns, overall pitch and song sequences (Tobias *et al.* 2011).

This study was conducted under permits from the Department of Conservation and the University of Canterbury Animal Ethics Committee.

2.7 Statistical analyses

All statistical analyses were performed in R (R Development Core Team, 2009, version: 3.1.0). Pearson's correlations were run to investigate the relationships between wattle size and sex. One-way ANOVA's were used to test differences in absolute and relative wattle length between sexes. Fisher's tests were used to test significance between the playback behavioural responses and the control tests. Wattle length was averaged between the left and right wattles for each individual because apart from the individuals with missing, damaged or malformed wattles (0.05% or 3/59), length was not significantly different between the left (mean = 9.98 ± 1.66) and right sides (mean = 9.57 ± 1.86) in hand-measured individuals (Welch's t-test: t = 0.236, df = 39.48, p = 0.81). Similarly, in digitally-measured wattles, the left (mean = 9.65 ± 1.88) and right (mean = 9.91 ± 2.11) wattle length were not significantly different (Welch's t-test: t = -0.555, df = 68.94, p = 0.58). Generalized linear models (glms) with a Gaussian error distribution were used to test relationships between a behavioural score that incorporated wattle engorgement (WE), speaker approach (SA), and counter singing (CS). Where sample sizes were large enough glms with a binary response were also used.

The behavioural score was calculated as follows:

$$\text{Behavioural score}_i = \frac{S_{WE_i}}{N_{WE_i}} + \frac{S_{SA_i}}{N_{SA_i}} + \frac{S_{CS_i}}{N_{CS_i}} \qquad [3]$$

where S is the summed binary response (1 or 0) for the three behavioural responses for a given individual (i). This is divided by N, the number of trials for each of the behavioural responses. This equation ensures that consistency in responses over time for individuals tested multiple times is accounted for, and yet produces a value that can still be compared with individuals that were only tested once.

The incorporation of multiple measures captures, albeit in a coarse way, the overall response. Because wattle size correlated significantly with body mass overall (r = 0.36, n = 286, p < 0.001), and for females (r = 0.19, n = 152, p <0.05) but not for males (r = - 0.13, n = 134, p = 0.13), I also carried out each analysis controlling for body mass as it could confound any relationship between wattle size and the predictor variables. I did this by regressing wattle size against body mass for each sex and using the residuals of both these relationships as the dependent variable in the analyses which controlled for weight. Residuals for relative wattle size were calculated and used in Generalized linear models in the same way. Pseudo-R^2 values were calculated using Nagelkerke's corrected function (Nagelkerke 1991).

Chapter 3. Results

3.1 Behavioural observations of wattle engorgement

Observations outside of the playback experiments showed that changes in wattle colour were variable. Some birds had reddish wattles even in their flaccid state that became slightly redder during engorgement. Others had yellow-orange wattles in their flaccid state, that became darker red when engorged. A reddening colour change was observed in all wattle engorgements (focal watches n = 10; playback responses n = 45). Wattle colour changes were not notably different between sexes (n = 38 males, n = 17 females). The majority of the wattle engorgements observed under natural conditions during focal watches (90%, n = 9/10) were part of a more complex multimodal display: the 'bow-fan-warble' (Higgins *et al.* 2006). This display included (often simultaneously) a fanned tail, presentation of the chestnut saddle by bowing forward, and presentation of the wattles (either engorged or un-engorged) in addition to vocalization (Blackburn 1964, Higgins *et al.* 2006) (Fig. 2.5). Tail movement and overall intensity of the displays varied among those observed. In some bow-fan-warble displays the tail was quickly flicked up and fanned out for a second or less (Fig. 2.5. b and c), whereas in other displays it was lifted high, completely fanned out and sustained in that position for up to 10 seconds as the bird moved on the branch. All naturally observed bow-fan-warbles involved quiet 'warbles' (n = 10). These consisted of variations on previously described male 'four-note' warbles and female 'triple-note' calls in North Island saddleback (Higgins *et al.* 2006).

Behavioural observations of wattle engorgements in both sexes were made on 58 occasions in a variety of contexts, including between members of a pair (n = 5), between neighbouring males (n =2), during 3 observations of bow-fan-warble assemblies (where a number of pairs meet, display and vocalize continuously for up to 15 minutes) and in aggressive responses to the speaker during the playback experiment (n = 45). Outside of these contexts wattles were never observed to be engorged. Wattles did not appear to engorge under stress during mist-netting or handling and bird were not observed to use them in response to heterospecifics.

Despite strong wattle engorgement in the playbacks (see section 3.2), bow-fan-warble displays towards the playback speaker were rare (n = 3 males, n = 1 female), and in both sexes these did not last for more than 3 seconds. The wattle size, based on visual observations, changed very little in some individuals during fast bow-fan-warbles, while in longer displays

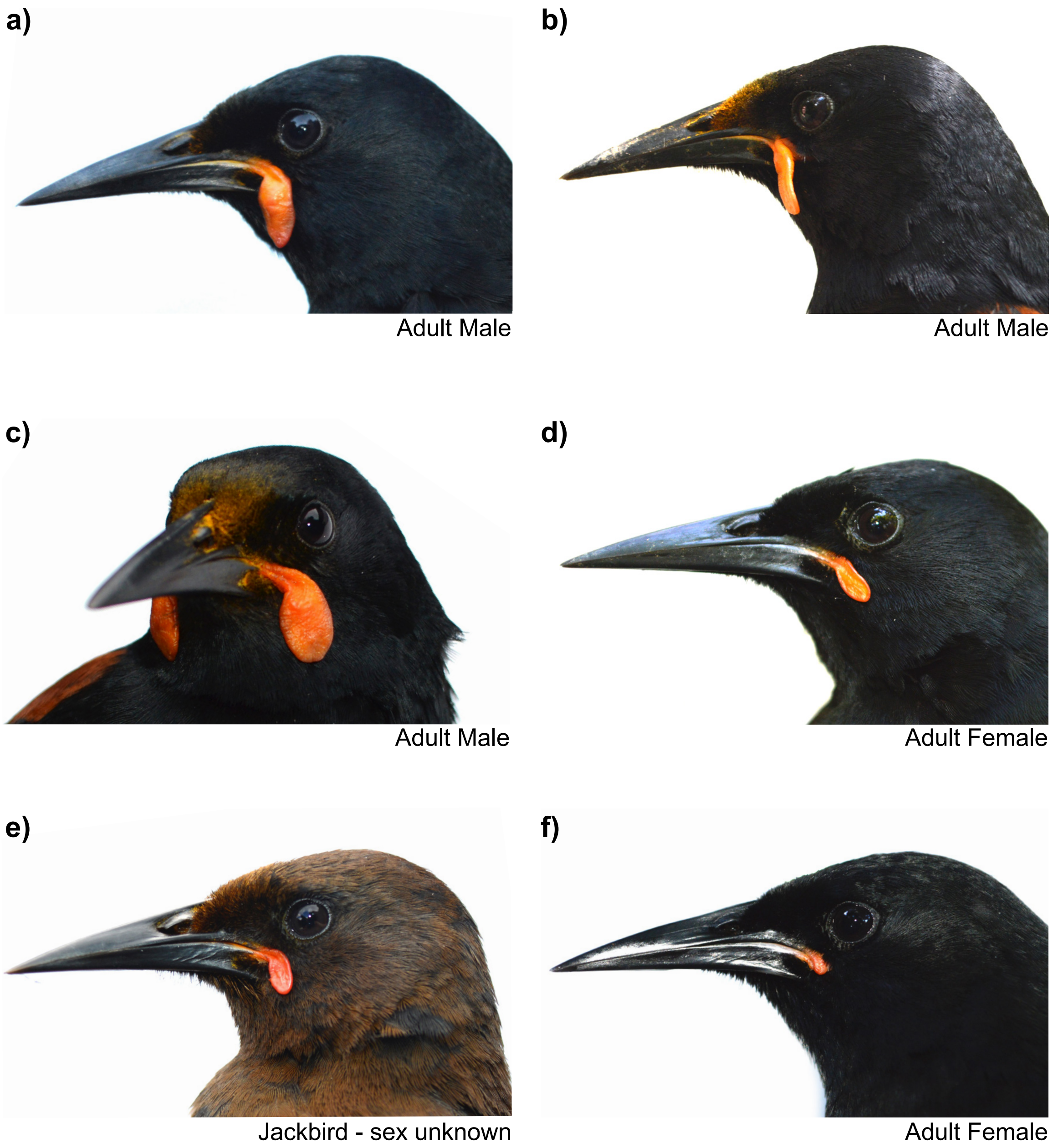

Fig. 3.1. (**a** - **f**) Variation in flaccid wattle size, colour and shape in South Island saddleback. The change in wattle orientation (or angle away from the head) can be compared between (**a**) unengorged wattle that lies flat against the head and (**b**) partially engorged wattle that has begun to rotate outwards. All photographs are of different individuals.

