

The copyright of this thesis vests in the author. No quotation from it or information derived from it is to be published without full acknowledgement of the source. The thesis is to be used for private study or non-commercial research purposes only.

Published by the University of Cape Town (UCT) in terms of the non-exclusive license granted to UCT by the author.

DETERMINANTS AND CONSEQUENCES OF TERRITORY QUALITY IN THE
BAR-THROATED APALIS *APALIS THORACICA*

BY

ADAMS ADAMANYIWA CHASKDA

Thesis presented for the degree of

DOCTOR OF PHILOSOPHY

In the Department of Zoology

UNIVERSITY OF CAPE TOWN

December 2011

Declaration

I hereby declare that this work is the product of my own research efforts; undertaken under the supervision of Prof. Philip A.R. Hockey and Dr. Penn Lloyd and has not been presented elsewhere for the award of a degree or certificate. However, all data collected prior to 2007, used particularly in Chapter 4, were generously provided by Dr. Penn Lloyd. Other sources have been duly identified and appropriately acknowledged in the thesis.

Signed by candidate

.....
Adams Adamanyiwa Chaskda

Acknowledgements

Once again another feather has been added to adorn my wretched hat! Thanks to the Supreme one who has enabled kind-hearted men/women to actualise this, notably Mr. A.P. Leventis who provided a full scholarship through the A.P. Leventis Foundation to undertake this study – *I will forever remain grateful for this kind gesture.*

I am also most grateful to my supervisor Prof. Phil Hockey and co-supervisor Dr. Penn Lloyd for their tremendous understanding, patience, intellectual contribution and guidance that made it possible for me to reach this destination.

Thanks also to the management of ESKOM, particularly Mr Hilton Westman, Mr Gert Greef, Mr Graeme Fick and the late Mr Frikkie Potgieter, for facilitating my research at the Koeberg Nature Reserve, Cape Town, South Africa.

To my dear wife, Faith Nanman Chaskda I say THANK YOU! I wish there are better words than that to express my gratitude for your patience, understanding and encouragement while this study lasted – *my dear, you are amazing!*

This work also wouldn't have been possible without the valuable field assistance received throughout the study from Mr. David Mbongeni-Nkosi – *hey man, can't thank you enough!* Several other individuals have also rendered invaluable academic and field assistance at different stages, namely Mr Alexander Neu, Ms Betina Christ, Dr. Andrew Taylor, Ms Juliet Taubman and Mr Philipp Becker. I am also grateful to Dr. Corine Eising whose preliminary work on the study species gave birth to this broader study – *Many thanks guys!*

Thanks also to Hilary Buchanan, Lionel Mansfield and Chris Tobler – the administrative and technical assistance you all render at the Percy FitzPatrick Institute of African Ornithology makes life a lot easier and particularly to you Hilary – your motherly disposition and humility is highly encouraging! *Thank you all!*

I am also most grateful to Sir Phil Hall, Drs. Peter Jones, Georgina Mwansat, Will Cresswell, Manu Shiiwua and Ulf Ottoson for sharing knowledge and for your encouragement and advice at different stages of the study – *Thanks greatly!*

To my extended family members – the Chaskda's and Mwansat's – *Thanks all for being there when I needed you most!*

Determinants and consequences of territory quality in the Bar-throated Apalis *Apalis thoracica*

Abstract

The underlying principles of territoriality propose that competition for resources compels individuals to defend areas (territories) that give them exclusive access to critical resources. The theory suggests that only high-quality individuals succeed in occupying areas rich in these resources with consequent benefits in terms of higher reproductive success and/or chances of survival. Successive studies have shown that specific factors determining territory quality and the consequences for the individuals that occupy them vary widely from one species to another. Some territorial species use morphological or plumage signals to denote status, but the information conveyed in these signals may vary also across species. Very few studies, however, have tested predictions about either territory quality effects or phenotypic signal messages on non-migratory, territorial and socially monogamous African passerines. Amongst these birds, we know very little about how patterns of territory occupancy constrain parental reproductive investment, pair stability and adult survival. The main aims of this study were: i) to determine the ecological factors influencing variation in territory size and quality among Bar-throated Apalises *Apalis thoracica*; ii) to investigate the consequences of these factors for reproductive effort and reward, pair stability and survival; and iii) to investigate the signalling properties of the species' black breast band (a prominent 'badge' emblazoned across the white underparts) in relation to both male and territory quality. The study used diet, vegetation characteristics and individual foraging behaviour to quantify prey density (territory quality). Using focal observations, direct measurements and video records of parental activities at nests, several measures of parental effort/investment were quantified *viz.* foraging path distances when provisioning mates and young, feeding rates, sizes of prey delivered, incubation nest attentiveness, clutch size/mass and nestling growth. Several morphometric measures of individual quality and multiple measures of breast-band size across years were also obtained. Pair stability and adult survival were analysed from resighting/re-trapping data gathered annually throughout the study period. In line with predictions, territory quality (prey density) constrained parental reproductive effort and reward in both sexes. Breast-band size conveyed honest signals of both male and territory quality: males with the largest breast bands defended the smallest, highest quality territories, attracted the highest quality females and achieved the highest direct fitness, conforming to models of optimal territory occupancy. Further embedded in the breast band was a signal of age, with the oldest birds (with the largest breast bands) occupying the highest quality territories. Birds occupying high-quality territories also had high survivorship, and high mate and territory fidelity, all traits that could contribute to improving individual fitness.

Contents

	Page
Declaration	i
Acknowledgements	ii
Abstract	iii
Table of contents	iv
Chapter One: <i>General introduction</i>	1
Chapter Two: <i>Bar-throated Apalis territories: size, prey density and vegetation structure</i>	23
Introduction	23
Methods	26
Results	31
Discussion	42
Chapter Three: <i>Relationships between breast-band size, individual quality and territory attributes in the Bar-throated Apalis</i>	49
Introduction	49
Methods	51
Results	55
Discussion	60
Chapter Four: <i>Consequences of variation in territory and individual quality on reproductive performance and fitness in the Bar-throated Apalis</i>	67
Introduction	67
Methods	70
Results	81
Discussion	91

Chapter Five:	<i>Mate fidelity, territory fidelity and adult survival in the Bar-throated Apalis</i>	105
	Introduction	105
	Methods	108
	Results	111
	Discussion	115
Chapter Six:	<i>Synthesis</i>	128

University of Cape Town

CHAPTER ONE

GENERAL INTRODUCTION

The outcome of natural selection may be determined by competition for scarce resources, as well as by predation, mate choice or diseases (Darwin 1859, Lack 1954). Some competitive interactions ensure exclusive use of an area and the critical resource(s) within it, which may in turn influence individual reproductive success and survival. Animals exhibiting this behaviour are termed 'territorial' and the behaviour 'territoriality'.

The concept of territoriality

The term 'territoriality' was first established in ornithological literature as early as the 19th Century by Barnard Altum and H. Eliot Howard (see Nice 1941 for historical perspective). From the mid 20th Century until the present, it has come to be acknowledged as a response by individuals to environmental changes (resource availability) and population density (Lack 1954, Fretwell and Lucas 1970, Calsbeek and Sinervo 2002). It is predicted to occur when resources are patchily distributed but predictable, leading to competition which results in high-quality individuals acquiring access to areas rich in resources (Fretwell and Lucas 1970, Dyson-Hudson and Smith 1978, Lederer 1981, Calsbeek and Sinervo 2002).

Territoriality has been variously defined (reviewed by Nice [1941] and Maher and Lott [1995]). This study adopts the definition of territoriality proposed by Maher and Lott (1995), namely "a fixed space within which an individual or group of mutually tolerant individuals actively exclude competitors from a specific resource or resources". The "fixed space" is the territory from which other individuals are

excluded by either or both sexes or, in cooperative breeders, by a group of closely related individuals (Theuerkauf *et al.* 2009). Territory defence can be achieved in several ways, e.g. by violent combat (fights), vocal displays, marking of the territory boundary with scents, or status signalling through morphological traits (Rohwer 1975, Lyon and Montgomerie 1985, Møller 1987, Rosell *et al.* 1998, Gerhardt and Huber 2002, Brumm and Todt 2004, Nakagawa *et al.* 2008, deKort *et al.* 2009).

Based on their functions, territories have been grouped into six different types (Nice 1941). However, these classifications are not rigid; some species display more than one type of territoriality.

1. TYPE A: All-purpose territories where mating, nesting and rearing of nestlings occur.
2. TYPE B: Mating and nesting territories, held for the purpose of attracting the opposite sex to achieve mating and subsequent nesting.
3. TYPE C: Territories defended purely for mating, as occurs in e.g. hummingbirds and mannikins.
4. TYPE D: Defence of nest sites alone.
5. TYPE E: Territories defended in the non-breeding season solely for the purpose of feeding.
6. TYPE F: Territories defended for roosting purposes.

The economics of territoriality

The optimal territory

Territoriality is ultimately regulated by the balance of costs and benefits (Fretwell and Lucas 1970, Both and Visser 2003): to understand this, Fretwell and Lucas (1970) proposed two types of distributions, ideal free and ideal despotic. Under an ideal free

distribution, individuals operate at low population density and can occupy as large an area as necessary (i.e. without hindrance) in order to maximise fitness (benefit). However, under ideal despotic distributions, individuals operate at high population density and resources are limiting, resulting in competition and eventually defence of space containing the required resources against conspecifics (territoriality). A territory occupant thus has to contend with the pressure of territory usurpation (a cost) from competing conspecifics seeking a breeding (or feeding) space. Often, the intensity of such pressure increases with territory quality (Temeles 1987, Marchesseault and Ewald 1991, Eberhard and Ewald 1994). When territory size is such that net benefits are greatest, then territory size is defined as optimal (Myers *et. al.* 1979, Schoener 1983, Both and Visser 2003). Both and Visser (2003) demonstrated this graphically (Fig. 1.1) for a situation where size of a breeding territory is assumed to be regulated primarily by food density.

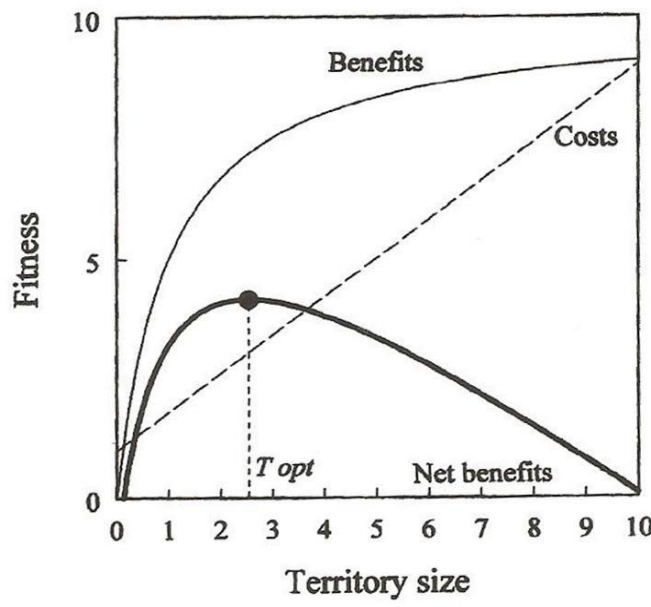


Figure 1.1: Territory size as a function of costs and benefits. The thin unbroken line is the benefit curve, the broken diagonal line is the cost curve and the black solid line is the net benefit curve. The net benefits (fitness) represent the benefits minus the costs. T_{opt} is the (optimal) territory size that maximises fitness. Reproduced from Both and Visser (2003).

Territory maintenance costs

Although territory acquisition allows exclusive access to resources (at the level of conspecifics), there are costs associated with maintaining such a territory, including regular fights with intruders (Norton *et al.* 1982, Johnsson *et al.* 2000). Such conflicts reduce the time available for other activities such as foraging, parental care (Studd and Robertson 1988, Ydenberg and Krebs 1987) and anti-predator vigilance (Jakobsson *et al.* 1995, Dunn *et al.* 2004). They also increase energy expenditure (Carpenter and Macmillen 1976) and the risk of injuries or even death arising from fights (Jakobsson 1995, Hammerstein and Reichert 1988).

Signals and their relevance in territory maintenance

Animals employ several strategies to minimise some of the costs associated with territory maintenance. Among these, threat and display postures/signals are preferable to violent combat (Brown 1964, Dunn *et al.* 2004) because they reduce energy expenditure and afford opportunities to assess an opponent's abilities before embarking on potentially costly conflict, potentially obviating the risk of injury (Dunn *et al.* 2004).

Vocalisation is largely selected by female choice (Searcy 1996), but some studies have also afforded it a role in male-male competition. In anurans, for example, the amplitude of vocal signals plays a role in repelling rival males (reviewed by Gerhardt and Huber 2002), while in European Blackbirds *Turdus merula* simulated song amplitude of rival males stimulates increased signal strength in male receivers. When the asymmetry in signal strength reaches a certain point, the (quieter) receiver terminates the interaction and flees, suggesting that such vocal competition allows birds to assess (using 'remote' information) whether to retreat or advance (Dabelsteen

1981, Todt 1981). Recent studies of counter-singing by male Carolina Wrens *Thryothorus ludovicianus* (Hyman 2003), Common Nightingales *Luscinia megarhynchos* (Brumm and Todt 2004) and Banded Wrens *Thryophilus pleurostictus* (deKort *et al.* 2009) suggest that this may be widespread as a means of competitor assessment.

Chemical signals (scent marking) represent a medium of olfactory communication involving the use of chemical signals transmitted through the air. These signals are received by competitors via receptors that can identify and integrate the signals and stimulate the receiver to respond appropriately, either behaviourally or physiologically (Rosell *et al.* 1998). In a territorial context it has advantages over violent combat in that it is effective even in the sender's absence (Wynne-Edwards 1962, Rosell *et al.* 1998). This type of territory maintenance is typical of mammals (Wynne-Edwards 1962, Rosell *et al.* 1998). Some birds have quite advanced olfactory senses, for example Brown Kiwi *Apteryx australis* (Davies 2003, Steiger *et al.* 2008, Terra Nature Trust 2009), Blue Petrel *Halobaena caerulea* and Thin-billed Prion *Pachyptila belcheri* (Cunningham *et al.* 2003), but there is no evidence that any bird uses chemical signalling as a part of its territorial defence repertoire.