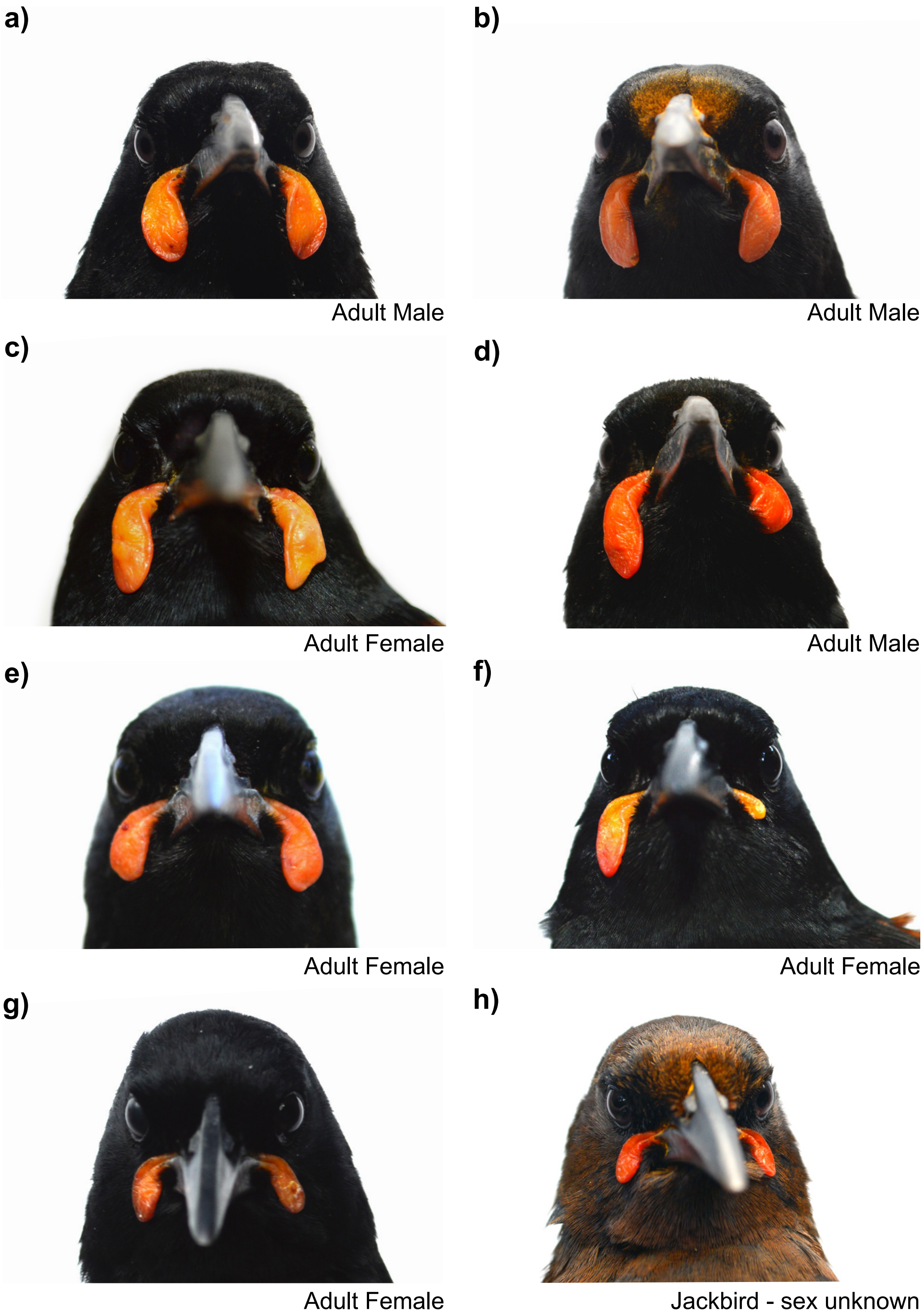

Fig. 3.2. (**a** - **h**) Left-right variation in flacid wattle symmetry, size, colour and shape in South Island saddleback. All photographs are of different individuals

the engorged wattles became twice as thick and approximately 20-30 percent longer (pers. obs). The quiet vocalizations during displays were not strongly stereotypical and in some cases, displays were very quiet with only one or two syllables uttered. In the playback experiment (n = 36 males, n = 20 females) after the male rhythmical song broadcast was started, approaching males jumped from branch to branch at the same height or above the playback speaker (placed 3m above the ground), engaged in counter singing (repeating the song broadcast from the speaker) and circled the speaker 2-3 times, gradually getting closer each time. When the speaker was first approached via hopping from branch to branch, the last few meters were often approached by flying over it in a swoop initiated from an adjacent tree. In 56 playbacks, none of the saddlebacks ever contacted or attacked the speaker in any way.

3.2 Wattles and saddleback morphology

3.2.1 Absolute wattle size in relation to body mass

A total of 59 saddlebacks were captured on Motuara Island and 57 were able to be sexed (n = 27 males, n = 30 females). There was a significant correlation between body mass and absolute wattle size (length) in the individuals measured ($r = 0.53$, $df = 44$, $p < 0.001$). When this relationship was tested for each sex separately, it was significant among males ($r = 0.49$, $df = 22$, $p = 0.016$), but not among females ($r = 0.16$, $df = 20$, $p = 0.46$). Absolute wattle length was significantly different between sexes (one-way ANOVA: $F_{1,44} = 12.01$, $p = 0.001$). However, when body mass was taken into account, there was no significant difference in wattle size between sexes (one-way ANOVA: $F_{1,44} = 0.32$, $p = 0.57$). Therefore, wattle size – when specifically measuring the wattle length – doesn't appear to be different among sexes, regardless of the mass of the individual.

3.2.2 Relative wattle size in relation to body mass

Relative wattle length was correlated with mass overall ($r = -0.45$, $df = 42$, $p = 0.002$). However, this relationship was not significant for females ($r = -0.32$, $df = 18$, $p = 0.172$), or for males ($r = -0.39$, $df = 22$, $p = 0.06$) when tested separately. The trend is negative because a smaller ratio represents a larger relative wattle size. Relative wattle length was significantly different between sexes prior to accounting for mass (one-way ANOVA: $F_{1,42} = 4.885$, $p = 0.033$).

Relative wattle size (surface area measurement) was not significantly correlated with mass ($r = 0.26$, $df = 39$, $p = 0.106$). When tested in each sex separately, the relationship was insignificant for both males ($r = 0.185$, $df = 22$, $p = 0.386$) and females ($r = 0.24$, $df = 20$, $p = 0.286$). Furthermore, relative wattle area was not significantly different between sexes (one-way ANOVA: $F_{1,39} = 1.47$, $p = 0.233$). Bill length was used to calculate relative size and was not correlated with mass ($r = 0.29$, $df = 57$, $p = 0.03$). When tested by sex, the relationship was insignificant for both males ($r = 0.23$, $df = 25$, $p = 0.23$) and females ($r = 0.26$, $df = 28$, $p = 0.16$).

Age was calculated for 2 males and 2 female saddlebacks that had been previously banded on Motuara Island. The two females were aged 12 and 7 years respectively and both had brood-patches, indicating that they were breeding over the 2013-2014 breeding season. The males were aged 12 and 9 years with unconfirmed breeding status. While wattles were unmeasured on the 12 year-old female, the 7 year-old female had a mean wattle length (averaged across both the left and right) of 9.59 mm. This was longer than the mean wattle length for females (mean = 8.96 ± 1.79 mm). On both the 12 and 7 year-old males, mean wattle length (13.26 and 11.15 mm) was greater than the average for males (mean = 10.33 ± 2 mm). The sample size of individuals with confirmed ages was not large enough to test for correlations with mass or wattle length and area.

3.3 Playback experiment results

3.3.1 Wattle engorgement with territorial intrusions

Male South Island saddlebacks were significantly more likely to engorge their wattles in response to the playback of an 'intruding' conspecific male compared to the control playbacks (Fisher's test: $n = 28$, $p < 0.001$). In contrast, female saddlebacks did not engorge their wattles differently between test playbacks and the control (Fisher's test: $n = 16$, $p = 0.55$). This was measured with each bird counted once, although rerunning the test with multiple trials on the same individual did not alter significance levels. Responses are summarised in Fig 3.3. Each individual in these analyses is a unique bird, and only the first response, if they were tested multiple times, was counted. Interestingly, there was a marked difference in female wattle engorgement from when their mate was present or absent (Fig. 3.2). Females engorged their wattles in 79% ($n = 11/14$) of trials in the absence of their mate but only 21% of the time when their mate was present (i.e. within sight) ($n = 6/14$) (Proportion test: $\chi^2 = 4.375$, $df = 1$, $p = 0.036$).

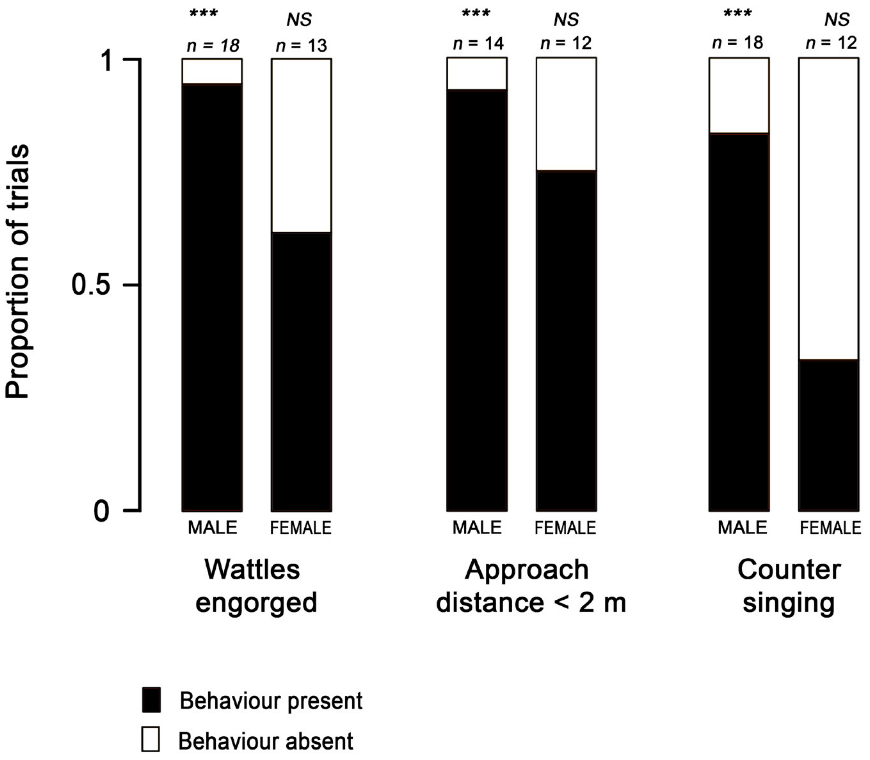

Fig. 3.3. Behavioural responses to the simulated territorial intrusion of a conspecific male. *** denotes $p < 0.001$ and NS for non-significant.

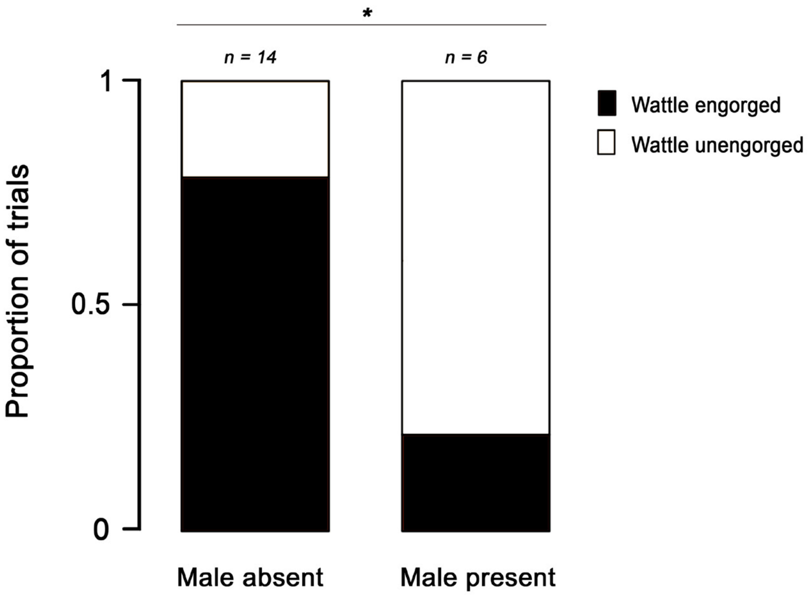

Fig. 3.4. Wattle engorgement responses of female South Island saddleback to the simulated territorial intrusion of a conspecific male, with and without their mate present. A proportion test was used to test for significant difference. * denotes $p < 0.05$.

3.3.2 Playback and counter singing responses to territorial intrusions

Male saddlebacks were significantly more likely to approach the speaker closely (< 2 m) during playback tests than during control tests (Fisher's test: $n = 23, p < 0.001$). In contrast, there was no significant difference in likelihood of approaching the speaker by females (Fisher's test: $n = 23, p = 0.242$). Counter singing behavioural responses followed the same pattern with males more likely to counter sing to a playback broadcast than during control tests (Fisher's test: $n = 26, p = 0.001$). Females were not more likely to do so (Fisher's test: $n = 26, p = 0.98$). All analyses were also run with the repeated trials (3 playback and 1 control trial for 12 birds), and the Fisher's test results remained the same. Of the males that were tested multiple times ($n = 12$) over different days, 83% (10/12) engorged their wattles in the second trial, and 75% (6/8) in the third trial. This does not include control trials. Few female saddlebacks were tested repeatedly ($n = 5$). In males the proportion of positive behavioural responses appeared to decline slightly when tested multiple times (changes in responses over time plotted in Fig. 3.3). In 13 of the 56 experimental trials (23%), males and females were tested together as a pair.

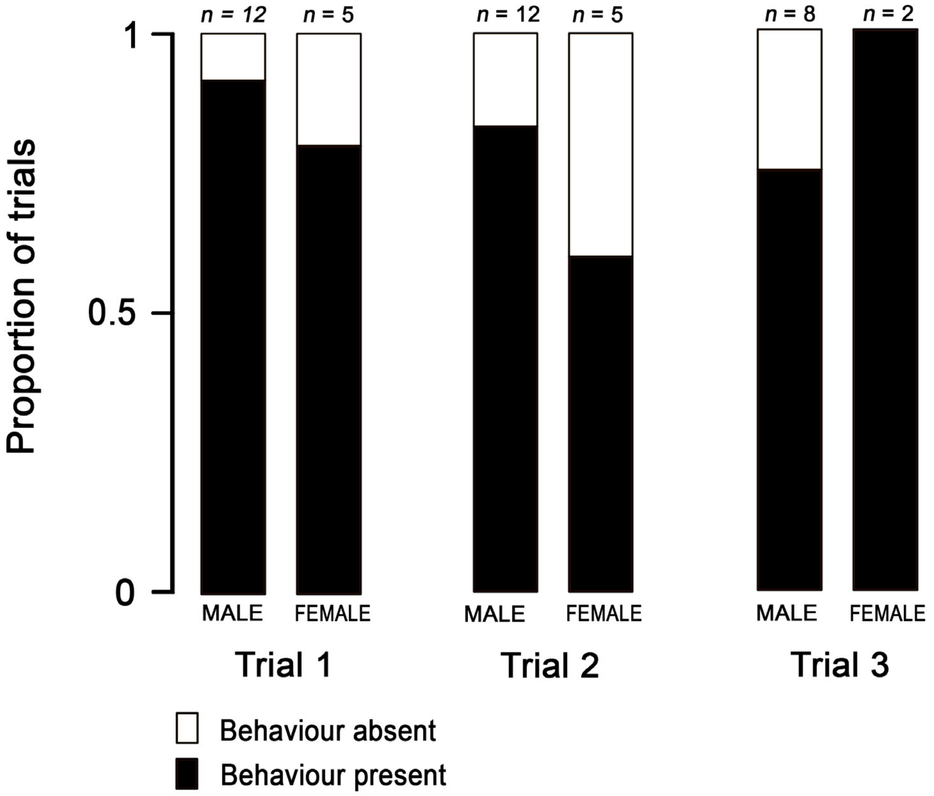

Fig. 3.5. Change in wattle engorgements by South Island saddlebacks across repeated trials.

3.3.3 Wattle size, body mass and behavioural response relationships

Heavier saddleback males were not significantly more likely to engorge their wattles (Binary response GLM: z = -0.371, p = 0.71, *AIC* = 10.98) or have larger wattles (Binary response GLM: z = 0.06, p = 0.95, *AIC* = 10.69), although this may be a product of a small sample size (n = 12). When a behavioural score that incorporated all three responses and the number of times that each individual was tested against mass and absolute (mm) wattle length, it was insignificant overall (GLM: F = 2.47, *df* = 17, p = 0.14, R^2 = 0.17). When separated by sex, absolute wattle length was insignificantly associated with behavioural responses in males (GLM: F = 2.57, *df* = 9, p = 0.14, R^2 = 0.33), and females (GLM: F = 0.69, *df* = 6, p = 0.45, R^2 = 0.18). When body mass was controlled, the overall relationship with absolute wattle size remained insignificant (GLM: F = 0.007, *df* = 17, p = 0.93, R^2 > 0.001). Separately, this relationship was insignificant for males (GLM: F = 0.86, *df* = 17, p = 0.38, R^2 =0.12) and female saddleback (GLM: F = 0.99, *df* = 6, p = 0.36, R^2 = 0.28)

When the wattle size – behavioural response relationships were re-tested using relative wattle size, it remained insignificant overall (GLM: F = 1.9, *df* = 16, p = 0.19, R^2 = 0.12). For only males this was also insignificant (GLM: F = 3.5, *df* = 9, p = 0.09, R^2 = 0.29), as it was for females (GLM: F = 2.82, *df* = 5, p = 0.15, R^2 = 0.39). When body size was accounted for, relative wattle size remained insignificantly related to the behavioural response score overall (GLM: F = 0.038, *df* = 16, p = 0.85, R^2 = 0.002). For both males (GLM: F = 0.84, *df* = 9, p = 0.38, R^2 = 0.09), and females (GLM: F = 2.90, *df* = 5, p = 0.15, R^2 = 0.40) separately it remained insignificant. When these relationships were plotted, most trends indicated a weak relationship (Fig. 3.6 and Fig 3.7).

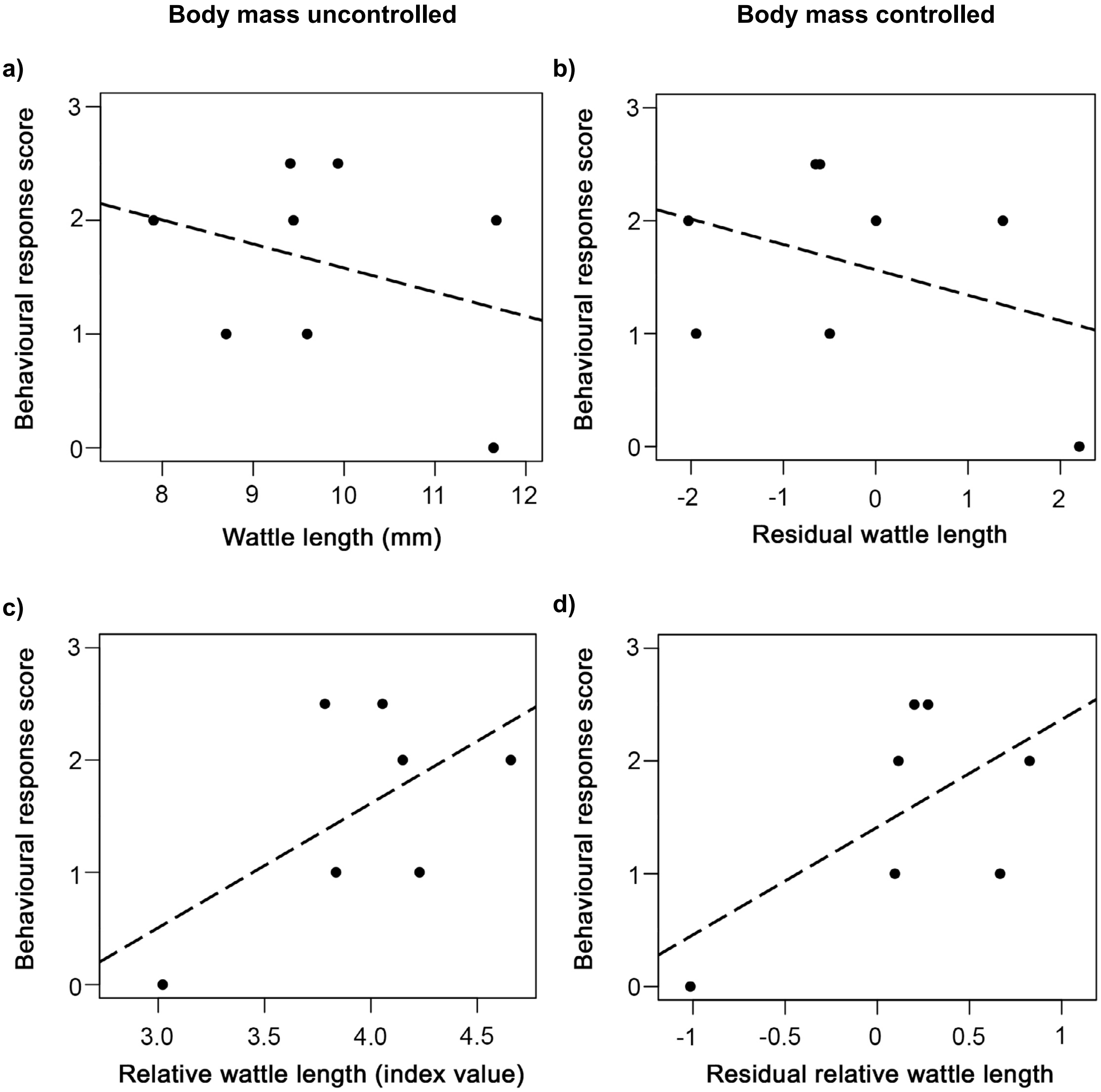

Fig. 3.6. Female saddleback wattle lengths in relation to the behavioural response score (a combined measure of wattle-engorgement, counter singing and speaker approach responses to a simulated conspecific territorial intrusion). (**a**) plot with actual wattle length values uncontrolled for body mass, (**b**) plot with actual wattle length values controlled for body mass, (**c**) plot with relative wattle length values uncontrolled for body mass, (**d**) plot with relative wattle length values controlled for body mass.