Morphological status signalling and territory maintenance

Signalling behaviour involves the advertisement of individual quality to conspecifics (Status Signalling – Rohwer 1975, Lyon and Montgomerie 1985). This can be achieved through morphological traits (ornaments) that may range from elongated feathers to patches of coloured feathers (Møller 1987, Andersson *et al.* 2002, Tarof *et al.* 2005, Dunn *et al.* 2008, Nakagawa and Burke 2008). Such ornaments are grouped according to their constituent pigments, namely carotenoid pigments (red, yellow and

orange) and melanin pigments (brown and black). Carotenoid-based signals are hypothesized to be selected by female choice (Johnson *et al.* 1993, Brooks and Coughlin 1999, Badyaev and Hill 2000, Jawor and Breitwisch 2006, Dunn *et al.* 2008) whereas melanin-based signals are hypothesized to be selected by male-male competition (Rohwer 1975, 1982, Senar 1993, McGraw *et al.* 2002, Dunn *et al.* 2008). However, some recent studies suggest that this simple division of functions may be an oversimplification. For example, the melanin-based bib (black facial mask) of the Common Yellowthroat *Geothlypis trichas* functions in both female choice and male-male competition (Tarof *et al.* 2005, Dunn *et al.* 2008). Similarly, the red gorget of the Red-collared Widowbird *Euplectes ardens*, even though carotenoid based, functions primarily in male-male competition, with tail length being under selection from female choice (Andersson *et al.* 2002). Nonetheless, most experimental manipulations have supported the notion that the primary function of melanin-based ornaments relates to male-male competition (Rohwer 1975, 1977, Gustafsson *et al.* 1995, McGraw *et al.* 2002). In the House Sparrow *Passer domesticus*, the black throat patch signals individual dominance: males with the largest bibs win more fights than do males with smaller bibs (Møller 1987, Nakagawa *et al.* 2008). In addition, the extent of the black eye-mask of male House Sparrows signals age (and is positively linked to status in a dominance hierarchy - Nakagawa and Burke 2008). Among King Penguins *Aptenodytes patagonicus* the size of the orange auricular patch is correlated with aggressiveness. Individuals with the largest ear patches gain high-quality territories in the centre of the colony, with attendant fitness benefits (Viera *et al.* 2008). The honesty of these signals in demonstrating individual quality is thought to maintain social hierarchies and help to reduce costs associated with 'contact

aggression' as well as confer fitness benefits on individuals (Rohwer 1975, Zahavi 1975, 2007, Lyon and Montgomerie 1985, Siitari and Huhta 2002, Viera *et al.* 2008).

Indices of territory quality

Territory quality is best reflected in the fitness consequences for the individuals occupying that territory (Johnson 2007). With this in mind, various direct and indirect measures of fitness have been proposed as indicative of territory quality (Sergio and Newton 2003):

1. The quantity and quality of resources present, including e.g. food and nest sites. This rests on the assumption that higher quality territories contain more and higher quality resources than do poorer territories.
2. The duration of occupancy of the territory. This assumes that territories with long occupancy periods are the most profitable. Poorer quality territories will be abandoned sooner.
3. The capacity of the territory to sustain high levels of survival and reproduction. Territories occupied by individuals with high survivorship and reproductive rates are likely to be those with high resource densities/quality.
4. The date of territory occupation during the seasonal sequence of settlement, with high-quality territories predicted to be occupied first.
5. The predictability of reproductive success in the territory, often measured as the coefficient of variation in reproductive success (Ferrer and Donázar 1996). This assumes that high-quality territories are identifiable through vegetation attributes or the reproductive success of neighbours. Such indirect cues may represent one of the ways in which floaters and newly settling individuals are

able to locate high-quality territories (Eason and Hannon 1994, Boulinier and Danchin 1997, Marshall and Cooper 2004).

Another indirect measure of habitat/territory quality is measurement of individual body condition, which can be made in two ways (Johnson 2007):

1. Morphological measures of condition that rely on external, visible and measurable features, such as body size.
2. Physiological measures of condition, including those that rely on analysis of sampled tissues, usually blood.

Irrespective of the measures of body condition, there are two further preconditions for this measure to be a useful indicator of habitat quality. Firstly, variation in body condition must be a result, rather than a cause, of differential habitat use. Secondly, differences in body condition should ultimately manifest in differential fitness (Bêty *et al.* 2003 and Johnson 2007). Measures of body condition that have been used as surrogates for habitat/territory quality include body mass (Pöysä *et al.* 2000), body mass corrected for body size (Latta and Faaborg 2002, Costantini *et al.* 2009), fat scores (Strong and Sherry 2000, Brown 1996), pigmentation (Doucet *et al.* 2005, Siefferman and Hill 2005), and hormone levels, e.g. of corticosterone (Marra and Holberton 1998, Lanctot *et al.* 2003).

Inferring links between body condition and territory quality needs to be approached with caution because individuals in better body condition could acquire high-quality territories rather than body condition being a consequence of occupying a high-quality territory. Thus, to tease these possibilities apart, it is important to check for the effect of territory quality on individual quality traits otherwise the interpretation of results may be confounded (e.g. Otter and Ratcliffe 1999). One

possible way of doing this is through experimental manipulations (e.g. Pérez-Rodríguez and Viñuela 2008).

Furthermore, because the definition of habitat quality is scale dependent, whichever approach is used for assessing territory quality should focus on those scales that provide reliable information, such as integrating behavioural observations with habitat/territory attributes (Wiens 1989, Marshall and Cooper 2004, Kristan *et al.* 2007).

Consequences of variation in territory quality

Territory quality can influence a variety of factors, including survival and reproduction. For example, the quantity or quality of resources that a male acquires may influence his attractiveness to females (over and above phenotype alone - Wittenberger [1981]) and consequently his mating success (Dhindsa *et al.* 1989, Bensch and Hasselquist 1991, Savalli 1994). Furthermore, variation in territory quality may influence the timing of breeding, with individuals occupying poorer territories delaying breeding past the point when conditions are most favourable, with potential ramifications for lifetime reproductive fitness (Stacey and Ligon 1987, Zack 1990, Zack and Stutchbury 1992). Among Black Kites *Milvus migrans*, for example, high-quality territories (those rich in food availability and/or containing few predators) have a positive influence on both territory occupancy and reproductive success (Sergio and Newton 2003).

Territory quality also plays a significant role in parental reproductive effort/investment and fitness. For example, the frequency which male Merlins *Falco columbarius* provision their incubating mates is proportional to prey availability within their foraging ranges (Sodhi 1993). In poor-quality territories, where prey

delivery rates are reduced, this may force reduced nest attentiveness by females, with negative outcomes for offspring quality and survival (Lyon and Montgomerie 1985, Sodhi 1993, Jawor and Breitwisch 2006). Variation in territory quality can also influence clutch size (Högstedt 1980) and may influence hatching date and offspring body condition, as in Blue Tits *Parus caeruleus* (Przybylo *et al.* 2001). Studies of Eurasian Oystercatchers *Haematopus ostralegus* have underscored the long-term effects of territory quality on offspring survival. Offspring raised on high-quality territories have a 30% higher juvenile survival, a 60% higher pre-breeding survivorship, and a higher probability of settling in high-quality habitat and achieving a lifetime reproductive success of more than double that of individuals raised on low-quality territories (Van de Pol 2006).

Territory size vs territory quality

Territories vary in size both within and between species (Nice 1941, Wortman-Wunder 1997, Adams 2001, Marshall and Cooper 2004). For example, territories of male Red-winged Blackbirds *Agelaius phoenecius* vary by an order of magnitude, ranging from 1188 m² to 18 456 m² (Pickman 1987), and territory sizes of Ovenbirds *Seiurus aurocapillus* range from 1300-3800 m² (Smith and Shugart 1987). Variation in territory size can also occur across seasons. For example, Little Owls *Athene noctua* defend larger territories during courtship than during the incubation and nestling periods (Finck 1990).

Optimal territory-size models predict an inverse relationship between territory size and resource density. This has been confirmed in several studies (e.g. Stenger, 1958, MacLean and Seastedt 1979, Smith and Shugart 1987, Turpie 1995, Marshall and Cooper 2004). For example, territory size of Red-eyed Vireos *Vireo olivaceus* is

inversely correlated with foliage density, the latter correlating positively with density of the birds' caterpillar food (Marshall and Cooper 2004). However, there are exceptions to this generalisation. For example, no relationship was found between territory size and food abundance in juvenile Steelhead Trout *Onchorhynchus mykiss* (Imre *et al.* 2004) or between territory size and vegetation composition in Lincoln's Sparrow *Melospiza lincolnii* (Wortman-Wunder 1997).

In addition to being regulated by resource density, territory size is likely to be further influenced by intruder pressure (Ewald 1980, Norton *et al.* 1982, Norman and Jones 1984, Mcfarland 1986, Marshall and Cooper 2004), as is the case for Bushbuck *Tragelaphus scriptus* (Wronski and Plat 2006). This expectation is based on the premise that high-quality territories will attract more potential settlers or competitors, placing pressure on the territory holder through incessant conflict and leading to a compromise in territory size determined by a balance between the resource benefits derived and the costs of territory defence (Riechart 1979, Johnsson *et al.* 2000). The 'Intruder Pressure Hypothesis' predicts that smaller territories will be found in high-quality habitat patches and larger territories in poorer areas.

Background to this study

Although the underlying factors that regulate territory size/quality in animal populations have been well explored, there is a geographic bias in these studies towards the Northern Hemisphere. Despite their relatively high diversity, information on non-migratory, territorial and socially monogamous African passerines is scant. Because the proximate factors regulating territory size/quality differ across species, there may be cause to question whether they also differ across geographical regions, in the same way that there are geographical asymmetries in the prevalence of

cooperatively breeding species (Jetz and Rubenstein 2011). Furthermore, previous studies of melanin-based ornaments have mostly focussed on signal variation among individuals in relation to male-male competition (Rohwer 1975, Senar 1993, McGraw *et al.* 2002, Dunn *et al.* 2008, Viera *et al.* 2008). However, we understand far less about whether the information signalled by such ornaments can ‘honestly’ indicate male reproductive effort and whether signallers receive proportional reciprocal fitness benefits in terms of female reproductive investment. There is also a lack of long-term studies involving multiple measures of ornaments in the same individuals over time, despite the fact that such studies may hold the key to teasing apart the relationship between ornament size, age and dominance status, as well as making it possible to control for the effect of territory quality on the development of signalling ornaments. How these factors and variables interact remains unclear (Otter and Ratcliffe 1999).

Study species

The focus of this study is a small, territorial and socially monogamous African passerine, the Bar-throated Apalis *Apalis thoracica* (Family: Cisticolidae). The bird is predominantly grey to olive green above and whitish below, measuring 120-130 mm in length. The outer tail feathers are white and inner tail feathers blackish: the tail is held cocked upwards. The eyes are creamy white, and the slender, black bill has a slightly decurved upper mandible. The white is bordered by a clear black breast band, largest in males. The feet and legs are brownish pink (Sinclair *et al.* 2002). The species’ range extends from the southern and eastern parts of South Africa, east and north to Kenya. Favoured habitats include evergreen forests, woodlands, wooded gorges, riverine areas, scrub and grasslands and. It feeds on arthropods gleaned from leaves and branches, including caterpillars, (Sinclair and Ryan 2003). The species is

highly vocal, giving a fast and repetitive *pillly pillly pillly pillly pillly pillly pillly pillly* song and duetting occurs regularly, especially during nest building. The nest is oval shaped, with a side entrance, typically constructed from rootlets, grass, spider webs, moss and silky plants. Incubation is by the female alone, provisioned by the male, but both parents feed the nestlings (Hockey *et al.* 2005).

Aims

This study aims to explore the ecological factors that determine variation in territory size among Bar-throated Apalises and their consequences for reproduction (effort and reward), pair stability and survival. The study also investigates the signalling ‘properties’ of the species’ prominent black breast band.

Specifically, the study has the following objectives:

1. To investigate variations in the sizes of breeding territories defended by male Bar-throated Apalises and the roles that vegetation structure and food density play in influencing this variability.
2. To determine the consequences of variation in territory size/quality for:
 - a. Key male functions such as mate and nestling provisioning rates and the effort required to achieve these.
 - b. Female reproductive investment (i.e. timing of initiation of breeding, clutch size and mass, incubation attentiveness, rate of nestling provisioning and breeding productivity).
 - c. Pair stability and adult survival.
3. To determine whether breast-band size is an ‘honest’ signal of territory quality and/or male quality and fitness.

Predictions

1. Breeding territory size will vary inversely with food density, with the smallest territories containing the most dense food resources. If this relationship holds, it is further predicted that foraging efficiency will increase with decreasing territory size
2. The consequences for pairs occupying large territories will include:
 - a. Delayed nest initiation.
 - b. Reduced clutch and brood sizes.
 - c. Reduced provisioning of incubating females by males, leading to reduced female nest attentiveness during incubation.
 - d. Reduced nestling feeding rates and hence reduced offspring condition and/or survivorship.
3. If breast-band size is an honest signal of male/territory quality, males with large bibs will gain proportional fitness benefits through high levels of reproductive investment by their mates.

Thesis structure

1. Chapter 2 quantifies food density based on the host-plant-specific foraging behaviour of the species. This in turn is used to develop an index of territory quality that is related to vegetation structure and territory size.
2. Chapter 3 quantifies variation in breast-band size between males and across years, and assesses how such variation relates to individual and territory quality.

3. Chapter 4 explores the consequences of territory quality for parental reproductive effort and investment and relates these variables to male status signalling.
4. Chapter 5 focuses on the effect of variation in territory quality on pair stability, territory fidelity and adult survival.
5. Chapter 6 provides a synthesis and places the study in a global perspective.