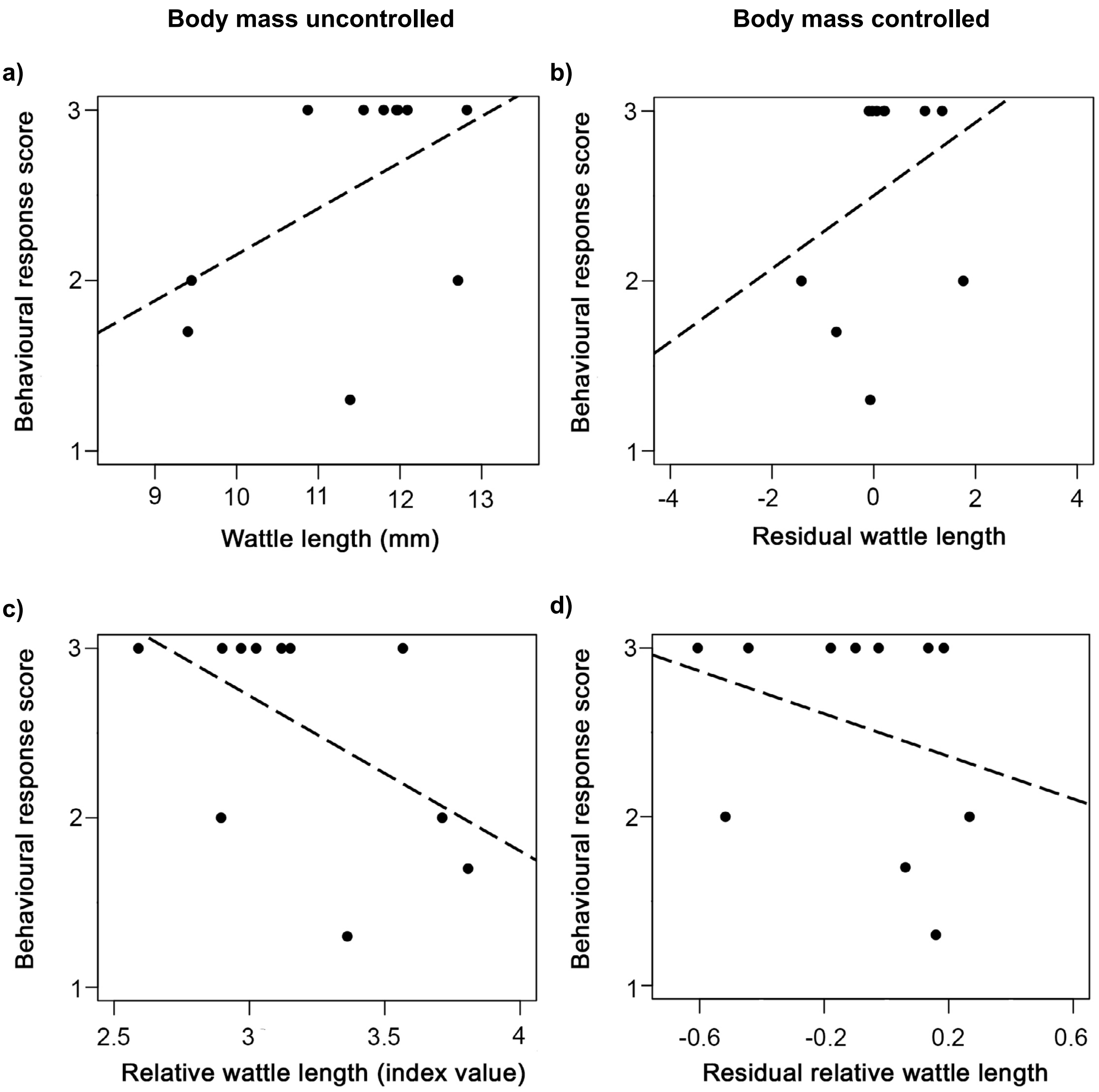

Fig. 3.7. Male saddleback wattle size in relation to the behavioural response score (a combined measure of wattle-engorgement, counter singing and speaker approach responses to a simulated conspecific territorial intrusion). (**a**) plot with actual wattle length values uncontrolled for body mass, (**b**) plot with actual wattle length values controlled for body mass, (**c**) plot with relative wattle length values uncontrolled for body mass, (**d**) plot with relative wattle length values controlled for body mass.

Chapter 4. Discussion

This study provides the first known experimental evidence for the function of wattles in South Island saddleback. Wattles were found to be an important visual signal used by both sexes in territory defence. Behavioural observations also confirm the use of wattles in intra-pair visual communication during the breeding season. Playback of unfamiliar male song elicited aggressive responses from both sexes of saddleback within their territory. Using both observational and experimental approaches, I found evidence of intra- and intersexual functions for wattle engorgement, although the emphasis on the intersexual function appears to be reduced in females under specific circumstances (Fig. 3.4). In the broader perspective, South Island saddleback appear to fit a general pattern of monomorphic ornamentation where females clearly use their ornaments, however they give fewer signals and generally display more infrequently than males (e.g., Penteriani *et al.* 2007, Illes & Yunes-Jimenez 2009, Price *et al.* 2009, Lyon & Montgomerie 2012). Overall evidence is insufficient to definitively state that social rather than sexual selection is operating on the ornaments in this species, or that selection is stronger in one sex. However, there is substantial evidence for dual functionality in wattles as they are used in visual displays during competition over territories (a non-sexual resource), and also in non-aggressive intrapair communication.

4.1 Wattles are monomorphic

Wattle length was found to be correlated with mass in males, but not in females. Hale (2007) measured South Island saddleback on Motuara Island for a study looking at the relationship between immune function and ornamentation and found that wattle length and body mass were significantly correlated in females but not males, which was the opposite of my findings. One explanation for this is that my sample sizes were considerably smaller than Hale's (2007) (e.g., $n = 30$ compared to $n = 152$ females). Another influencing factor may be the capture of females at the beginning of nesting, when body mass can fluctuate (Lima 1986, Moreno 1989, Thomson *et al.* 2010). In this study, 70 percent of the saddlebacks netted were captured during the egg laying and brooding period and this may have affected the measured mass of the females. A female about to lay an egg may be several grams heavier than an equivalent bird who has just laid (Thomson *et al.* 2010). Overall, male saddleback have bigger wattles than females in absolute terms, yet when body mass was accounted for, I found no significant difference in wattle size between sexes. This finding provides evidence for monomorphism in saddlebacks, and corresponds with past research (Hale 2007).

Nevertheless, visual judgement of wattle size among saddlebacks, assuming saddlebacks assess the size of wattles on other individuals, is most likely to be a size judgment relative to other body features such as bill length or overall body size rather than absolute size, which is what is usually compared in most studies (Kraaijeveld *et al.* 2007). Therefore, I calculated wattle size relative to bill length to see if either sex had wattles that were larger relative to their body size. Finding that males have bigger wattles relative to the body would suggest that directional selection, probably via mate choice, was operating on the ornament size (Clutton-Brock 2007). Instead, I found that relative wattle length did not correlate with mass in either sex, which suggests that beak and wattle lengths are traits that are linked to other genetic and ecological factors (e.g., food and habitat quality). Relative wattle area, another measure of relative size, was also insignificantly related to mass. It should be noted that both measures of relative size suffered from a small sample size, and the possibility remains that this may have obscured weaker trends. Bill length in males and females was insignificantly related to mass, so it is possible that both the wattle and beak fluctuate with the quality of resources available (Botero & Rubenstein 2012) and testosterone levels (Bonisoli-Alquati *et al.* 2011).

Measuring wattles during displays when they are engorged is very difficult under field conditions and was not attempted in this study. Thus I could not determine if engorged wattles were similar in size between males and females. However, measurements of engorged wattles would represent the ideal for testing how wattle traits are related to individual fitness in passerines. Other studies have combined both mass and tarsus into an overall fitness score for a more representative indicator of condition (e.g., Pryke *et al.* 2001) that could then be related to ornament size. In preliminary tests, tarsus length in saddlebacks was closely correlated in both sexes with mass. Consequently, I did not combine both measures for the analyses to reduce the potential for increased error and unnecessary complexity. Nevertheless, one of the major drawback of my study design was that all morphological measures of wattles were made when they were flaccid, but they engorge when used in signalling. It is possible that higher immune function may enable 'better' engorgement of wattles and thus two individuals with equally-sized flaccid wattles may have different degrees of engorgement.

4.2 The function of wattle engorgement

Wattle engorgement responses towards unfamiliar conspecific males were strong in male saddlebacks (Fig. 3.3). By simulating conspecific territorial intrusion, the playback experiment provided evidence for the territorial function of wattles (i.e. their use in male-male and male-female territorial interactions). Several past studies have made observations on wattle engorgements in saddlebacks and their use (e.g., Lovegrove 1980, Jenkins & Veitch 1991). Until now however, wattle function in saddlebacks has not been tested experimentally (Higgins *et al.* 2006). I found that males engorged their wattles when defending their territories in 94 % of responses and this was significantly associated with aggressive counter singing and speaker approach behaviour in males (Fig. 3.2). Females also engorged their wattles in territorial encounters but this response was reduced when their mate was present. Females engorged their wattles in 79% of trials in the absence of males but only 21% of the time when a male was in the area. This suggests a sharing of territorial defence roles, which is characteristic of monomorphic mating systems (Kraaijeveld *et al.* 2007). Wattle engorgement was also observed to be a component of the bow-fan-warble displays in both bow-fan-warble assemblies (n = 3) and during responses to playback (n = 45). Engorgement responses to playback were initially tested with each bird only used once in statistical analyses to avoid pseudoreplication, although rerunning the test with multiple trials on the same individual did not alter the levels of significance. A low habituation or learning response was apparent because, of the males that were tested multiple times over different days, 83% engorged their wattles in the second trial compared to 91%, but this was reduced to 75% in the third trial.

While this study tested the *context* of a signalling behaviour more that the actual signalling receiver response (e.g., Smith & Evans 2013), wattle signalling in saddleback appears to function differently from that reported in non-passerines. In junglefowl, a sexually dimorphic species where the male has much more prominent ornaments than the female, wattles increased the conspicuousness of visual food-related 'tidbitting' displays in the male (Smith *et al.* 2009). In saddlebacks (and unlike junglefowl), wattles are the only fleshy ornament present. With my results I cannot rule out the possibility that wattles are selected for an ancillary 'signalling enhancing function' to non-integumentary ornaments such as the rufous 'saddle'. In every case when wattle engorgement was viewed under natural conditions it was as part of the bow-fan-warble display. In the playback experiment, the lack of a visible opponent appeared to prevent most saddlebacks tested from initiating a full bow-fan-warble display towards the speaker.

However, when other individuals are present, such as at bow-fan-warble assemblies ('social gatherings') there can be vigorous displaying between sexes – involving many individuals from a number of territories (Blackburn 1964). Many of these interactions also appear to be extra-pair (i.e. not with their mate) and certainly deserve further study. From my two observations of bow-fan-warble assemblies, wattles are engorged in most individuals that could be properly sighted, thus supporting the idea that wattles are central to close-range visual displays.

Drawing together this evidence it is possible to hypothesize how selection on wattle engorgement in the South Island saddleback may operate. Zahavi (1975) suggested that sexual selection is effective because it improves the ability of the selecting sex to detect quality in the selected sex. In North Island saddleback, both sexes appear to be selected and selectors (Higgins *et al.* 2006), and this may also be the case in South Island saddleback. Wattle engorgement may function both as short term signals of fitness whereby features such as colour, surface quality (e.g. compare the wattle skin in Fig. 3.2 a and g), or mottling in the engorged wattle may serve as indicators of immune function over the short term (Hale & Briskie 2007, Bonisoli-Alquati *et al.* 2011). In contrast, overall wattle size and symmetry when engorged, could be long-term indicators of fitness, although it is yet unknown just how much fluctuating asymmetry (Polak & Starmer 2005) may affect a saddleback's breeding opportunities.

As noted in the introduction, ornamental traits can be classified as either dynamic (e.g. integument colouration) or non-dynamic (e.g. feather length) (Tobias *et al.* 2012). Integument colouration, and in this study, engorged wattle size and colouration, may be used to continually assess a partner's quality and adjust parental investment accordingly. In such situations high quality individuals may elicit enhanced parental care from their partner through ornament display (Tobias *et al.* 2012). Roulin (1999) and Griggio *et al.* (2003) have shown that monomorphically ornamented male barn owls (*Tyto alba*), and rock sparrows (*Petronia petronia*), adjust their provisioning rate according to their partner's ornamentation, suggesting that mutual ornaments may indeed be used in this way. If the difficulties in measuring engorged wattle size in saddlebacks in the field can be overcome, then it may be possible to further test how variation in wattle engorgement affects the outcome of interactions between birds, and ultimately how it may affect their fitness.