REFERENCES

- Adams E.S. (2001) Approaches to the study of territory size and shape. *Annual Review of Ecological Systems*, **32**, 277–303.
- Andersson, S., Pryke, S.R., Örnborg, J., Lawes, M.J. and Andersson, M. (2002) Multiple receivers, multiple ornaments, and a trade-off between agonistic and epigamic signaling in a widowbird. *American Naturalist*, **160**, 683–691.
- Baydaev, A.V. and Hill, G.E. (2000) Evolution of sexual dichromatism: contribution of carotenoid- versus melanin-based coloration. *Biological Journal of the Linnaean Society*, **69**, 153–172.
- Bensch, S. and Hasselquist, D. (1991) Territory infidelity in the polygynous Great Reed Warbler *Acrocephalus arundinaceus*: the effect of variation in territory attractiveness. *Journal of Animal Ecology*, **60**, 857–871.
- Bêty, J., Gauthier, G. and Giroux, J.F. (2003) Body condition, migration and timing of reproduction in Snow Geese: a test of the condition-dependent model of optimal clutch size. *American Naturalist*, **162**, 110–121.
- Both, C. and Visser, M.E. (2003) Density dependence, territoriality, and divisibility of resources: from optimality models to population processes. *American Naturalist*, **161**, 326–336.
- Boulinier, T. and Danchin, E. (1997) The use of conspecific reproductive success for breeding patch selection in territorial migratory species. *Evolutionary Ecology*, **11**, 505–517.
- Brooks, R. and Couldridge, V. (1999) Multiple sexual ornaments co-evolve with multiple mating preferences. *American Naturalist*, **154**, 37–45.
- Brown, J.L. (1964) The evolution of diversity in avian territorial systems. *Wilson Bulletin*, **76**, 160–169.

- Brown, M. E. (1996) Assessing body condition in birds. *Current Ornithology*, **13**, 67–135.
- Brumm, H. and Todt, D. (2004) Male-male vocal interactions and the adjustment of song amplitude in a territorial bird. *Animal Behavior*, **67**, 281–286.
- Calsbeek, R. and Sinervo, B. (2002) An experimental test of the ideal despotic distribution. *Journal of Animal Ecology*, **71**, 513–523.
- Carpenter, F.L. and Macmillen, R.E. (1976) Energetic costs of feeding territories in an Hawaiian honeycreeper. *Oecologia*, **26**, 1432–1939.
- Costantini, D., Casagrande, S., Carello, L. and Dell’Omo, G. (2009) Body condition variation in Kestrel *Falco tinnunculus* nestlings in relation to breeding conditions. *Ecological Research*, **24**, 1213–1221.
- Cunningham, G.B., Van Buskirk, R.W., Bonnadona, F. Weimerskirch, H. and Nevitt, G.A. (2003) A comparison of the olfactory abilities of three species of procellariiform chicks. *Journal of Experimental Biology*, **206**, 1615–1620.
- Dabelsteen, T. (1981) The sound pressure level in the dawn song of the Blackbird *Turdus merula* and a method for adjusting the level in experimental song to the level in natural song. *Zeitschrift für Tierpsychologie*, **56**, 137–149.
- Darwin, C. (1859) <http://www.literature.org/authors/darwin-charles/the-origin-of-species/chapter-04.html>.
- Davies, S.J.J.F. (2003) "Kiwis". in Hutchins, Michael. *Grzimek's Animal Life Encyclopedia*. 8 Birds, I Tinamous and Ratites to Hoatzins (2nd ed.). Farmington Hills, MI: Gale Group. Pp.89–90.
- de Kort, S.R., Eldermer, E.R.B., Cramer, E.R.A., Vehrencamp, S.L. (2009) The deterrent effect of bird song in territory defense. *Behavioural Ecology*, **20**, 200–206.
- Dhindsa, M.S., Boag, D.A. and Komers, P.E. (1989) Mate choice in Black-billed Magpies: the role of male quality versus quality of defended resources. *Ornis Scandinavica*, **20**, 193–203.
- Doucet, S.M., Mennill, D.J., Montgomerie, R., Boag, P.T. and Ratcliffe, L.M. (2005) Achromatic plumage reflectance predicts reproductive success in male Black-capped Chickadees. *Behavioral Ecology*, **16**, 218–222.
- Dunn, M., Copelston, M. and Workman, L. (2004) Trade-offs and seasonal variation in territorial defence and predator evasion in the European Robin *Erithacus rubecula*. *Ibis*, **146**, 77–84.
- Dunn, P.O., Whittingham, L.A., Freeman-Gallant, C.R. and DeCoste, J. (2008) Geographic variation in the function of ornaments in the Common Yellowthroat *Geothlypis trichas*. *Journal of Avian Biology*, **39**, 66–72.

- Dyson-Hudson, R. and Smith E.A. (1978) Human territoriality: an ecological reassessment. *American Anthropologist*, **80**, 21–41.
- Eason, P. K. and S. J. Hannon. (1994) New birds on the block: new neighbours increase defensive costs for territorial male Willow Ptarmigan. *Behavioral Ecology and Sociobiology*, **34**, 419–426.
- Eberhard, J.R. and Ewald, P.W. (1994) Food availability, intrusion pressure and territory size: an experimental study of Anna's Hummingbirds (*Calypte anna*). *Behavioral Ecology and Sociobiology*, **34**, 11–18.
- Ewald, P.W. (1980) Territory size in Western Gulls: importance of intrusion pressure, defense investments, and vegetation structure. *Ecology*, **61**, 80–87.
- Ferrer, M. and Donazar, J.A. (1996) Density-dependent fecundity by habitat heterogeneity in an increasing population of Spanish Imperial Eagles. *Ecology*, **77**, 69–74.
- Finck, P. (1990) Seasonal variation of territory size with the Little Owl *Athene noctua*. *Oecologia*, **83**, 68–75.
- Fretwell, S.D. and Lucas, H.J., Jr. (1970) On territorial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheoretica*, **19**, 16–36.
- Gerhardt, H.C and Huber, F. (2002) Acoustic communication in insects and anurans. Chicago: University of Chicago.
- Gustafsson, L., Qvarnström, A. and Sheldon, B.C. (1995) Trade-offs between life history traits and a secondary sexual character in male Collared Flycatcher. *Nature*, **375**, 311–313.
- Hammerstein, P. and Reichert, S.E. (1988) Payoffs and strategies in territorial contests: ESS analysis of two ecotypes of the spider *Agelenopsis aperta*. *Evolutionary Ecology*, **2**, 115–138.
- Hockey, P.A.R., Dean, W.R.J. and Ryan, P.G. (eds) (2005) *Roberts - Birds of Southern Africa*, 7th ed. The Trustees of the John Voelcker Bird Book Fund, Cape Town.
- Högstedt, G. (1980) Evolution of clutch-size in birds: adaptive variation in relation to territory quality. *Science*, **210**, 1148–1150.
- Hyman, J. (2003) Counter-singing as a signal of aggression in a territorial songbird. *Animal Behaviour*, **65**, 1179–1185.
- Imre, I., Grant, J.W.A., Keeley, E.R. (2004) The effect of food abundance on territory size and population density of juvenile Steelhead Trout *Oncorhynchus mykiss*. *Oecologia*, **138**, 371–378.

- Jakobsson, S., Brick, O. and Kullberg, C. (1995) Escalated fighting behaviour incurs increased predation risk. *Animal Behaviour*, **49**, 235–239.
- Jawor, J.M. and Breitwisch, R. (2006) Is mate provisioning predicted by ornamentation? A test with Northern Cardinals *Cardinalis cardinalis*. *Ethology*, **112**, 888–895.
- Jetz, W. and Rubenstein, D.R. (2011) Environmental uncertainty and the global biogeography of cooperative breeding in birds. *Current Biology*. **21**, 72–78.
- Johnson, D. (2007) Measuring habitat quality: a review. *Condor*, **109**, 489–504.
- Johnson, K., Dalton, R. and Burley, N. (1993) Preferences of female American Goldfinches *Carduelis tristis* for natural and artificial male traits. *Behavioral Ecology*, **4**, 138–143.
- Johnsson, J.I., Carlsson M. and L.F. Sundstöm (2000) Habitat preference increases territorial defence in Brown Trout *Salmo trutta*. *Behavioral Ecology and Sociobiology*, **48**, 373–377.
- Kristan, W.B. III, Johnson, M.D. and Rottenberry, J.T. (2007) Choices and consequences of habitat selection for birds. *Condor*, **109**, 485–488.
- Lack, D. (1954). *The Natural Regulation of Animal Numbers*. Clarendon Press, Oxford. pp.11–19.
- Lancot, R. B., Hatch, S. A., Gill, V. A. and Eens, M. (2003) Are corticosterone levels a good indicator of food availability and reproductive performance in a Kittiwake colony? *Hormonal Behaviour*, **43**, 489–502.
- Latta, S. C. and Faaborg, J. (2002) Demographic and population responses of Cape May Warblers wintering in multiple habitats. *Ecology*, **83**, 2502–2515.
- Lederer, R. J. (1981) Facultative territoriality in Townsend's Solitaire *Myadestes townsendi*. *The Southwestern Naturalist*, **25**, 461–467.
- Lyon, B.E. and Montgomerie, R.D. (1985) Incubation feeding in Snow Buntings: female manipulation or indirect male parental care? *Behavioral Ecology Sociobiology*, **17**, 279–284.
- MacLean, S.F. and Seastedt, T.R. (1979) Avian territoriality: sufficient resources or interference competition. *American Naturalist*, **114**, 308–312.
- Maher, C.R. and Lott, D.F. (1995) Definitions of territoriality used in the study of variation in vertebrate spacing systems. *Animal Behavior*, **49**, 1581–1597.
- Marchesseault, L. and Ewald, P.W. (1991) Effect of territory quality on intrusion rate in non-breeding hummingbirds. *Behavioral Ecology and Sociobiology*. **28**, 305–308.

- Marra, P.P. and Holberton, R.L. (1998) Corticosterone levels as indicators of habitat quality: effects of habitat segregation in a migratory bird during the non-breeding season. *Oecologia*, **116**, 284–292.
- Marshall, M.R. and Cooper, R.J. (2004) Territory size of a migratory songbird in response to caterpillar density and foliage structure. *Ecology*, **85**, 432–445.
- Mcfarland, D.C. (1986) Responses of territorial New Holland Honey-eaters *Phylidonyris novaehollandiae* to short term fluctuations in nectar productivity. *Emu*, **94**, 193–200.
- McGraw K.J, Mackillop E.A., Dale J. and Hauber M.E. (2002) Different colours reveal different information: how nutritional stress affects the expression of melanin- and structurally based ornamental plumage. *Journal of Experimental Biology*, **205**, 3747–3755.
- Møller, A.P. (1987) Variation in badge size in male House Sparrows *Passer domesticus*: evidence for status signalling. *Animal Behavior*, **35**, 1637–1644.
- Myers, J.P., Connors, P.G. and Pitelka, F.A. (1979) Territory size in wintering Sanderlings: the effects of prey abundance and intruder density. *Auk*, **99**, 551–561.
- Nakagawa, S. and Burke, T. (2008) The mask of seniority? A neglected age indicator in House Sparrows *Passer domesticus*. *Journal of Avian Biology*, **39**, 222–225.
- Nakagawa, S., Lee, J.W., Woodward, B.K., Hatchwell, B.J. and Burke, T. (2008) Differential selection according to the degree of cheating in a status signal. *Biological Letters*, **4**, 667–669.
- Nice, M.M. (1941) The role of territory in bird life. *American Midland Naturalist*, **26**, 441–487.
- Norman, M.D. and Johnes G.P. (1984) Determinants of territory size in the pomacentrid reef fish *Parma victoriae*. *Oecologia*, **61**, 60–69.
- Norton, M.E., Arcese, P. and Ewald, P.W. (1982) Effect of intrusion pressure on territory size in Black-chinned Hummingbirds *Archilocus alexandri*. *Auk*, **99**, 761–764.
- Otter, K. and Ratcliffe, L. (1999) Relationship of bib size to age and sex in the Black-capped Chickadee. *Journal of Field Ornithology*, **70**, 567–577.
- Pérez-Rodríguez, L. and Viñuela, J. (2008) Carotenoid-based bill and eye coloration as honest signals of condition: an experimental test in the Red-legged Partridge (*Alectoris rufa*). *Naturwissenschaften*, **95**, 821–830.
- Pickman, J. (1987) Territory establishment, size and tenacity by male Red-winged Blackbirds. *Auk*, **104**, 405–412.

- Pöysä, H., Elmberg, J., Sjöberg, K. and Nummi, P. (2000) Nestling Mallards *Anas platyrhynchos* forecast brood stage food limitation when selecting habitat: experimental evidence. *Oecologia*, **122**, 582–586.
- Przybylo, R., Wiggins, D.A. and Merillä, J. (2001) Breeding success in Blue Tits: good territories or good parents? *Journal of Avian Biology*, **32**, 214–218.
- Riechart S.E. (1979) Games spiders play. II. Resource assessment strategies. *Behavioral Ecology and Sociobiology*, **6**, 121–128.
- Rohwer, S. (1982) The evolution of reliable and unreliable badges of fighting ability. *American Zoologist*, **22**, 531–546.
- Rohwer, S. (1975) The social significance of avian winter plumage variability. *Evolution*, **29**, 593–610.
- Rohwer, S. (1977) Status signaling in Harris's Sparrows: some experiments in deception. *Behaviour*, **61**, 107–128.
- Rosell, F., Bergan, F. and Parker, H. (1998) Scent-marking in the Eurasian Beaver *castor fiber* as a means of territory defense. *Journal of Chemical Ecology*, **24**, 207–219.
- Savalli, U.M. (1994) Mate choice in the Yellow-shouldered Widowbird: correlates of male attractiveness. *Behavioral Ecology and Sociobiology*, **35**, 227–234.
- Searcy, W.A. (1996) Sound-pressure levels and song preferences in female Red-winged Blackbirds *Aegelaius phoeniceus* (Aves, Emberizidae). *Ethology*, **102**, 187–196.
- Senar, J.C., Camerino, M., Copete, J.L. and Metcalfe, N.B. (1993) Variation in black bib of the Eurasian Siskin *Carduelis spinus* and its role as a reliable badge of dominance. *Auk*, **110**, 924–927.
- Sergio, F. and Newton, I. (2003) Occupancy as a measure of territory quality. *Journal of Animal Ecology*, **72**, 857–865.
- Schoener, T.W. (1983) Simple models of optimal feeding-territory size: a reconciliation. *American Naturalist*, **121**, 608–629.
- Sinclair, I. and Ryan, P. (2003) Birds of Africa South of the Sahara. Struik Publishers, Cape Town.
- Smith, T.M. and Shugart, H.H. (1987) Territory size variation in the Ovenbird: the role of habitat structure. *Ecology*, **68**, 695–704.
- Sodhi, N.S. (1993) Proximate determinants of foraging effort in breeding male Merlins. *Wilson Bulletin*, **105**, 68–76.

- Stacey, P.B. and Ligon, J.D. (1987) Territory quality and dispersal options in the Acorn Woodpecker, and a challenge to the habitat saturation model of cooperative breeding. *American Naturalist*, **130**, 654–676.
- Steiger, S.S., Fidler, A.E., Valcu, M. and Kempenaers, B. (2008) Avian olfactory receptor gene repertoires: evidence for a well-developed sense of smell in birds? *Proceedings of the Royal Society B: Biological Sciences*, **275**, 2309–2317.
- Stenger, J. (1958) Food habits and available food of Ovenbirds in relation to territory size. *Auk*, **75**, 335–346.
- Siefferman, L. and Hill, G.E. (2005) UV-blue structural coloration and competition for nest boxes in male Eastern Bluebirds *Sialia sialis*. *Animal Behavior*, **69**, 67–72.
- Siitari H. and Huhta E. (2002) Individual color variation and male quality in Pied Flycatchers *Ficedula hypoleuca*: a role of ultraviolet reflectance. *Behavioral Ecology*, **13**, 737–741.
- Studd, M.V. and Robertson, R.J. (1988) Differential allocation of reproductive effort to territorial establishment and maintenance by male Yellow Warblers (*Dendroica petechia*). *Behavioral Ecology and Sociobiology*, **23**, 199–210.
- Strong, A.M. and Sherry, T.W. (2000) Habitat-specific effects of food abundance on the condition of Ovenbirds wintering in Jamaica. *Journal of Animal Ecology*, **69**, 883–895.
- Tarof, S., Dunn, P.O. and Whittingham, L.A. (2005) Dual function of a melanin based ornament in the Common Yellow-throat. *Proceedings of the Royal Society B: Biological Sciences*, **272**, 1121–1127.
- Temeles, E.J. (1987) The relative importance of prey availability and intruder pressure in feeding territory size regulation by Harriers *Circus cyaneus*. *Oecologia*, **74**, 286–297.
- Terra Nature Trust (2009) New Zealand ecology: flightless birds.
<http://www.terranature.org/kiwi1.htm>
- Theuerkauf, J., Rouys, S., Mériot, J.M. and Gula, R. (2009) Group territoriality as a form of cooperative breeding in the flightless Kagu *Rhynochetos jubatus* of New Caledonia. *Auk*, **126**, 371–375.
- Todt, D. (1981) On functions of vocal matching: effect of counter replies on song post choice and singing. *Ethology*, **57**, 73–93.
- Turpie, J.K. (1995) Nonbreeding territoriality: causes and consequences of individual and seasonal variation in Grey Plover *Pluvialis squatarola* behaviour. *Journal of Animal Ecology*, **64**, 429–438.

- Van de Pol, M., Bruinzeel, L.W., Heg, D., Van der Jeugd, H.P. and Verhulst, S. (2006) A silver spoon for a golden future: long-term effects of natal origin on fitness prospects of Oystercatchers *Haematopus ostralegus*. *Journal of Animal Ecology*, **75**, 616–626.
- Viera, V.M., Nolan, P.M., Côté, S.T., Jouventin, P. and Groscolas, R. (2008) Is territory defence related to plumage ornaments in the King Penguin *Aptenodytes patagonicus*? *Ethology*, **114**, 146–153.
- Wiens, J.A. (1989) Spatial scaling in ecology. *Functional Ecology*, **3**, 385–397.
- Wittenberger, J.F. (1981) Male quality and polygyny: the “sexy son” hypothesis revisited. *American Naturalist*, **117**, 329–342.
- Wortman-Wunder, E. (1997) Territory size in Lincoln’s Sparrow *Melospiza lincolnii*. *The Southwestern Naturalist*, **42**, 446–453.
- Wronski, T. and Plat, M. (2006) Mate availability and intruder pressure as determinants of territory size in male Bushbuck *Tragelaphus scriptus*. *Acta Ethologica*, **9**, 37–42.
- Wynne-Edwards, V. C. (1962) Animal dispersal in relation to social behavior. Oliver and Boyd, Edinburgh, Scotland.
- Ydenberg, R.C. and Krebs, J.R. (1987) The trade off between territorial defence and foraging in the Great Tit *Parus major*. *American Zoologist*, **27**, 337–346.
- Zack, S. (1990) Coupling delayed breeding with short-distance dispersal in cooperatively breeding birds. *Ethology*, **86**, 265–286.
- Zack, S. and Stutchbury, B.J. (1992) Delayed breeding in avian social systems: the role of territory quality and "floater" tactics. *Behaviour*, **123**, 194–219.
- Zahavi, A. (1975) Mate selection - a selection for a handicap. *Journal of Theoretical Biology*, **53**, 205–214.
- Zahavi, A. (2007) Sexual selection, signal selection and the handicap principle: in *Reproductive Biology and Phylogeny of Birds* (B. G. M. Jamieson, Ed.). Science Publishers, Plymouth. Pp.143–157.

CHAPTER TWO

BAR-THROATED APALIS TERRITORIES: SIZE, PREY DENSITY AND VEGETATION STRUCTURE

Introduction

Competition for resources may compel individuals to become territorial: this is suggested to occur when resources are both relatively dense and predictable (the Economic Defensibility Model - Fretwell 1970, Dyson-Hudson and Smith 1978, Lederer 1981). Resource density often varies across territories and this variability may determine not only territory size (e.g. Pickman 1987, Smith and Shugart 1987, Turpie 1995, Marshall and Cooper 2004), but also the relative reproductive success and survival of territory occupants (Steury and Murray 2003, Van de Pol *et al.* 2006, Grande *et al.* 2009). . For example, territory sizes of Lincoln's Sparrows *Melospiza lincolnii* vary from 1000–9100 m² (Wortman-Wunder 1997) and those of Red-winged Blackbirds *Agelaius phoeniceus* from 1188-18 456 m² (Pickman 1987).

Optimal territory size is determined by the balance between costs and benefits of territory defence (Both and Visser 2003 – see Chapter 1). Environmental factors that regulate territory size may include food (the Food-value Hypothesis - Stenger 1958, Gill and Wolf 1975); specific habitat features that account for the abundance and dispersion of food within territories (the Structural Cues Hypothesis – Marshall and Cooper 2004), as reported for Ovenbirds *Seiurus aurocapillus* (Smith and Shugart 1987) and Red-eyed Vireos *Vireo olivaceus* (Marshall and Cooper 2004); intruder pressure (the Intraspecific Competition Hypothesis – Hinde 1956), as in Western Gulls *Larus occidentalis* and Anna's Hummingbirds *Calypte anna* (Ewald *et al.* 1980; Eberhard and Ewald, 1994); or a combination of these (Marshall and Cooper 2004). There has been considerable evidence and counter-evidence for food density

determining territory size, even within same species. For example, Askenmo *et al.* (1994) reported a non-significant relationship between territory size and food density in the Rock Pipit *Anthus petrosus*, while a subsequent experimental study of the same species found a significant positive relationship when controlling for the effect of intruder pressure (Arvidsson *et al.* 1997). In the case of the Nuthatch *Sitta europaea*, a negative relationship exists between territory size and food density (Enoksson and Nilsson 1983). In terms of behavioural determinants of territory size, inference about the role of intruder pressure should be approached with caution because a) it is difficult to quantify, and b) those parameters that are the easiest to measure (such as number of neighbouring territories, local density of competitors) may not necessarily be those with the strongest effects on territory occupants (Adams 2001). However, it is unlikely that both food value and intraspecific competition operate independently of one another, simply because high resource density in high-quality territories may increase the probability of intrusion by conspecifics (Adams 2001, Marshall and Cooper 2004). This co-variation probably explains why several studies have found that territory size varies inversely with both food density and intruder pressure (e.g. Myers *et al.* 1979, Turpie 1995). Bar-throated Apalises *Apalis thoracica* rarely engage in direct territorial conflict (i.e. overt aggression), this study explores whether the food-value hypothesis is adequate to explain intra-specific variation in territory size.

If apalises do not resolve territorial disputes through direct conflict, it seems likely that territory boundaries are maintained through a combination of visual and vocal signalling of individual status. Neighbouring male apalises regularly perch conspicuously on tall shrubs at the edge of their territories and call aggressively towards one another, after which they disperse. However, cognisant of the importance of multivariate approaches in enhancing understanding of the factors that regulate

territory size in animal species (Adams 2001), this study did not restrict itself to measurements of food density alone. The study also considered other elements of the habitat to which territory occupants cue to ensure an adequate food supply and that may act as cues to intruders in recognising resource-rich areas (as assumed under the structural cue hypothesis - Smith and Shuggart 1987, Marshall and Cooper 2004).

Attempts to link environmental factors to territory size are most likely to produce robust results if they are made at the appropriate scale (Kristan *et al.* 2007). Monitoring individual behaviour is regarded as a scale that should provide reliable information on the habitat features that should be measured and how these might affect fitness (Wiens 1989, Johnson 2007, Kristan *et al.* 2007). This study explored the foraging behaviour of Bar-throated Apalises during the breeding season to determine those habitat features that in turn may determine territory size/quality. Individual foraging behaviour has a well-established potential to 'swiftly' unlock key habitat features that constrain survival and reproduction in animal populations (Lyon and Montgomerie 1985, Sodhi 1993, Johnson 2007). Foraging behaviour was studied during the breeding season, when food is expected to be a major determinant of individual fitness (through constraints it imposes on the [differential] ability of adults to provision nestlings). Any indices of territory quality that explain general patterns of territory occupancy at this time of year may represent the general quality of territories for the rest of the year. Specifically, the objectives of the study were:

1. To investigate foraging behaviour of the Bar-throated Apalis in relation to a) foraging substrata and b) prey abundance.
2. To use information from (1) to quantify food density across territories and establish its relationship with territory size and vegetation structure within territories.

Because territory maintenance is an energetically costly behaviour (Chapter 1), I further predicted that:

1. Individuals will concentrate their foraging efforts at those plant species that deliver the greatest rewards in terms of access to favoured prey.
2. Territory size will be determined by the abundance of favoured foraging substrata.

METHODS

Study site

The study was carried out at Koeberg Nature Reserve, South Africa (33°41'S, 18°27'E; Fig. 2.1). The site is coastal, covering *ca* 1.9 km² and lying 20 m a.s.l. The climate is Mediterranean, with annual rainfall concentrated in the winter, immediately prior to the birds' breeding season. The site is characterised by two main habitats occurring in a diffuse mosaic - Dune Thicket and Sand Plain Fynbos (Mucina and Rutherford 2006). The former occurs on coastal sand dunes and is characterised by denser and taller shrubs (up to 3 m) than the Sand Plain Fynbos. Bar-throated Apalises occupy breeding territories in both habitats. Common shrub species include *Rhus glauca*, *Olea europaea*, *Euphorbia camerunica*, *Chrysanthemoides monilifera*, *Euclea racemosa* and grasses of the genus *Staberoha*. Bird ringing has been carried out at the study site since 2001, with targeted ringing of apalises since 2004.

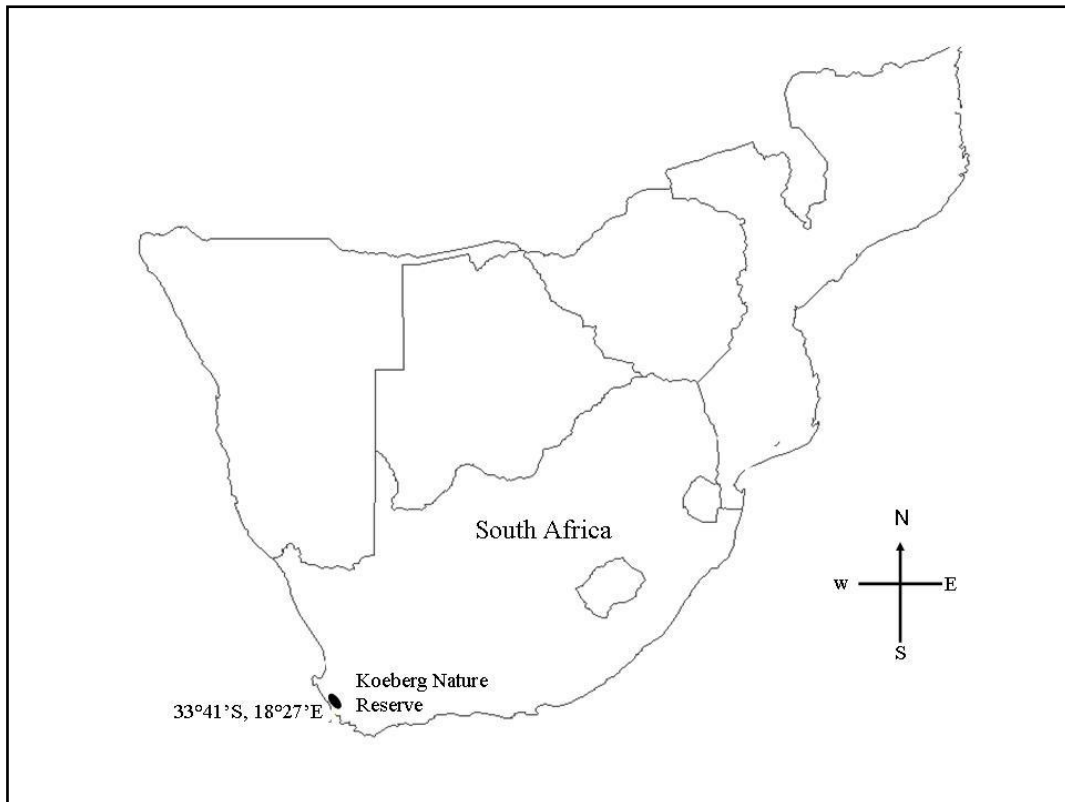


Figure 2.1: Map of southern Africa showing location of the study area.