4.3 Wattles and territoriality

In South Island saddleback, female wattle engorgement changed depending on the presence of their mate. This was unexpected and is preliminary evidence of the importance of territories for both members of a pair. It is a finding that could be tested in the future to gain better understanding of monomorphic ornamentation in the species. This finding was consistent with the hypothesis that success in competition by both members of a pair can be an important evolutionary driver of monomorphic ornamentation (Kraaijeveld *et al.* 2007). From my limited data, competition appears to occur mainly over territories (pers. obs.) but may also occur in partnership formation (Higgins *et al.* 2006). In future studies it would be useful to test whether females remain faithful to their territories when their mates are removed (see mate-removal experiments in Morton *et al.* 2000, Stutchbury & Morton 2001). This would enable the value of territories to South Island saddleback to be quantified and with it, the costs and benefits of territory-related signals such as wattles.

Emphasis on resource defence and its intricate link to visual signalling and wattle engorgement may be rooted in one key life history trait of saddleback: year-round territoriality (Pierre 2000). Although this form of avian territoriality may be one of the most common its evolutionary implications remain poorly understood (Stutchbury & Morton 2001, Tobias *et al.* 2011). Generally, it is associated with low adult mortality, delayed dispersal and social monogamy with little or no extra-pair copulation (Fleischer *et al.* 1997, Russell *et al.* 2004). These are all features of saddleback systems, although levels of extra-pair copulation are yet untested (Higgins *et al.* 2006). The main implications of this are intense territorial competition and increased value of breeding partnerships (Morton *et al.* 2000). My results do not contradict the two broad predictions arising out of this: firstly, year-round resource competition is likely to exert positive selection on elaborate traits in both sexes (West-Eberhard 1983) and secondly, long-term monogamy leads to choosiness and therefore ornamentation in both sexes. A final alternative hypothesis for wattle use may be that displaying individuals are trying to attract a secondary mate (e.g. male starlings, Komdeur *et al.* 2005), or extrapair copulations (as in many passerine birds). However, I did not detect any differences, other than the clearly different vocalisations, between female displays with their mate, and with non-paired males.

If saddlebacks place high value on territories, which appears to be the case (Pierre 2001), then this is inconsistent with evidence from other socially monogamous passerines in temperate climates (Tobias *et al.* 2011). In some socially monomorphic tropical passerines, females have been found to be more faithful to territories than partners (Gill & Stutchbury 2006), and dusky antbird (*Cercomacra tyrannina*) females have been found to hold solo territories for up to a year if the male disappears (Morton *et al.* 2000). In contrast, experimental male-removal in temperate zones species has revealed that females will abandon their territories soon after their mate is removed and seek a new mate (e.g., Harper 1985, Klatt & Ritchison 1994). This implies that ecological resources are of greater value to females in stable tropical systems, where the benefits of defending resources year-round are likely to be greater (Tobias *et al.* 2011). In an avian system comparable to saddlebacks, male *Hypocnemis* antbirds were temporarily removed from their territories, after which the females defended them and then in some cases appeared to use the territories for attracting another male (Seddon & Tobias 2006). This territorial basis for monomorphism suggests that the reasons for display using an ornament (monomorphic song in antbirds and wattles in saddleback) may be the same in males and females; i.e. they both function in mate attraction and territory defence (Catchpole & Slater 2008).

Interestingly, it appears that monomorphism and territoriality in saddlebacks is more similar to the previously studied tropical (Seddon 2005), rather than temperate monomorphically ornamented species (Catchpole & Slater 2008). If saddlebacks are experimentally shown to use their wattles for mate attraction as well as for territorial defence (as presented in this study) then they would provide a rare example of a temperate bird where female ornaments have dual functions in intra- and intersexual interactions (Tobias *et al.* 2012). Demonstrating that saddleback wattles have the same functions in territoriality and mate choice strongly implies that selection pressures on the ornaments themselves are the same across sexes. This contrasts with many systems in which selection appears to act asymmetrically and sexually dimorphic ornamentations are seen (Clutton-Brock 2007, Clutton-Brock & Huchard 2013). Overall, my observations on wattle use by saddlebacks in territorial displays closely align with the findings regarding vocal ornaments in *Hypocnemis* antbirds (Seddon & Tobias 2006, Tobias & Seddon 2009, Tobias *et al.* 2011). Further work on both these and other species should shed light on the dynamics of selection by revealing the evolutionary pathway by which long-term monogamy and elevated resource competition can lead to both sexes converging towards the same signalling strategy.

4.4 Dual functionality for wattles

An alternative hypothesis to the view that wattles perform dual functions (i.e both in aggressive territorial defence and non-aggressive mate attraction) is that the monomorphic ornaments function exclusively in intrapair communication. This would be between the male and female when they are interacting with an unfamiliar conspecific in both aggressive and non-aggressive interactions. However, three findings suggest that the intended receiver of wattle engorgement and bow-fan-warble signalling behaviour is not exclusively the mate. Firstly, both male and female saddlebacks engorged their wattles in response to the playback of an unfamiliar male within their territory regardless of whether their mate was present, although the presence of a male appears to alter the level of female responses (Fig. 3.4). Secondly, in the closely-related North Island saddleback, pairs spend extended periods of time foraging in proximity with each other, and communicate using 'quiet song' warbles (Higgins *et al.* 2006), yet no engorgement was observed in conjunction with these vocalisations, unless a bow-fan-warble display was initiated. Observations in the South Island saddleback are similar (pers. obs.). Thirdly, in North Island saddleback, loud male rhythmical song has been shown to play a key role in 'mutual avoidance behaviour' of adult males, where they frequently communicate vocally but rarely visually interact with neighbours during territory defence (Jenkins 1978). Parker *et al.* (2013) and Pierre (2001) have noted that South Island saddleback behave similarly, which is supported by my observations during this study. This evidence of a link between loud male song and wattle engorgement when the level of aggression is 'scaled-up' suggests that wattle engorgement is not solely used in intrapair interactions.

Unfortunately, I was unable to collect data on wattle-use outside of the breeding season. Therefore, it is possible that the signalling function (and thus selection pressures) on wattles vary with season. Exploring how wattle engorgement vary between seasons is an important next step in quantifying the relative levels of wattle use in intra- and intersexual interactions (Tobias *et al.* 2011). Therefore, with this in mind, I cannot rule out the possibility that wattle function changes with season, possibly reduced to a function in maintaining contact between pair members or strengthening pair-bonds in the non-breeding season. However, the strength of responses to an unfamiliar conspecific and evidence of year-round territoriality in saddlebacks indicate that wattle-use likely occurs outside the breeding season (Blackburn 1964, Jenkins 1978, Lovegrove 1980).

4.5 Selection for monomorphism

As discussed by Tobias *et al.* (2009), convergent signals used for territoriality make sense, yet convergent mating signals appear to contradict deep-rooted evolutionary ideas about species recognition and character displacement. If wattle engorgements (and associated bow-fan-warble displays) are adaptive in intraspecific territorial species (e.g., Grether *et al.* 2009), then this raises the interesting question of why sexual functions are maintained as part of the same signal, rather than transferred to a less ambiguous one? My results do not conclusively answer this question; however, they are consistent with the theory that females should assess the most informative male trait only if the benefits of doing so outweigh the costs of mistaken identity (Gröning & Hochkirch 2008). It may be that wattles are the most distinct ornament that a saddleback has (other than its song), and therefore females benefit from detecting and selecting males based on a socially-enforced honest ornament such as wattles (Kodric-Brown & Brown 1984). Hale (2008), demonstrated using the immunocompetence hypothesis that in female saddlebacks, wattle condition could serve as a honest 'short-term' signal of immune condition and parasite load (Hamilton & Zuk 1982). Over time, the overall size and symmetry may also function as honest signals of genetic fitness (West-Eberhard 2003).

Another interesting idea for future testing would be whether wattles are also used in the visual identification of other specific saddleback individuals. Signalling theory suggests that both females and males should rely on a suite of signals to identify specific individuals (in saddlebacks they could range from the vocal song to the visual signals of the wattles, saddle and tail fanning) where some act as 'back-up' (e.g., Hankison & Morris 2003). These 'perceptual and visual safety nets' would bring developmental and energetic costs of their own, thus possibly explaining positive selection on dual functionality in ornaments such as wattles (Tobias *et al.* 2011).

4.6 Wattles and mate-pairing hypotheses

Kraaijeveld *et al.* (2007) found in their review of monomorphism that mutual mate preferences based on mutual ornaments may be common. The prediction of the mutual sexual selection hypothesis is that it should result in assortative mating (Trivers 1972). Theoretically, there are four (not mutually exclusive) processes that may result in a pattern of assortative paring (Burley 1983): (1) Directional mate preferences where both sexes pair preferentially with a highly ornamented individual. In this process, highly ornamented individuals would

would obtain highly ornamented partners, leaving less ornamented individuals to pair among themselves. If the degree of ornamentation reflects some aspect of individual fitness (which has been suggested in female saddleback by Hale 2008), directional mate preferences should lead to directional selection on the ornament. (2) Assortative mate preferences occur in only one or both sexes. This occurs when highly ornamented individuals prefer highly ornamented individuals and less ornamented individuals prefer less ornamented partners. This mate-paring process should lead to assortative pairing if one or both sexes are selective and could result in disruptive selection (Burley 1983). No evidence was found in this study of disruptive selection in wattles (Figs. 3.6 and 3.7). (3) Convergence in degree of ornamentation among partners: this could arise because partners in a long-term pair bond may tend to occupy a similar physical and social environment and via phenotypic plasticity result in increased resemblance between both individuals over time (West-Eberhard 2003). (4) Finally, pair formation and ornamentation could be correlated to a third factor, such as age or arrival date in the breeding area, leading to a positive correlation between ornament size in the male and female of a pair (e.g., Kraaijeveld *et al.* 2007).

How assortative pairing operates in saddleback is not fully understood, and answering this question was beyond the scope of this study. This does not however exclude preferential selection by saddlebacks with smaller ornaments towards other individuals with smaller ornaments, and this remains something which would need to be specifically tested. Assortative pairing, according to Burley (1983), assumes that mate choice is not linked to non-sexual resources such as territories, however based on the importance of territoriality this is unlikely to be the case in saddleback (see Seddon & Tobias 2006). An often over-looked factor when investigating signalling quality and mate choice is the effect of age on ornaments (Kraaijeveld *et al.* 2007). In study systems where the level of ornamentation is highly correlated with age, the strength of the correlation can make it difficult to statistically separate the relative influences of age and ornamentation on partner choice and the measured fitness variables (e.g., Komdeur *et al.* 2005). In some species, ornaments may be even used to directly assess the preferred age of a mate. For example, in species with biparental care, choosing an older mate may provide direct fitness benefits due to improved reproductive performance with age (Forslund & Pärt 1995). In this study, correlates of age with wattle size or mass could not be tested. However, wattles in three birds (aged 7, 12 and 12 years respectivley) were larger than the mean wattles size and two females aged 9 and 12 were found to be breeding, thus indicating that wattles don't reduce with age, and that even 9 and 12 year-old birds are capable of maintaining a territory.