Establishing territory sizes

All pairs on the site were monitored once weekly for a period of one hour throughout the breeding season from August to October in 2007 (25 territories) and 2008 (15 territories). All points where pairs were observed calling, feeding or perching were recorded onto a handheld GPS (Garmin® Etrex H). Time of sampling was randomized (between 06h00 and 16h00) to reduce any effect of time of day on individual activity. Territory sizes were calculated from cumulative resightings of colour-ringed pairs using the computer software ArcView 3.2 (ESRI 1999): the minimum convex polygon enclosing all identified locations for a pair was used to define the breeding territory of that pair (Marshall and Cooper 2004).

Foraging substrata

Foraging behaviour was observed during both male-mate incubation feeding and nestling provisioning. For the male-mate incubation feeding period, data on foraging substrata were obtained during the weekly 1-hour territory delineation period; males were monitored to record the plant species from which food was obtained for delivery to the incubating females. During the nestling phase, a period of 1-hour (randomised for nestlings of different age) was spent identifying the plant species from which food was obtained by parents for provisioning nestlings. Heights (m) of plants visited were also recorded. Favoured foraging substrata were later quantified per territory on four randomly stratified 100 m transects, each separated by 30 m. Each transect was subdivided into 1 m sections (a total of 400 sections per territory). At each 1 m interval, plant species type and height was recorded. From these measurements, the abundance of favoured foraging substrata per territory was computed (accounting for the fact that birds foraged exclusively in shrubs >1 m tall).

Diet composition

Diet of Bar-throated Apalises was determined from video recordings made during both male-mate incubation feeding (25 territories) and nestling feeding (17 territories). A Spy camera (SW211-SPY, Swann Communication Pty. Ltd., Australia) was camouflaged in vegetation close to each nest: each recording used in analyses lasted for the five hours after sunrise. Video footage for nestling feeding was standardised at day 1 (24-hours old) and day 9 after hatching. Arthropods brought to nests were identified mostly to family level and in some cases to genus level.

Prey density

Prey abundance was quantified in three separate sampling periods spread across the breeding season. Sampling was conducted in the first two weeks of August, September and October 2008 (representing early, mid and late breeding season). For each of the three major plant species that were identified as the favoured foraging substrata (see results), three individuals per plant species per territory were selected (minimum 10 m apart) and two samples were taken per plant. Using the knock-down-technique (Southwood 1978, Southwood *et al.* 1982), arthropods were collected in a 0.096 m² rectangular tray by inserting the tray into the shrub canopy and vigorously shaking branches. Arthropods were sorted by taxon and weighed in the field using a Scout[®] Pro SPU123 balance (Ohaus Corporation, USA). Only arthropod taxa that had been identified through video recordings as contributing to the diet of the Bar-throated Apalises were counted and weighed. The arthropods were subsequently returned to the shrubs from which they had been collected.

To obtain prey biomass, the number of each arthropod taxon on each plant species was multiplied by the mean weight for individuals of that taxon during the sampling period. The biomass for each taxon per plant species was then averaged per sampling period (to control for within-season variation) and per territory. Prey biomass per plant species per territory was multiplied by the number of favoured foraging plants >1 m tall within the territory and divided by the size of each territory to obtain a measure of prey density per territory (cf. Komdeur *et al.* 1997).

Differences in arthropod biomass between foraging and non-foraging substrata

In order to determine whether the favoured foraging substrata were particularly prey rich, arthropod samples were also collected from shrubs within the territories that

were not used for foraging (one plant per territory and comprising seven plant species in 27 territories). Samples were collected and analysed as described above.

Statistical analyses

Data were analysed using the statistical package SPSS 17 (SPSS incorporated, USA).

All data were explored for normality and equality of variance using One-Sample Kolmogorov-Smirnov Tests and Levene statistics, as well as using visual exploration (Zuur *et al.* 2009).

Comparisons and relationships

A paired-sample t-test was used to determine whether territory sizes changed in size between 2007 and 2008. An independent-sample t-test was used to compare arthropod biomass on plant species that were favoured *vs* avoided as foraging substrata.

Separate regression analyses were used to examine relationships between territory size, food density and territory vegetation structure (vegetation cover and average shrub height). Pearson correlation was used to check for the relationship between territory area and number of sampling points per territory to ensure that calculated territory size was not simply a correlate of sampling intensity (because the number of points sampled per territory was not standardised). A one-sample analysis of variance (ANOVA) was used to compare mean arthropod density across the three sampling periods in the breeding season.

Analysis of diet selectivity

Diet selectivity was assessed by comparing the proportion of prey observed in the birds' diets (both during male-mate incubation feeding and during the nestling period)

with their availability on the three favoured foraging substrata. This analysis involved five arthropod orders (Araneae, Hemiptera, Lepidoptera, Orthoptera and Phasmatodea) common to all territories and for which sample sizes were sufficiently large to make meaningful comparisons. Comparisons were made using Generalised Linear Mixed Models (GLMM), following the modelling approach of Maguire (2006). Territory identity, sample type (diet or environment), arthropod order and their interactions were included as random factors. The main questions explored were: 1) is prey choice non-random (tested by the significance of a 2-way interaction between arthropod order and sample type); and 2) does the relative availability of arthropod groups vary significantly across territories (tested by the significance of a 2-way interaction between arthropod order and territory identity). In both cases, the proportions of arthropods sampled in the diet and in the environment were used as the dependent variables.

RESULTS

Foraging substrata

During incubation feeding, males obtained food (arthropods) for incubating females primarily from two plant species, *Rhus glauca* and *Chrysanthemoides monilifera*.

During nestling feeding birds broadened their foraging habitat niche slightly to include *Olea europaea* (Figs 2.2a, b).

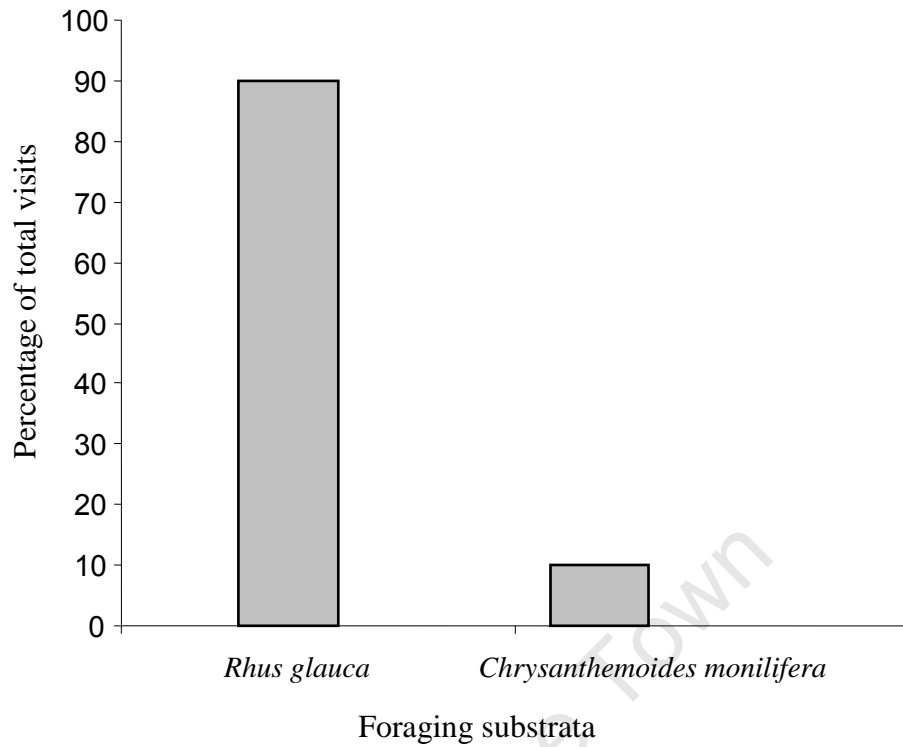


Figure 2.2a: Foraging substrata utilised by male Bar-throated Apalis during mate incubation feeding ($n = 20$ males, 40 visits).

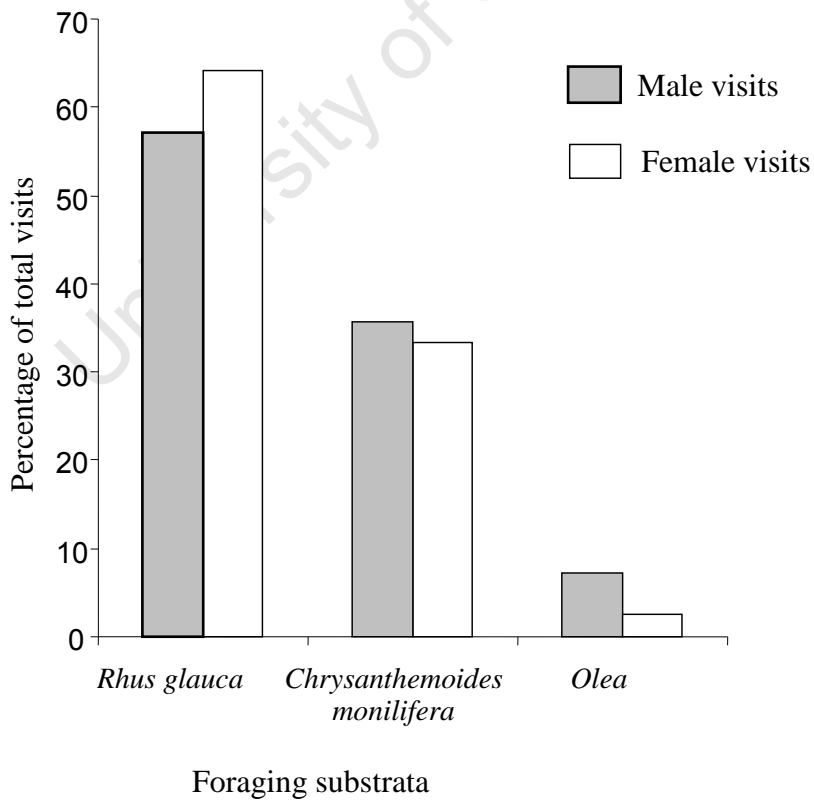


Figure 2.2b: Foraging substrata utilised by male and female Bar-throated Apalises during nestling feeding ($n = 13$ males, 70 visits and 13 females, 39 visits).

Diet composition

During male-mate incubation feeding, males were recorded bringing arthropods to incubating females in a total of 155 visits across 25 territories. In addition, both parents brought arthropods to nestlings in a total of 1306 visits in 17 territories.

Arthropods could be identified in 108 of 155 incubation feeds (70%) and 970 of 1306 nestling feeding (74%), giving a total, identifiable prey sample size of 1078 (Table 2.1).

Table 2.1: Arthropods brought to the nest by Bar-throated Apalises during incubation (males only) and nestling feeding (both sexes). *N INCF* = numbers recorded during incubation feeding; *N NSTLF* = numbers recorded during nestling feeding; % *INCF* = percentage recorded during incubation feeding; % *NSTLF* = percentage recorded during nestling feeding.

Order	Family	Genus	Common name	<i>N</i>	<i>N</i>	%	%
				<i>INCF</i>	<i>NSTLF</i>	<i>INCF</i>	<i>NSTLF</i>
Orthoptera	Acrididae	<i>Acanthacris</i>	Grasshopper	9	81	8.3	8.4
	Pneumoridae	<i>Bullacris</i>	Bladder grasshopper	9	64	8.3	6.6
Phasmatodea	Bacillidae	<i>Phalces</i>	Cape stick-insect	6	37	5.6	3.8
Araneae	Pisauridae		Spider		115		11.8
Hemiptera*			Bug	7	19	6.5	2.0
Lepidoptera			Caterpillar	69	527	63.9	54.3
			Moth	7	96	6.5	9.9
			Butterfly	1	23	0.9	2.4
Hymenoptera	Apoidea	<i>Apis</i>	Bee		5		0.5
	Apoidea		Wasp		1		0.1
Dictyoptera	Blattidae	<i>Periplaneta</i>	Cockroach (nymphs)		2		0.2
Total				108	970	100	100

* = all hemipterans were grouped together

Arthropod biomass on favoured and avoided foraging substrata

Average arthropod biomass was significantly higher on favoured foraging substrata (*Rhus glauca*, *Chrysanthemoides monilifera* and *Olea europaea* collectively – 0.20 ± 0.03 S.E. g.m^{-2}) than on those that were avoided (0.11 ± 0.02 g.m^{-2} ; $t = 2.363$, $df = 42$, $P = 0.023$). A closer examination of arthropod biomass based on grouping by Order showed that favoured foraging substrata supported a significantly higher biomass of lepidopterans and their larvae than plants that were avoided as foraging substrata (Table 2.2).

Table 2.2: Differences in arthropod biomass between favoured and avoided foraging substrata of Bar-throated Apalises.

Arthropod Order	Favoured substrata, mean \pm S.E. g.m^{-2}	Avoided substrata, mean \pm S.E. g.m^{-2}	df	t	P
Lepidoptera	0.032 ± 0.004	0.008 ± 0.003	42	4.132	< 0.001
Araneae	0.126 ± 0.036	0.069 ± 0.010	42	1.536	0.132
Hemiptera	0.025 ± 0.006	0.024 ± 0.009	42	0.110	0.913
Phasmatodea	0.001 ± 0.001	0.000 ± 0.000	42	0.444	0.659
Orthoptera	0.013 ± 0.003	0.009 ± 0.003	42	0.722	0.474
Dictyoptera	0.004 ± 0.001	0.000 ± 0.000	42	3.198	0.004

Diet selectivity

Prey selection by Bar-throated Apalises was significantly non-random (GLMM, arthropod order/sample type interaction: $F_{1,9} = 5.552$, $P = 0.043$). Lepidoptera and Phasmatodea were over-represented relative to their occurrence in the environment, whilst Araneae and Hemiptera were under-represented. The proportional occurrences of Orthoptera in the diet and in the environment were very similar (Fig. 2.3).

Similarly, arthropod assemblages differed significantly in their taxonomic make-up

across territories (GLMM, arthropod order/territory identity interaction: $F_{1, 189} = 85.988$, $P < 0.001$).

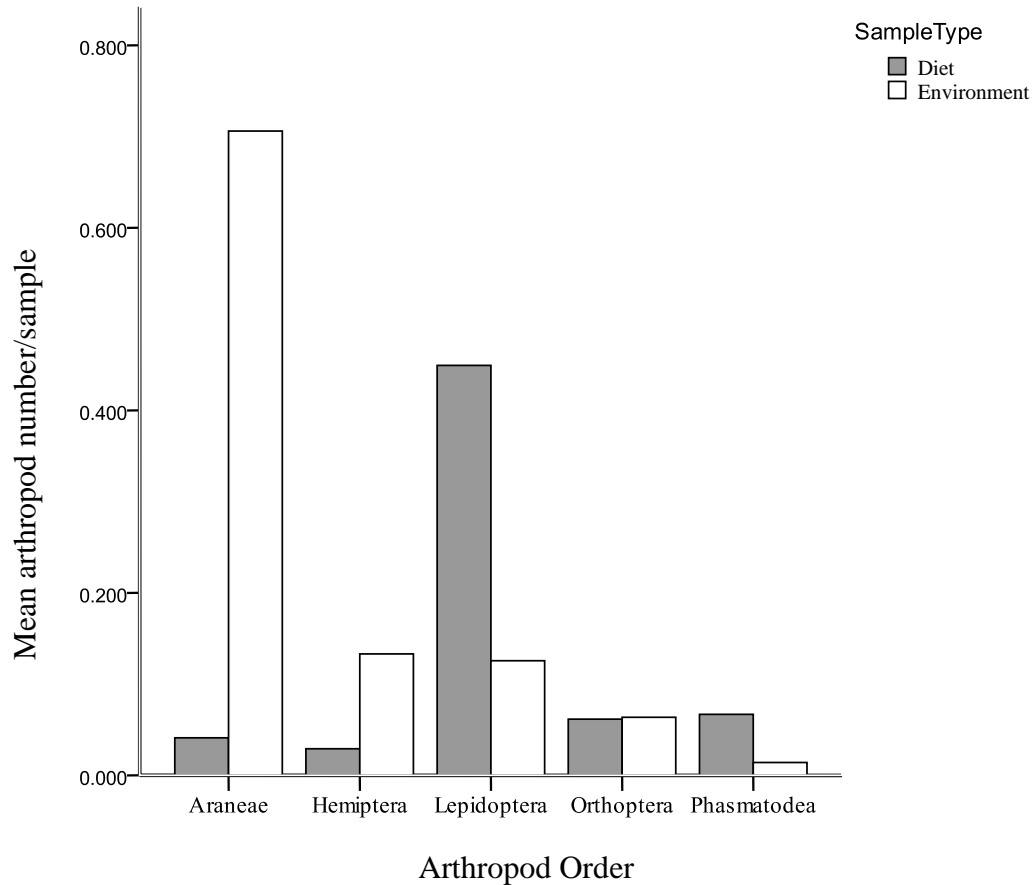


Figure 2.3: Differences in arthropod numbers as collected using the knock-down technique (environment) and as observed in Bar-throated Apalis diet through video observations at nests across 19 territories during both incubation and nestling feeding.

Prey abundance within territories

Across the breeding season, average arthropod abundance per territory on favoured substrata was 2.25 ± 0.12 individuals.m⁻² (range 1.20 – 3.41 individuals.m⁻²). As a necessary corollary, prey density across territories increased significantly with an increasing density of favoured foraging substrata ($n = 27$ territories, $r^2 = 0.76$, $F_{1, 26} = 34.817$, $P < 0.001$; Fig. 2.4a). Across the breeding season, however, arthropod

abundance decreased steadily and significantly (one-sample ANOVA, $F_{2, 88} = 55.034$, $P < 0.001$; Fig. 2.4b).

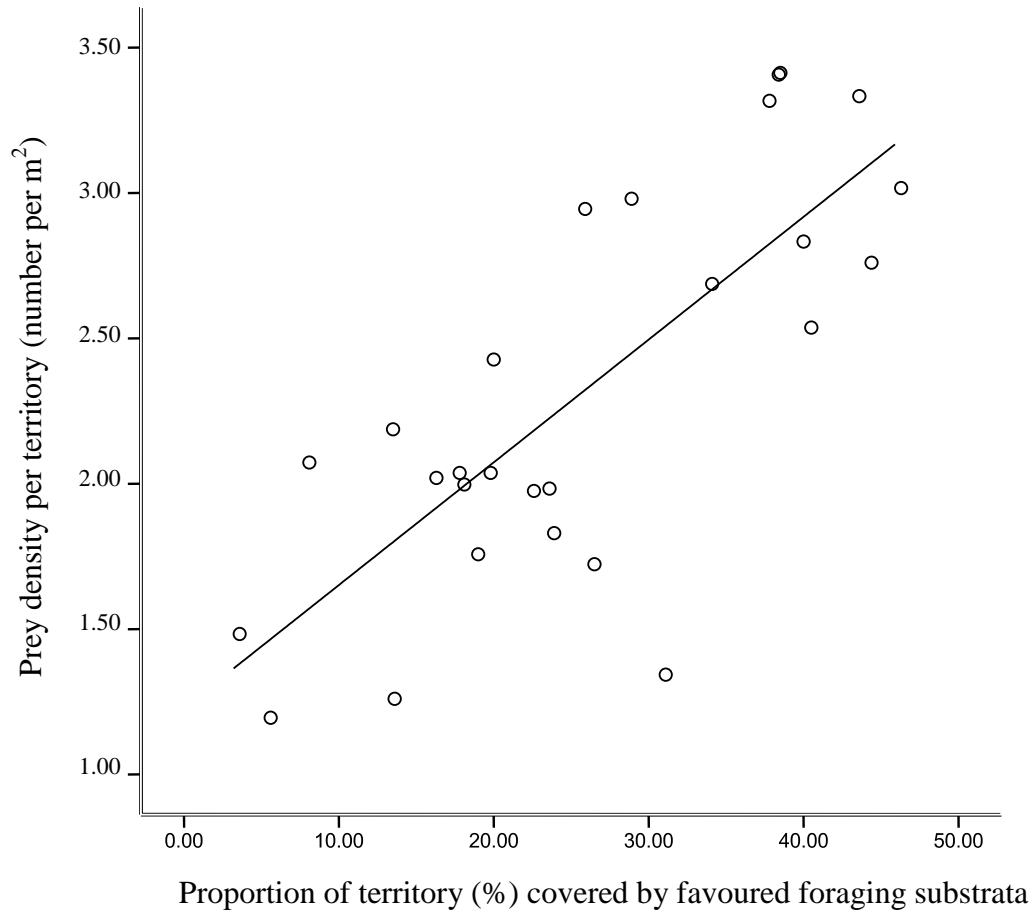


Figure 2.4a: Average apalis prey density per territory as a function of the relative abundance of favoured foraging substrata ($y = 0.042x + 1.223$; $P < 0.05$).

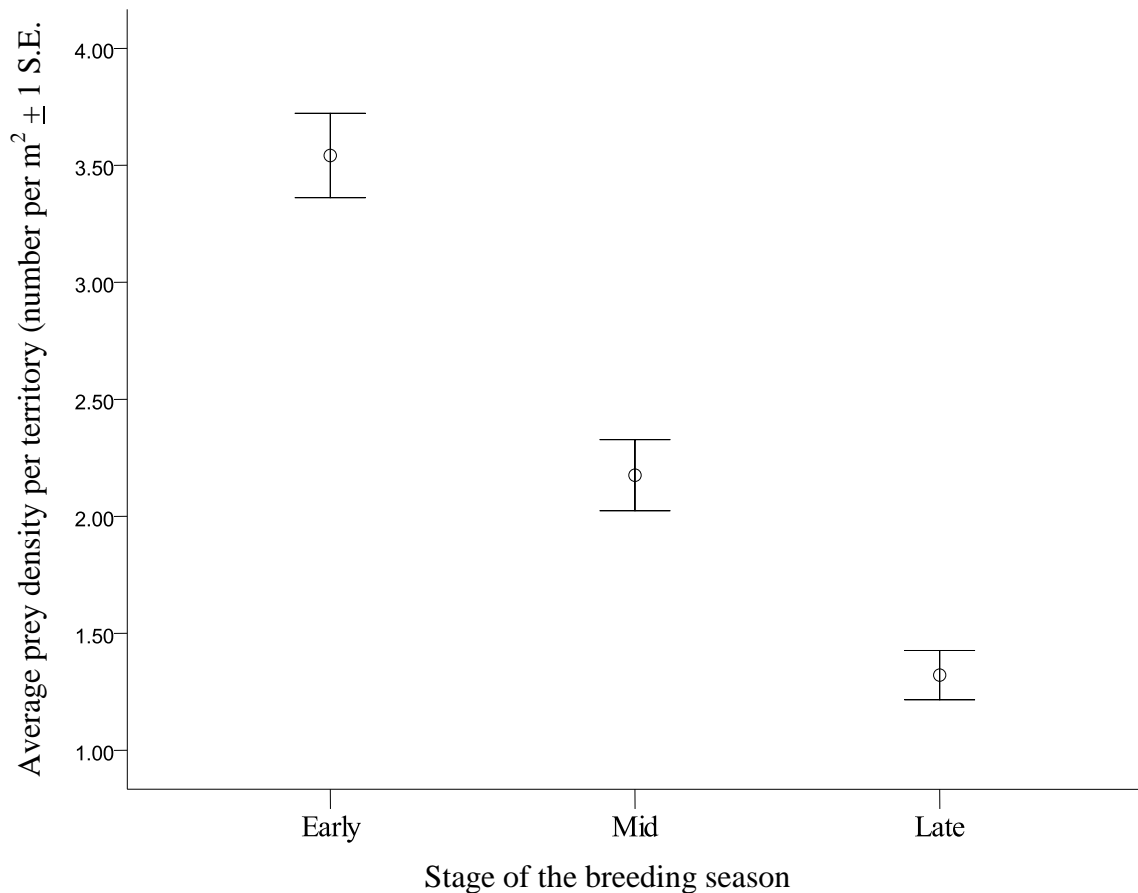


Figure 2.4b: Average apalis prey density per territory as a function of stage of the breeding season (August, September and October 2008).

Prey density and vegetation structure

Prey biomass density across 27 territories averaged 0.0017 ± 0.0004 (S.E.) g.m^{-2} and was positively correlated with proportional overall vegetation cover per territory ($n = 27$ territories, $F_{1\ 26} = 5.453$, $r^2 = 0.42$, $P = 0.028$; Fig. 2.5a) and with average overall vegetation height ($n = 27$ territories, $F_{1\ 26} = 13.962$, $r^2 = 0.59$, $P = 0.001$; Fig. 2.5b).

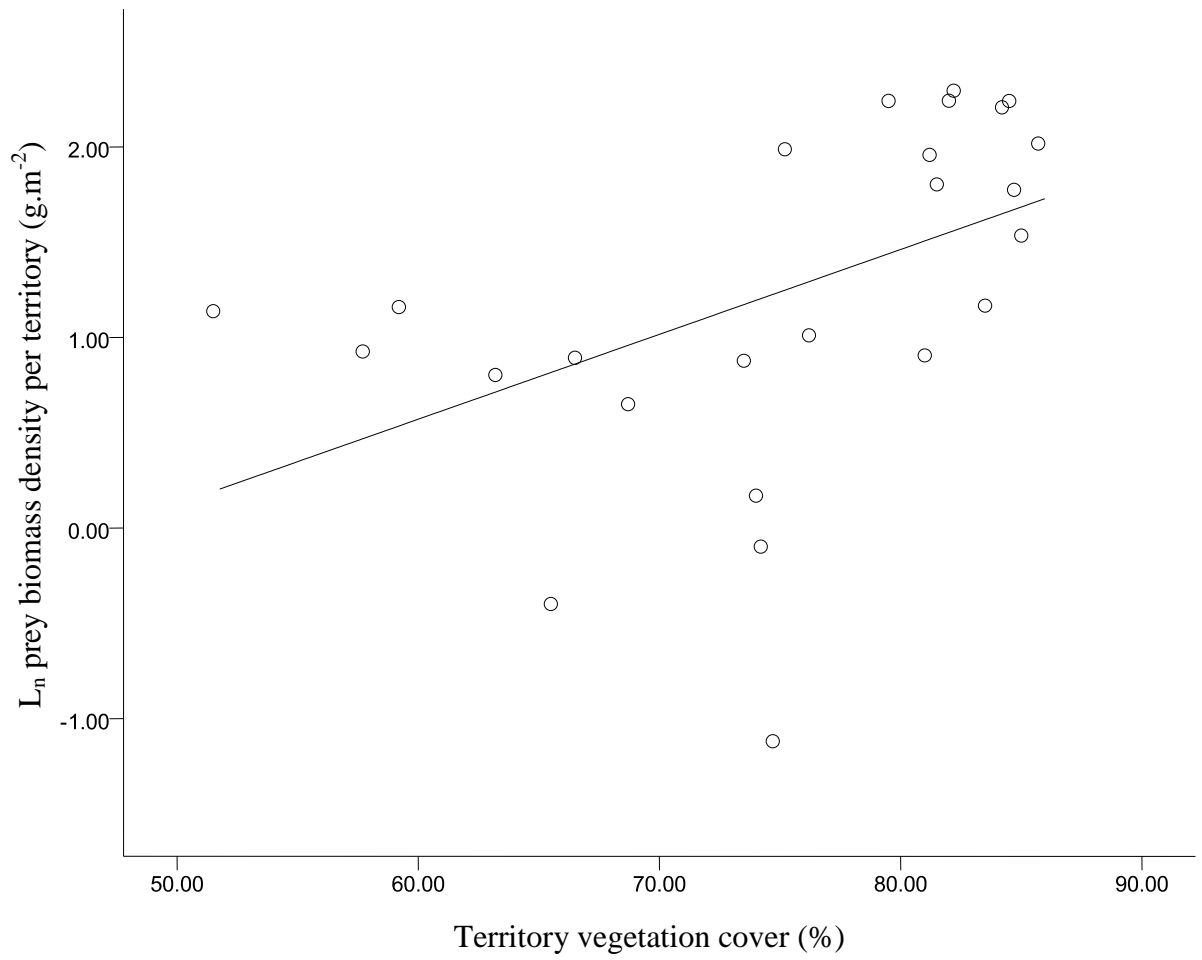


Figure 2.5a: *Apalis* prey density in relation to overall vegetation cover per territory ($y = 1.02E-04 x - 0.06$; $P < 0.05$).