4.7 Wattles and social selection

A common assumption in behavioural ecology exists stating that sexual selection is the predominant process behind the evolution of ornaments (e.g., Leitão & Riebel 2003), but this is not necessarily always the case (Lyon & Montgomerie 2012). Evidence for competition over non-sexual resources in birds is growing, and with it the recognition that social selection mechanisms can be a more comprehensive framework with which to understand species' ornaments. West-Eberhard (1983) was among the first to note a correlation between monomorphically bright signal colouration and territoriality. Although this concept has yet to be widely tested or accepted (Clutton-Brock & Huchard 2013), it is being revisited with greater frequency (Lyon & Montgomerie 2012; Roughgarden 2012; Tobias *et al.* 2012). The wider perspective of social selection can help to explain puzzling patterns in phenotypic evolution. For example, Friedman et al. (2009) first noted that species with migratory life-histories were often associated with a loss of bright plumage in female birds. Similarly, Price *et al.* (2009) used a phylogenetic approach to show that several factors appear to select against female song, including brood parasitism and colonial breeding. Within the framework of sexual selection these two observations are not easily explained. However, in the framework of social selection they make more sense as indirect relationships driven by the relaxation of social competition. In other words, with migration and colonialism comes the loss of year-round territoriality that in turn better explains the de-ornamentation of females across evolutionary time.

The significant insights that social selection theory has to offer are only relevant if saddlebacks (or any study species) are using their ornaments to compete for resources that fall outside the bounds of sexual selection theory. Tobias *et al.* (2011) highlight that the relevance of sexual selection theory depends on whether competition relates solely to mates and mating opportunities. As previously discussed, this can be difficult to determine, and I cannot unequivocally show that competition in saddleback was over non-sexual resources. My results provide several lines of evidence suggesting that saddleback use wattles and wattle engorgement in territorial defence, however possible changes in the non-breeding season are unquantified. Tobias *et al.* (2011) provide one of the few studies on mutual ornamentation that look at a species year-round, and while a number of comparisons with their findings can be drawn, further studies on saddlebacks are required to unequivocally show that territorial competition in saddlebacks is over non-sexual resources. This would require determining territorial defence during non-breeding and also investigating solo defence by unpaired individuals (e.g., Sogge *et al.* 2007, Townsend *et al.* 2010).

In conclusion, the results of this study offer evidence of wattles and wattle engorgement as an important visual signal used in both territorial and non-territorial interactions. I found no evidence of strong directional selection on wattles, although this could be the result of small sample sizes. My results add to what is known about visual signalling in saddleback, and also add to the growing body of empirical and theoretical research suggesting that social competition for non-sexual resources contributes to selection on exaggerated or ornamental traits. Territoriality is an important trait in South Island saddleback, and that the selection pressures on wattle ornaments are currently best explained in a social selection theory framework (West-Eberhard 1983, Lyon & Montgomerie 2011).

Acknowledgements

I thank my supervisor, Dr. Jim Briskie, for his support, dry humour, keen scientific insight and willingness to let me take on this project. Field work on a remote New Zealand island was more than I ever hoped for in an honours project, and for enabling that, I am immensely grateful. I also thank my co-supervisor, Dr. Ximena Nelson, for her encouraging feedback, wide-ranging advice and refreshing lack of pretence.

The Department of Conservation (DOC) granted permission to work on Motuara Island, and I thank the DOC Picton office for all their assistance. I am particularly grateful to Frank Rosie for his friendliness and help – especially when it involved his weekends and public holidays. I thank Cougar Line and particularly Fred Gaudin and Jill Evans for their help with transport to Motuara and back (several times over), as well as their continuous interest in my research.

I am very grateful to Paolo Garrido and Julian Krönert for working as my field assistants on Motuara. Their patience, good humour, close interest in the project and willingness to put up with my idiosyncrasies made the long days in the bush immeasurably more enjoyable. Robyn White, Christina Wu, Nyil Khwaja and Tina Sandersfeld all helped multiple times with transport from Christchurch to Kaikoura to Picton. All were great company on the island for the short times they were there – thanks for being so willing to help.

Although they had little direct involvement in this project, Dr. Jason Tylianakis and Dr. Daniel Stouffer greatly enriched my learning and ecological understanding this year. They pushed me to embrace and tackle ecological and statistical problems head-on. This has proved immensely gratifying, which in turn made tacking the analysis part of this project all the more enjoyable. I would not be writing this if it weren't for the people responsible for fuelling my interest in biology: David Moyer, Neil and Liz Baker, Sue Stolberger, Rob Glen, Patrick O'Brian and Jonathan Kingdon (via *East African Mammals: An Atlas of Evolution in Africa*) – thank you all very much.

I thank my fellow honours students (Billy, Chris, Olivia, Roseanna, Rosie and Simona) for their encouragement and good humour. There is little doubt that this year would have been very different, less fun and a lot more predictable without you. Many thanks go to Laura Azzani for encouragement and vital statistical advice. Aude Thierry's help in organising field equipment was also much appreciated. Thanks also go to Patrick Cotter for his support in numerous practical ways: he's helped with a place to live, a vehicle to drive and, along with Brent Granger, has been a dependable mate. Many *asantes* to Shera Moyer for being an understanding friend and incredible proof-reader throughout the year. Last but not least, I thank my family and especially my parents; Tim & Adrienne Lloyd-Jones, for their constant love, support, proof-reading and encouragement.

References

Amundsen T. 2000. Why are female birds ornamented? *Trends in Ecology and Evolution* 15: 149-155.

Amundsen T, Forsgren E, Hansen LT. 1997. On the function of female ornaments: male bluethroats prefer colourful females. *Proceedings of the Royal Society B-Biological Sciences* 264: 1579-1586.

Amundsen T, Pärn H. 2006. Female coloration: review of functional and non-functional hypothesis. In: Hill GE, McGraw KJ. (eds.), *Bird coloration, vol. II: Function and evolution*. Cambridge, MA: Harvard University Press, pp. 280-345

Andersson M, Simmons LW. 2006. Sexual selection and mate choice. T*rends in Ecology & Evolution* 21: 296-302.

Andersson MB. 1994. *Sexual selection*. Princeton, NJ: Princeton University Press.

Azar JF, Bell BD, Burns KC. 2013. Chatter-call harmonics in the North Island Saddleback: Do they play a role in ranging? *Emu* 113: 161-167.

Badyaev AV, Hill GE. 2000. The evolution of sexual dimorphism in the house finch. I. Population divergence in morphological covariance structure. *Evolution* 54: 1784-1794.

Badyaev AV, Hill GE. 2003. Avian sexual dichromatism in relation to phylogeny and ecology. *Annual Review of Ecology, Evolution, and Systematics* 34: 27-49.

Baker RR, Parker G. 1979. The evolution of bird coloration. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 287: 63-130.

Baratti M, Ammannati M, Magnelli C, Massolo A, Dessì-Fulgheri F. 2010. Are large wattles related to particular MHC genotypes in the male pheasant? *Genetica* 138: 657-665.

Beaman M, Madge S. 1998. *The handbook of bird identification: for Europe and the western Palearctic.* London: A&C Black.

Bennett PM, Owens IP. 2002. *Evolutionary ecology of birds: Life histories, mating systems and extinction.* Oxford: Oxford University Press.

Bernatchez L, Landry C. 2003. MHC studies in nonmodel vertebrates: what have we learned about natural selection in 15 years? *Journal of Evolutionary Biology* 16: 363-377.

Blackburn A. 1964. Some observations on behaviour of the North Island saddleback in August. *Notornis* 11: 87-92.

Bleiweiss R. 1992. Reversed plumage ontogeny in a female hummingbird: implications for the evolution of iridescent colours and sexual dichromatism. *Biological Journal of the Linnean Society* 47: 183-195.

Bonisoli-Alquati A, Rubolini D, Caprioli M, Ambrosini R, Romano M, Saino N. 2011. Egg testosterone affects wattle color and trait covariation in the ring-necked pheasant. *Behavioral Ecology and Sociobiology* 65: 1779-1790.

Botero CA, Rubenstein DR. 2012. Fluctuating environments, sexual selection and the evolution of flexible mate choice in birds. *PloS ONE* 7: e32311.

Briganti F, Papeschi A, Mugnai T, Dessí-Fulgheri F. 1999. Effect of testosterone on male traits and behaviour in juvenile pheasants. *Ethology Ecology & Evolution* 11: 171-178.

Buchholz R. 1997. Male dominance and variation in fleshy head ornamentation in wild turkeys. *Journal of Avian Biology* 28: 223-230.

Burley N. 1981. The evolution of sexual indistinguishability. In: Alexander RD & Tinkle DW. (eds.), *Natural Selection and Social Behaviour*. New York: Chiron Press.

Burley N. 1983. The meaning of assortative mating. *Ethology and Sociobiology* 4: 191-203.

Butcher GS, Rohwer S. 1989. The evolution of conspicuous and distinctive coloration for communication in birds. *Current Ornithology* 6: 51-108.

Cash B, Gaze P. 2000. Restoration of Motuara Island–Queen Charlotte Sound. *Ecological Management* 8: 31-36.

Catchpole CK, Slater PJ. 2008. *Bird Song: Biological Themes and Variations.* Cambridge: Cambridge University Press.

Chaine AS, Tjernell KA, Shizuka D, Lyon BE. 2011. Sparrows use multiple status signals in winter social flocks. *Animal Behaviour* 81: 447-453.

Childress RB, Bennun LA. 2002. Sexual character intensity and its relationship to breeding timing, fecundity and mate choice in the great cormorant *Phalacrocorax carbo lucidus*. *Journal of Avian Biology* 33: 23-30.

Clutton-Brock T. 2007. Sexual selection in males and females. *Science* 318: 1882-1885.

Clutton-Brock T, Huchard E. 2013. Social competition and selection in males and females. *Philosophical Transactions of the Royal Society B: Biological Sciences* 368: 201-217.

Clutton-Brock T, Sheldon BC. 2010. Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. *Trends in Ecology & Evolution* 25: 562-573.

Clutton-Brock T, Huchard E. 2013. Social competition and its consequences in female mammals. *Journal of Zoology* 289: 151-171.

Cornwallis CK, Uller T. 2010. Towards an evolutionary ecology of sexual traits. *Trends in Ecology & Evolution* 25: 145-152.

Cunningham E, Birkhead T. 1998. Sex roles and sexual selection. *Animal Behaviour* 56: 1311-1321.

Darwin C. 1871. *The descent of man, and selection in relation to sex.* London: John Murray.