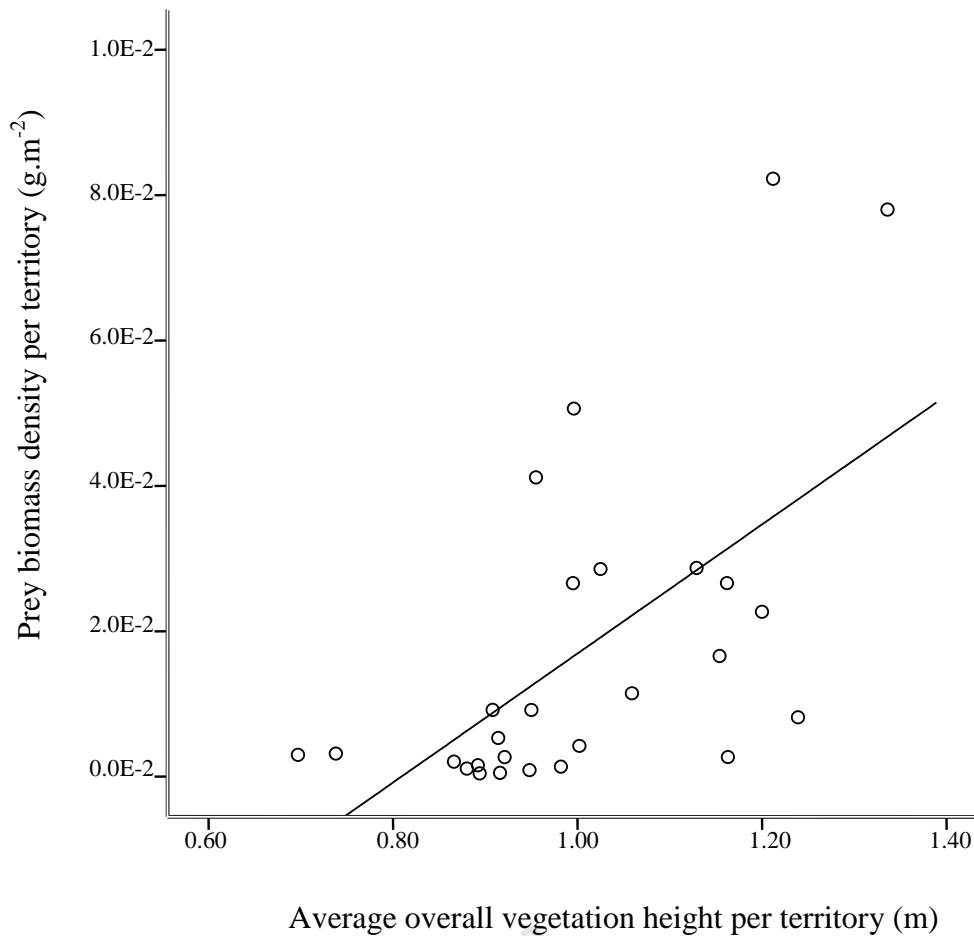


Figure 2.5b: Apalis prey biomass density in relation to average vegetation height per territory ($y = 0.009x - 0.007$; $P < 0.05$).

Territory size and its determinants

The areas of 40 Bar-throated Apalis territories measured during both the 2007 and 2008 breeding seasons were determined from an average of 16 sampling points per territory per year (range 12 – 36). Calculated territory areas were not correlated with number of points sampled per territory (Pearson correlation, $n = 40$, $r = 0.17$, $P = 0.282$) and are thus not an artefact of sampling intensity. Territory size ranged from 804 - 20 584 m² (Mean \pm S.E. = 6114 \pm 783 m²) and individual territories did not change significantly in size across the two breeding seasons (Paired sample t-test, $n = 15$ territories, $t = 1.660$, $df = 14$, $P = 0.119$).

Prey density accounted for 61.3 % of the variation in territory size, with smaller territories having higher prey density than larger ones ($n = 27$ territories, $F_{1, 26} = 15.073$, $r = -0.61$, $P = 0.001$; Fig. 2.6a). Territory size was also negatively correlated with both overall vegetation cover ($n = 30$ territories, $F_{1, 28} = 9.773$, $r^2 = -0.50$, $P = 0.004$; Fig. 2.6b) and average vegetation height ($n = 30$ territories, $F_{1, 28} = 6.111$, $r^2 = -0.42$, $P = 0.02$; Fig. 2.6c) Vegetation height and overall vegetation cover were themselves autocorrelated ($n = 30$ territories, $F_{1, 28} = 24.594$, $r^2 = 0.68$, $P < 0.001$), but vegetation cover contributed more to explaining prey density than did vegetation height.

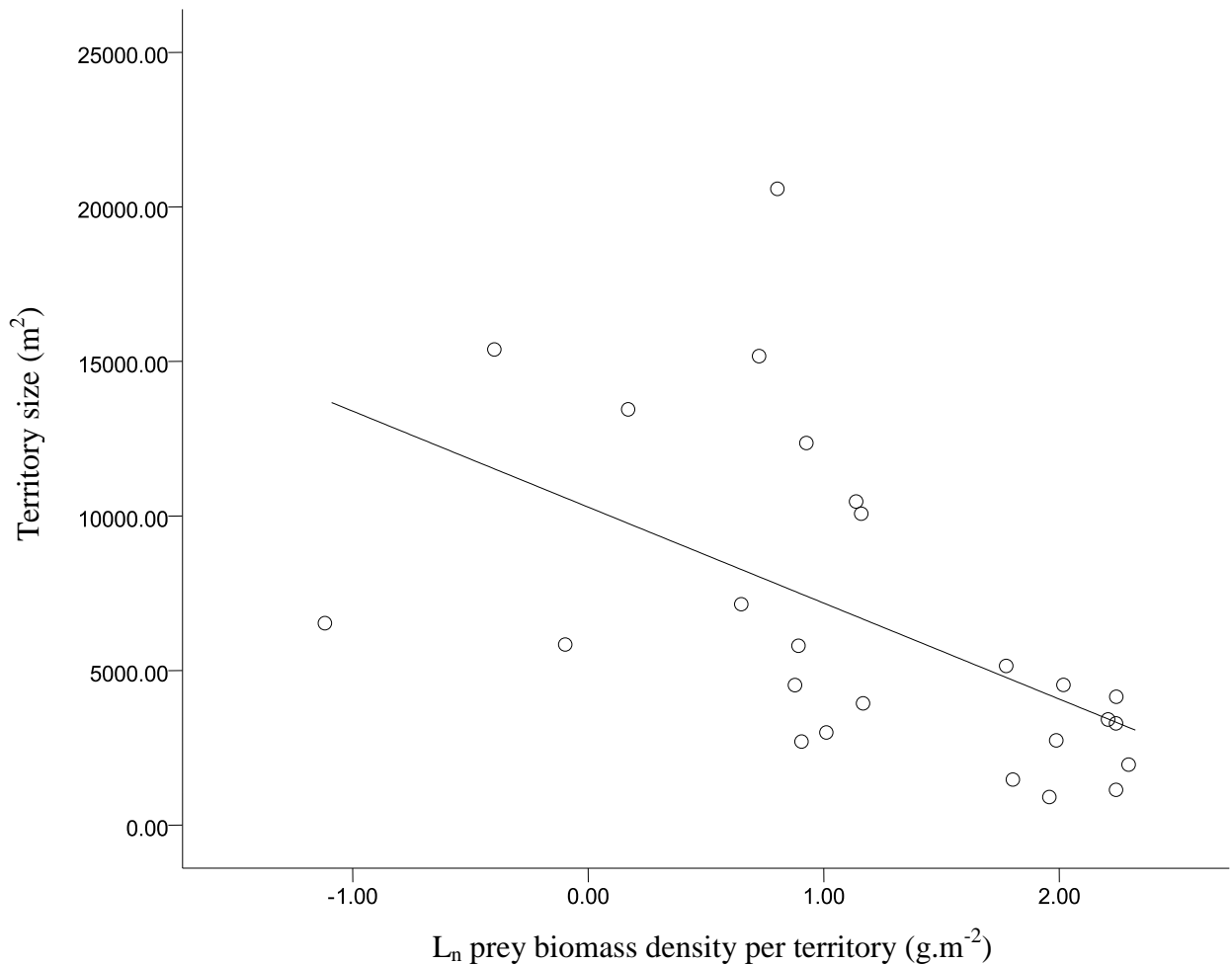


Figure 2.6a: The relationship between territory sizes of Bar-throated Apalises and average prey density per territory ($n = 27$ territories, $r^2 = -0.69$, $F_{1, 25} = 58.088$, $P < 0.001$).

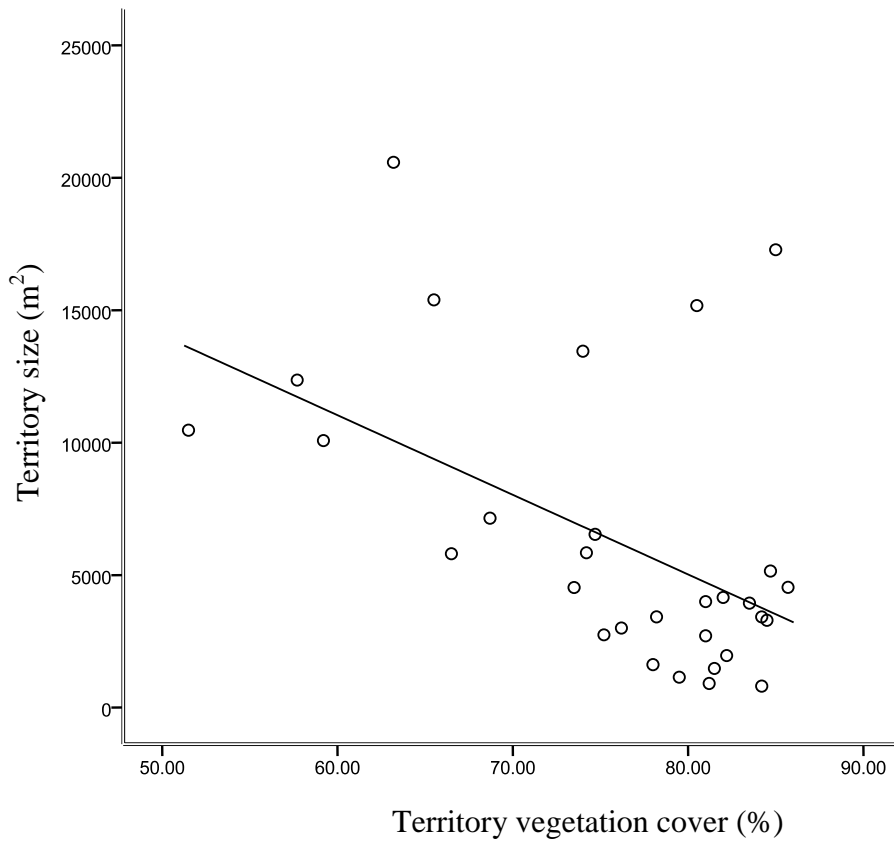


Figure 2.6b: The relationship between territory sizes of Bar-throated Apalises and vegetation cover within territories ($y = 29\,347.24 - 301.94 x$; $P < 0.05$).

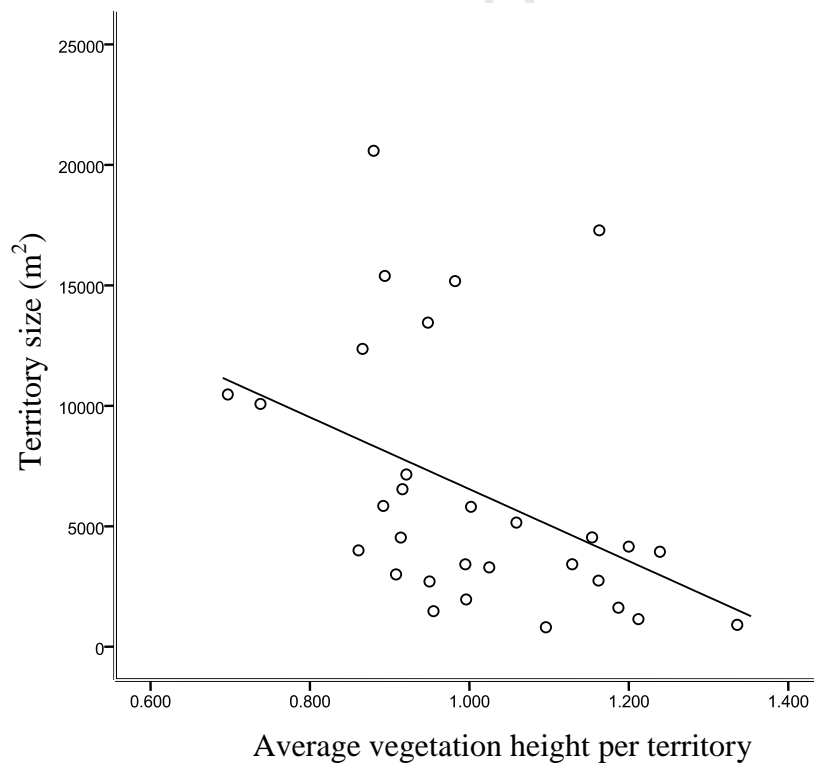


Figure 2.6c: The relationship between territory sizes of Bar-throated Apalises and average vegetation height within territories ($Y = 21\,615.51 - 1.5E4 x$; $P < 0.05$).