Doutrelant C, Grégoire A, Gomez D, Staszewski V, Arnoux E, Tveraa T, Faivre B, Boulinier T. 2013. Colouration in Atlantic puffins and blacklegged kittiwakes: monochromatism and links to body condition in both sexes. J*ournal of Avian Biology* 44: 451-460.

Dunn PO, Whittingham LA, Pitcher TE. 2001. Mating systems, sperm competition, and the evolution of sexual dimorphism in birds. *Evolution* 55: 161-175.

Endler JA, McLellan T. 1988. The processes of evolution: toward a newer synthesis. *Annual Review of Ecology and Systematics* 19: 395-421.

Figuerola J, Green AJ. 2000. The evolution of sexual dimorphism in relation to mating patterns, cavity nesting, insularity and sympatry in the Anseriformes. *Functional Ecology* 14: 701-710.

Fisher RA. 1958. *The genetical theory of natural selection.* NY: Dover Press.

Fleischer RC, Tarr CL, Morton ES, Sangmeister A, Derrickson KC. 1997. Mating system of the dusky antbird, a tropical passerine, as assessed by DNA fingerprinting. *Condor* 512-514.

Fleishman LJ, Leal M, Sheehan J. 2006. Illumination geometry, detector position and the objective determination of animal signal colours in natural light. *Animal Behaviour* 71: 463-474.

Folstad I, Karter AJ. 1992. Parasites, bright males, and the immunocompetence handicap. A*merican Naturalist* 603-622.

Forslund P, Pärt T. 1995. Age and reproduction in birds—hypotheses and tests. *Trends in Ecology & Evolution* 10: 374-378.

Friedman NR, Hofmann CM, Kondo B, Omland KE. 2009. Correlated evolution of migration and sexual dichromatism in the New World orioles (Icterus). *Evolution* 63: 3269-3274.

Gallistel CR, Gelman R. 2000. Non-verbal numerical cognition: From reals to integers. *Trends in Cognitive Sciences* 4: 59-65.

Gil D, Gahr M. 2002. The honesty of bird song: multiple constraints for multiple traits. *Trends in Ecology & Evolution* 17: 133-141.

Gill SA, Stutchbury BJ. 2006. Long-term mate and territory fidelity in neotropical buff-breasted wrens (*Thryothorus leucotis*). *Behavioral Ecology and Sociobiology* 61: 245-253.

Grafen A. 1990. Biological signals as handicaps. *Journal of Theoretical Biology* 144: 517-546.

Grether GF, Losin N, Anderson CN, Okamoto K. 2009. The role of interspecific interference competition in character displacement and the evolution of competitor recognition. *Biological Reviews* 84: 617-635.

Griggio M, Matessi G, Pilastro A. 2003. Male rock sparrow (*Petronia petronia*) nest defence correlates with female ornament size. *Ethology* 109: 659-669.

Griggio M, Zanollo V, Hoi H. 2010. Female ornamentation, parental quality, and competitive ability in the rock sparrow. J*ournal of Ethology* 28: 455-462.

Gröning J, Hochkirch A. 2008. Reproductive interference between animal species. *The Quarterly Review of Biology* 83: 257-282.

Guilford T, Dawkins MS. 1991. Receiver psychology and the evolution of animal signals. *Animal Behaviour* 42: 1-14.

Hale KA. 2007. Population bottlenecks and the risk of parasitic and microbiological infections in the endangered saddleback (*Philesturnus caruncuatus*) and South Island robin (*Petroica australis*). Unpub. MSc thesis, University of Canterbury: Christchurch.

Hale KA. 2008. Disease outbreak amongst South Island saddlebacks (*Philesturnus carunculatus carunculatus*) on Long Island. Science & Technical Pub., Department of Conservation.

Hale KA, Briskie JV. 2007. Decreased immunocompetence in a severely bottlenecked population of an endemic New Zealand bird. *Animal Conservation* 10: 2-10.

Hale KA, Briskie JV. 2009. Rapid recovery of an island population of the threatened South Island Saddleback (*Philesturnus c. carunculatus*) after a pathogen outbreak. *Bird Conservation International* 19: 239-253.

Hamilton WD. 1964. The genetical evolution of social behaviour. I. *Journal of Theoretical Biology* 7: 1-16.

Hamilton WD, Zuk M. 1982. Heritable true fitness and bright birds: a role for parasites? *Science* 218: 384-387.

Hankison SJ, Morris MR. 2003. Avoiding a compromise between sexual selection and species recognition: female swordtail fish assess multiple species-specific cues. *Behavioral Ecology* 14: 282-287.

Harper D. 1985. Pairing strategies and mate choice in female robins *Erithacus rubecula. Animal Behaviour* 33: 862-875.

Harper DGC. 1999. Feather mites, pectoral muscle condition, wing length and plumage coloration of passerines. *Animal Behaviour* 58: 553-562.

Hawkins GL, Hill GE, Mercadante A. 2012. Delayed plumage maturation and delayed reproductive investment in birds. *Biological Reviews* 87: 257-274.

Hettyey A, Hegyi G, Puurtinen M, Hoi H, Török J, Penn DJ. 2010. Mate choice for genetic benefits: time to put the pieces together. *Ethology* 116: 1-9.

Higgins PJ, Peter JM, Cowling SJ. (2006) *Handbook of Australian, New Zealand & Antarctic birds. Volume 7: Boatbill to Starlings.* Melbourne: Oxford University Press, pp 986-1012

Holdaway RN, Worthy TH, Tennyson AJ. 2001. A working list of breeding bird species of the New Zealand region at first human contact. *New Zealand Journal of Zoology* 28: 119-187.

Hooper PL, Miller GF. 2008. Mutual mate choice can drive costly signalling even under perfect monogamy. *Adaptive Behavior* 16: 53-70.

Hooson S, Jamieson IG. 2003. The distribution and current status of New Zealand Saddleback Philesturnus carunculatus. *Bird Conservation International* 13: 79-95.

Hooson S, Jamieson IG. 2004. Variation in breeding success among reintroduced island populations of South Island Saddlebacks *Philesturnus carunculatus carunculatus. Ibis* 146: 417-426.

Illes AE, Yunes-Jimenez L. 2009. A female songbird out-sings male conspecifics during simulated territorial intrusions. *Proceedings of the Royal Society B: Biological Sciences* 276: 981-986.

Jamieson IG, Grant JL, Beaven BM. 2005. Capture and handling of saddlebacks during pre-nesting does not affect timing of egg-laying or reproductive success. *Notornis* 52: 81-87.

Jenkins PF. 1978. Cultural transmission of song patterns and dialect development in a free-living bird population. *Animal Behaviour* 26: 50-78.

Jenkins PF, Veitch CR. 1991. Sexual dimorphism and age-determination in the North Island saddleback (*Philesturnus carunculatus rufaster*). *New Zealand Journal of Zoology* 18: 445-450.

Johnsen TS, Hengeveld JD, Blank JL, Yasukawa K, Nolan Jr V. 1996. Epaulet brightness and condition in female red-winged blackbirds. *Auk* 113: 356-362.

Johnsgard PA. 1999. *The pheasants of the world: biology and natural history.* Washington, DC: Smithsonian Institution Press.

Jones AG, Ratterman NL. 2009. Mate choice and sexual selection: what have we learned since Darwin? *Proceedings of the National Academy of Sciences* 106: 10001-10008.

Jones IL, Hunter FM. 1998. Heterospecific mating preferences for a feather ornament in least auklets. *Behavioral Ecology* 9: 187-192.

Kimball RT, Braun EL. 2008. A multigene phylogeny of galliformes supports a single origin of erectile ability in non-feathered facial traits. *Journal of Avian Biology* 39: 438-445.

Kirkpatrick M. 1982. Sexual selection and the evolution of female choice. *Evolution* 1-12.

Klatt PH, Ritchison G. 1994. The effect of mate removal on the vocal behavior and movement patterns of male and female eastern screech-owls. *Condor* 485-493.

Kodric-Brown A, Brown JH. 1984. Truth in advertising: the kinds of traits favored by sexual selection. *American Naturalist* 309-323.

Kokko H, Brooks R, Jennions MD, Morley J. 2003. The evolution of mate choice and mating biases. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 270: 653-664.

Komdeur J, Oorebeek M, van Overveld T, Cuthill IC. 2005. Mutual ornamentation, age, and reproductive performance in the European starling. *Behavioral Ecology* 16: 805-817.

Kraaijeveld K, Kraaijeveld-Smit FJ, Komdeur J. 2007. The evolution of mutual ornamentation. *Animal Behaviour* 74: 657-677.

Kroodsma DE. 1989. Suggested experimental designs for song playbacks. *Animal Behaviour* 37: 600-609.

Kroodsma DE, Byers BE, Goodale E, Johnson S, Liu W. 2001. Pseudoreplication in playback experiments, revisited a decade later. *Animal Behaviour* 61: 1029-1033.

Lande R. 1980. The genetic covariance between characters maintained by pleiotropic mutations. *Genetics* 94: 203-215.

Lande R, Arnold SJ. 1985. Evolution of mating preference and sexual dimorphism. *Journal of Theoretical Biology* 117: 651-664.

Langmore N, Bennett A. 1999. Strategic concealment of sexual identity in an estrilid finch. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 266: 543-550.

Langmore NE. 1998. Functions of duet and solo songs of female birds. *Trends in Ecology & Evolution* 13: 136-140.

LeBas NR. 2006. Female finery is not for males. T*rends in Ecology & Evolution* 21: 170-173.

Leitão A, Riebel K. 2003. Are good ornaments bad armaments? Male chaffinch perception of songs with varying flourish length. *Animal Behaviour* 66: 161-167.

Lima SL. 1986. Predation risk and unpredictable feeding conditions: determinants of body mass in birds. *Ecology* 377-385.

Lindstedt SL, Calder WA. 1976. Body size and longevity in birds. *Condor* 78: 91-94.

Lovegrove TG. 1980. *The saddleback pair bond.* Unpub. M.Sc thesis. University of Auckland: Auckland.

Lovegrove TG. 1996. Island releases of saddlebacks Philesturnus carunculatus in New Zealand. *Biological Conservation* 77: 151-157.

Lovegrove TG, O'Callaghan AP. 1982. Recent studies of the North Island saddleback on Cuvier Island. *Forest and Bird* 14: 26-30.

Ludwig K, Jamieson IG. 2007. Phrase types, repertoire size and repertoire overlap in the South Island saddleback (*Philesturnus carunculatus carunculatus*). *Notornis* 54: 201-213.

Lyon BE, Montgomerie R. 2012. Sexual selection is a form of social selection. *Philosophical Transactions of the Royal Society B: Biological Sciences* 367: 2266-2273.

Majerus M, O'Donald P, Weir J. 1982. Female mating preference is genetic. *Nature* 300: 521-523.

Martin TE, Badyaev AV. 1996. Sexual dichromatism in birds: importance of nest predation and nest location for females versus males. *Evolution* 50: 2454-2460.

Mays Jr HL, Hill GE. 2004. Choosing mates: good genes versus genes that are a good fit. *Trends in Ecology & Evolution* 19: 554-559.

Michel P, Dickenson K, Barratt BI, Jamieson IG. 2008. Multi-scale habitat models for reintroduced bird populations: a case study of South Island saddlebacks on Motuara Island. *New Zealand Journal of Ecology* 32: 18.

Milinski M. 2006. The major histocompatibility complex, sexual selection, and mate choice. *Annual Review of Ecology, Evolution, and Systematics* 159-186.

Møller A, Pomiankowski A. 1993. Why have birds got multiple sexual ornaments? *Behavioral Ecology and Sociobiology* 32: 167-176.

Møller AP. 1991. Sexual ornament size and the cost of fluctuating asymmetry. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 243: 59-62.

Møller AP, Alatalo RV. 1999. Good-genes effects in sexual selection. *Proceedings of the Royal Society B-Biological Sciences* 266: 85-91.

Moreno J. 1989. Strategies of mass change in breeding birds. *Biological Journal of the Linnean Society* 37: 297-310.

Morton ES. 1977. On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. *American Naturalist* 111: 855-869.

Morton ES, Derrickson KC, Stutchbury BJ. 2000. Territory switching behavior in a sedentary tropical passerine, the dusky antbird (*Cercomacra tyrannina*). *Behavioral Ecology* 11: 648-653.

Nagelkerke NJ. 1991. A note on a general definition of the coefficient of determination. *Biometrika* 78: 691-692.

Neff BD, Pitcher TE. 2005. Genetic quality and sexual selection: an integrated framework for good genes and compatible genes. *Molecular Ecology* 14: 19-38.

Ohlsson T, Smith HG, Råberg L, Hasselquist D. 2002. Pheasant sexual ornaments reflect nutritional conditions during early growth. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 269: 21-27.

Omland KE. 1997. Examining two standard assumptions of ancestral reconstructions: repeated loss of dichromatism in dabbling ducks (Anatini). *Evolution* 51: 1636-1646.

Owens IP. 2006. Where is behavioural ecology going? T*rends in Ecology & Evolution* 21: 356-361.

Owens IP, Short RV. 1995. Hormonal basis of sexual dimorphism in birds: implications for new theories of sexual selection. *Trends in Ecology & Evolution* 10: 44-47.

Papeschi A, Briganti F, Dessı-Fulgheri F. 2000. Winter androgen levels and wattle size in male common pheasants. *Condor* 102: 193-197.

Papeschi A, Dessı-Fulgheri F. 2003. Multiple ornaments are positively related to male survival in the common pheasant. *Animal Behaviour* 65: 143-147.

Parker KA, Hauber ME, Brunton DH. 2010. Contemporary cultural evolution of a conspecific recognition signal following serial translocations. *Evolution* 64: 2431-2441.

Parker KA, Ludwig K, King T, Brunton DH, Scofield PR, Jamieson IG. 2013. Differences in vocalisations, morphology and mtDNA support species status for New Zealand saddleback *Philesturnus spp. New Zealand Journal of Zoology* 41: 79-94.

Penteriani V, del Mar Delgado M, Alonso-Alvarez C, Sergio F. 2007. The importance of visual cues for nocturnal species: eagle owls signal by badge brightness. *Behavioral Ecology* 18: 143-147.

Pierre JF. 2001. Habitat use and foraging patterns of a reintroduced population of the South Island saddleback (*Philesturnus carunculatus carunculatus*), the first breeding season after release. *Notornis* 48: 63-71.

Pierre JP. 1999. Reintroduction of the South Island saddleback (*Philesturnus carunculatus carunculatus*): dispersal, social organisation and survival. Biological Conservation 89: 153-159.

Pierre JP. 2000. Foraging behaviour and diet of a reintroduced population of the South Island saddleback (*Philesturnus carunculatus carunculatus*). *Notornis* 47: 7-12.

Platt JR. 1964. Strong inference. *Science* 146: 347-353.

Polak M, Starmer WT. 2005. Environmental origins of sexually selectd variation and a critique of the fluctuating asymmetry-sexual selection hypothesis. *Evolution* 59: 577-585.

Potti J, Canal D, Serrano D. 2013. Lifetime fitness and age-related female ornament signalling: evidence for survival and fecundity selection in the pied flycatcher. *Journal of Evolutionary Biology* 26: 1445-1457.

Price JJ, Lanyon SM, Omland KE. 2009. Losses of female song with changes from tropical to temperate breeding in the New World blackbirds. *Proceedings of the Royal Society B: Biological Sciences* 276: 1971–1980.

Price T. 1998. Sexual selection and natural selection in bird speciation. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 353: 251-260.

Price T, Birch GL. 1996. Repeated evolution of sexual color dimorphism in passerine birds. *Auk* 113: 842-848.

Pryke SR, Andersson S, Lawes MJ. 2001. Sexual selection of multiple handicaps in the red-collared widowbird: female choice of tail length but not carotenoid display. *Evolution* 55: 1452-1463.

Rice WR. 1984. Sex chromosomes and the evolution of sexual dimorphism. *Evolution* 38: 735-742.

Roberts ML, Buchanan KL, Evans M. 2004. Testing the immunocompetence handicap hypothesis: a review of the evidence. *Animal Behaviour* 68: 227-239.

Rosen RF, Tarvin KA. 2006. Sexual signals of the male American goldfinch. *Ethology* 112: 1008-1019.

Rosvall KA. 2011. Intrasexual competition in females: evidence for sexual selection? *Behavioral Ecology* 22: 1131-1140.

Roughgarden J. 2012. The social selection alternative to sexual selection. *Philosophical Transactions of the Royal Society B: Biological Sciences* 367: 2294-2303.

Roulin A. 1999. Nonrandom pairing by male barn owls (*Tyto alba*) with respect to a female plumage trait. *Behavioral Ecology* 10: 688-695.

Rowe C. 1999. Receiver psychology and the evolution of multicomponent signals. *Animal Behaviour* 58: 921-931.

Rubenstein DR, Lovette IJ. 2009. Reproductive skew and selection on female ornamentation in social species. *Nature* 462: 786-789.

Russell EM, Yom-Tov Y, Geffen E. 2004. Extended parental care and delayed dispersal: northern, tropical, and southern passerines compared. *Behavioral Ecology* 15: 831-838.

Seddon N. 2005. Ecological adaptation and species recognition drives vocal evolution in neotropical suboscine birds. *Evolution* 59: 200-215.

Seddon N, Tobias JA. 2006. Duets defend mates in a suboscine passerine, the warbling antbird (*Hypocnemis cantator*). *Behavioral Ecology* 17: 73-83.

Seddon N, Tobias JA, Eaton M, Ödeen A. 2010. Human vision can provide a valid proxy for avian perception of sexual dichromatism. *Auk* 127: 283-292.

Selander RK. 1966. Sexual dimorphism and differential niche utilization in birds. *Condor* 68: 113-151.

Shine R. 1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. *Quarterly Review of Biology* 64: 419-461.

Smith CL, Evans CS. 2013. A new heuristic for capturing the complexity of multimodal signals. *Behavioral Ecology and Sociobiology* 67: 1389-1398.

Smith CL, Van Dyk DA, Taylor PW, Evans CS. 2009. On the function of an enigmatic ornament: wattles increase the conspicuousness of visual displays in male fowl. *Animal Behaviour* 78: 1433-1440.

Sogge MK, Koronkiewicz TJ, van Riper III C, Durst SL. 2007. Willow flycatcher nonbreeding territory defense behavior in Costa Rica. *Condor* 109: 475-480.

Stettenheim PR. 2000. The integumentary morphology of modern birds—an overview. *American Zoologist* 40: 461-477.

Studd MV, Robertson RJ. 1985. Life span, competition, and delayed plumage maturation in male passerines: the breeding threshold hypothesis. *American Naturalist* 126: 101-115.

Stutchbury BJ, Morton ES. 2001. *Behavioral ecology of tropical birds.* San Diego: Academic Press

Taylor SS, Jamieson I. 2007. Determining sex of South Island saddlebacks (*Philesturnus carunculatus carunculatus*) using discriminant function analysis. *Notornis* 54: 61.

Thomson RL, Tomás G, Forsman JT, Broggi J, Mönkkönen M. 2010. Predator proximity as a stressor in breeding flycatchers: mass loss, stress protein induction, and elevated provisioning. *Ecology* 91: 1832-1840.

Tobias J, Gamarra-Toledo V, Garcia-Olaechea D, Pulgarin P, Seddon N. 2011. Year-round resource defence and the evolution of male and female song in suboscine birds: social armaments are mutual ornaments. J*ournal of Evolutionary Biology* 24: 2118-2138.

Tobias JA, Montgomerie R, Lyon BE. 2012. The evolution of female ornaments and weaponry: social selection, sexual selection and ecological competition. *Philosophical Transactions of the Royal Society B: Biological Sciences* 367: 2274-2293.

Tobias JA, Seddon N. 2009. Signal design and perception in *Hypocnemis* antbirds: evidence for convergent evolution via social selection. *Evolution* 63: 3168-3189.

Townsend JM, Rimmer CC, McFarland KP. 2010. Winter territoriality and spatial behavior of Bicknell's Thrush (*Catharus bicknelli*) at two ecologically distinct sites in the Dominican Republic. *Auk* 127: 514-522.

Trail PW. 1990. Why should lek-breeders be monomorphic? *Evolution* 44: 1837-1852.

Trivers R. 1972. Parental investment and sexual selection. In: Campbell B. (eds.), *Sexual Selection and the Descent of Man*, Chicago: Aldine, pp. 136-79.

Vehrencamp SL. 2001. Is song-type matching a conventional signal of aggressive intentions? *Proceedings of the Royal Society B-Biological Sciences* 268: 1637-1642.

Walls G. 1984. Scenic and allied reserves of the Marlborough Sounds: a biological survey of reserves in the Marlborough Land District, north of the Wairau River. *Biological Survey of Reserves No. 13*. Wellington, Department of Lands and Survey.

Walther BA, Clayton DH. 2005. Elaborate ornaments are costly to maintain: evidence for high maintenance handicaps. *Behavioral Ecology* 16: 89-95.

Wedekind C, Folstad I. 1994. Adaptive or nonadaptive immunosuppression by sex hormones? *American Naturalist* 143: 936-938.

West-Eberhard MJ. 1983. Sexual selection, social competition, and speciation. *Quarterly Review of Biology* 58: 155-183.

West-Eberhard MJ. 2003. *Developmental plasticity and evolution.* Oxford: Oxford University Press.

West-Eberhard MJ. 2014. Darwin's forgotten idea: the social essence of sexual selection. *Neuroscience & Biobehavioral Reviews* 14: 0149-7634 (preprint).

Whittingham LA, Kirkconnell A, Ratcliffe LM. 1996. Breeding behavior, social organization and morphology of red-shouldered (*Agelaius assimilis*) and tawny-shouldered (*A. humeralis*) blackbirds. *Condor* 68: 832-836.

Wiley RH. 2006. Signal detection and animal communication. *Advances in the Study of Behavior* 36: 217.

Zahavi A. 1975. Mate selection—a selection for a handicap. *Journal of Theoretical Biology* 53: 205-214.