DISCUSSION

Bar-throated Apalises fed on a wide diversity of arthropod taxa, but throughout the breeding cycle gleaned these from a low diversity of plant species. The favoured foraging substrata are probably selected on the basis of the high density of caterpillars (the favoured prey) that they support (Tables 2.1, 2.2). The non-random distribution of potential prey across plant species affected not only the birds' foraging behaviour, but also strongly influenced territory size. Small territories had high densities of favoured plants, and most of the variation in territory size was explained by prey density, with overall vegetation cover and average vegetation height being secondary (negative) correlates of territory size. Territory sizes of Red-eyed Vireos *V. olivaceus* are also inversely related to caterpillar density, with the birds hypothesised to use foliage density as the structural cue to assess caterpillar abundance (Marshall and Cooper 2004). These results both support models of optimal territoriality which propose that territory size varies inversely with resource abundance (Fretwell and Lucas 1970, Both and Visser 2003): similar conclusions have been reached in several other studies (e.g. Stenger, 1958, MacLean and Seastedt 1979, Smith and Shugart 1987, Turpie 1995, Marshall and Cooper 2004). The findings also highlight the fact that a combination of food density and specific habitat structures that account for food density can together provide a reliable method for explaining intra-specific variation in territory size. This forms the essence of the Structural Cues Hypothesis (Smith and Shuggart 1987, Marshall and Cooper 2004, Hagar *et al.* 2007) whereby landscape-level features (in this case vegetation structure) offer a short-cut to predicting territory quality and thus to evaluating whether a) territory defence is viable, and b) the costs

of attempting to usurp a territory are worth incurring (Fretwell and Lucas 1970, Dyson-Hudson and Smith 1978, Smith and Shugart 1987).

However, habitat choices based on environmental cues alone can be deceptive, leading individuals into 'ecological traps' (*sensu* Dwernychuk and Boag, 1972, Gates and Gysel, 1978) or perceptual errors (Kokko and Sutherland 2001). This happens because information about habitat quality is inevitably incomplete at the time of settlement if territories are selected based on structural parameters before it is possible to assess secondary correlates of territory quality such as prey abundance (Orians and Wittenberger 1991) or predation risk. Kentish Plovers *Charadrius alexandrinus*, for example, select favoured nesting sites based on food abundance. However, pairs on these ostensibly high-quality territories later suffer high rates of nest predation with the result that their productivity is lower than pairs that settle in relatively food-poor territories (Székely 1992).

The disproportionately large numbers of caterpillars fed to both the incubating female and to nestlings may have a nutritional basis. For insectivorous Collared Flycatchers *Ficedula albicollis* it has been proposed that caterpillar food eaten prior to egg-laying is important both in providing the calcium required for eggshell and bone development (Schowalter and Crossley Jr 1983, Hagar *et al.* 2007), and in increasing the availability of carotenoids during yolk formation (Török *et al.* 2007). From egg-laying onwards, carotenoids play a major role in antioxidant protection in birds, protecting the vulnerable lipid-rich tissues of bird embryos from attack by free radicals and other reactive oxygen metabolites (Surai *et al.* 1996, Chaple 1997, Edge *et al.* 1997, Von Schantz *et al.* 1999). Steroid hormones such as carotenoids also stimulate and regulate immune responses and play an important role in gene expression with positive consequences for the growth rate and competitive ability of

nestlings (Bendich 1989, Haq *et al.* 1996, Shwable 1996, Bertram 1999, Lipar and Ketterson 2000, Eising *et al.* 2001, Wilkin *et al.* 2009). Although some temperate bird species show dependence on caterpillars of one or only a few lepidopterans during reproduction (Cresswell and McCleery 2003, Visser *et al.* 2006, García-Navas and Sanz 2011), video recordings showed that Bar-throated Apalises prey on caterpillars of multiple species, but poor resolution precluded these from being identified to species level.

Small territories were more densely vegetated and contained taller plants than did large territories: these differences may have ecological consequences for territory occupants. For example, dense vegetation cover has been suggested to militate against nest predation by reducing the diversity of cues available to potential nest predators (Bowman and Harris 1980, Martin and Roper 1988).

Conclusion

Territory sizes of Bar-throated Apalises during the breeding season were regulated primarily by the density of preferred arthropods. This in turn was influenced by the relative densities of a small suite of favoured foraging substrata, with vegetation cover and vegetation height being secondary (and negative) correlates of territory size. The finding that territory size is governed by resource availability conforms to predictions of models of optimal territoriality and confirms findings from other empirical studies. The link between territory size and resource density potentially has far-reaching implications for important aspects of the species' biology that relate to fitness, such as male quality and energy delivery rates to both incubating females and to young (e.g. Fretwell and Lucas 1970, Dyson-Hudson and Smith 1978, Sodhi 1993). These potential fitness correlates of territory quality are explored in subsequent chapters.

REFERENCES

- Adams E.S. (2001) Approaches to the study of territory size and shape. *Annual Review of Ecological Systems*, **32**, 277–303.
- Arvidsson, B., Askenmo, C. and Neergaard, R. (1997). Food supply for settling male Rock Pipits affects territory size. *Animal Behaviour*, **54**, 967–972.
- Askenmo, C., Neergaard, R. and Arvidsson, B.L. (1994). Food supplementation does not affect territory size in Rock Pipits. *Animal Behavior*, **47**, 1235–1237.
- Bendich, A. (1989) Carotenoids and the immune response. *Journal of Nutrition*, **119**, 112–115.
- Bertram, J.S. (1999) Carotenoids and gene regulation. *Nutrition Review*, **57**, 182–191.
- Both, C. and Visser, M.E. (2003) Density dependence, territoriality, and divisibility of resources: from optimality models to population processes. *American Naturalist*, **161**, 326–336.
- Bowman, G.B. and Harris, L.D. (1980) Effect of spatial heterogeneity on ground-nest depredation. *Journal of Wildlife Management*, **44**, 806–813.
- Chapple, I.L.C. (1997) Reactive oxygen species and antioxidants in inflammatory diseases. *Journal of Clinical Periodontology*, **24**, 287–296.
- Cresswell, W. and McCleery, R. (2003). How Great Tits maintain synchronization of their hatch date with food supply in response to long-term variability in temperature. *Journal of Animal Ecology*, **72**, 356–366.
- Dwernychuk, L.W. and Boag, D.A. (1972) Ducks nesting in association with gulls – an ecological trap? *Canadian Journal of Zoology*, **50**, 559–563.
- Dyson-Hudson, R. and Smith E.A. (1978) Human territoriality: an ecological reassessment. *American Anthropologist*, **80**, 21–41.
- Eberhard, J.R. and Ewald, P.W. (1994) Effects of food availability and intrusion pressure on territory size: an experimental study of Anna's Hummingbirds *Calypte anna*. *Behavioral Ecology and Sociobiology*, **34**, 11–18.
- Edge, R., McGarvey, D.J. and Truscott, T.G. (1997) The carotenoids as antioxidants – a review. *Journal of Photochemical Photobiology*, **41B**, 189–200.
- Eising, C.M., Eikenaar, C., Schwabl, H. and Groothuis, T.G.G. (2001) Maternal androgens in Black-headed Gull (*Larus ridibundus*) eggs: consequences for chick development. *Proceedings of Royal Society B: Biological Sciences*, **268**, 839–846.

- Enoksson, B and Nilsson, S.G. (1983). Territory size and population density in relation to food supply in the Nuthatch *Sitta europaea* (Aves). *Journal of Animal Ecology*, **52**, 27–35.
- Ewald, P W., Hunt G.L, and Warner, M. (1980) Territory size in Western Gulls: importance of intrusion pressure, defense investments, and vegetation structure. *Ecology*, **61**, 80–87.
- Fretwell, S.D. and Lucas, H.J., Jr. (1970) On territorial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheoretica*, **19**, 16–36.
- García -Navas, V. and Sanz, J.J. (2011) The importance of a main dish: nestling diet and foraging behaviour in Mediterranean Blue Tits in relation to prey phenology. *Oecologia*, **165**, 639–649.
- Gates, J.E. and Gysel, L.W. (1978) Avian nest dispersion and fledging success in field-forest ecotones. *Ecology*, **59**, 871–883.
- Gill, F.B. and Wolf, L.L. (1975) Economics of feeding territoriality in the Golden-winged Sunbird. *Ecology*, **56**, 333–345.
- Grande, J.M., Serrano, D., Tavecchia, G., Carrete, M., Ceballos, O., Diaz-Delgado, R., Tella, J.L. and Donazar, J.A. (2009) Survival in a long-lived territorial migrant: effects of life-history traits and ecological conditions in wintering and breeding areas. *Oikos*, **118**, 580–590.
- Hagar, J.C., Dugger, K.M. and Starkey, E.E. (2007) Arthropod prey of Wilson's Warblers in the understory of Douglas-fir forests. *The Wilson Journal of Ornithology*, **119**, 533–546.
- Haq, A., Bailey, C.A. and Chinnah, A. (1996) Effect of β -carotene, canthaxanthin, lutein, and vitamin E on neonatal immunity of chicks when supplemented in the broiler breeder diet. *Poultry Science*, **75**, 1092–1097.
- Hinde, R.A. (1956) The biological significance of the territories of birds. *Ibis*, **98**, 340–369.
- Hockey, P.A.R., Dean, W.R.J. and Ryan, P.G. (eds) (2005) *Roberts - Birds of Southern Africa*, 7th ed. The Trustees of the John Voelcker Bird Book Fund, Cape Town.
- Johnson, D. (2007) Measuring habitat quality: a review. *Condor*, **109**, 489–504.
- Kokko, H. and Sutherland, W.J. (2001) Ecological traps in changing environments: ecological and evolutionary consequences of a behaviourally mediated Allee effect. *Evolutionary Ecology Research*, **3**, 537–551.
- Komdeur, J., Daan, S., Tinbergen, J. and Mateman, C. (1997) Extreme adaptive modification in sex ratio of the Seychelles Warbler's eggs. *Nature*, **385**, 522–525.

- Kristan, W.B. III; Johnson, M.D. and Rotenberry, J.T. (2007) Choices and consequences of habitat selection for birds. *Condor*, **109**, 485–488.
- Lederer, R.J. (1981) Facultative territoriality in Townsend's Solitaire (*Myadestes townsendi*) *The Southwestern Naturalist*, **25**, 461–467.
- Lipar, J.L. and Ketterson, E.D. (2000) Maternally derived yolk testosterone enhances the development of the hatching muscle in the Red-winged Blackbird *Agelaius phoeniceus*. *Proceedings of the Royal Society B: Biological Sciences*, **267**, 2005–2010.
- Lyon, B.E. and Montgomerie, R.D. (1985) Incubation feeding in Snow Buntings: female manipulation or indirect male parental care? *Behavioral Ecology and Sociobiology*, **17**, 279–284.
- MacLean, S.F. and Seastedt, T.R. (1979) Avian territoriality: sufficient resources or interference competition. *American Naturalist*, **114**, 308–312.
- Maguire, G.S. (2006) Territory quality, survival and reproductive success in Southern Emu-Wrens *Stipiturus malachurus*. *Journal of Avian Biology*, **37**, 579–593.
- Marshall, M.R. and Cooper, R.J. (2004) Territory size of a migratory songbird in response to caterpillar density and foliage structure. *Ecology*, **85**, 432–445.
- Martin, T.E. and Roper, J.J. (1988) Nest predation and nest-site selection of a western population of Hermit Thrush. *Condor*, **90**, 51–57.
- Mucina, L. and Rutherford, M.C. (eds.) (2006) *The Vegetation of South Africa, Lesotho and Swaziland*. Strelitzia 19, South African National Biodiversity Institute, Pretoria.
- Myers, J.P., Connors, P.G. and Pitelka, F.A. (1979). Territory size in wintering Sanderlings: the effects of prey abundance and intruder density. *Auk*, **96**, 551–561.
- Orians, G.H. and Wittenberger, J.F. (1991) Spatial and temporal scales in habitat selection. *American Naturalist*, **137**, S29–S49.
- Schowalter, T.D. and Crossley Jr, D.A. (1983) Forest canopy arthropods as sodium, potassium, magnesium and calcium pools in forests. *Forest Ecology and Management*, **7**, 143–148.
- Schwabl, H. (1996) Maternal testosterone in the avian egg enhances postnatal growth. *Comparative Biochemistry and Physiology A*, **114**, 271–276.
- Smith, T.M. and Shugart, H.H. (1987) Territory size variation in the ovenbird: the role of habitat structure. *Ecology*, **68**, 695–704.
- Sodhi, N.S. (1993) Proximate determinants of foraging effort in breeding male Merlins. *Wilson Bulletin*, **105**, 68–76.

- Southwood, T.R.E. (1978) *Ecological Methods*, 2nd ed. Chapman and Hall, London.
- Southwood, T.R.E., Moran, V.C. and Kennedy, C.E.J. (1982) The assessment of arboreal insect fauna: comparisons of knockdown sampling and faunal lists. *Ecology and Entomology*, **7**, 331–340.
- Stenger, J. (1958) Food habits and available food of Ovenbirds in relation to territory size. *Auk*, **75**, 125–140.
- Steury, T.D. and Murray, D.L. (2003) Causes and consequences of individual variation in territory size in the American Red Squirrel. *Oikos*, **101**, 147–156.
- Surai, P.F., Noble, R.C. and Speake, B.K. (1996) Tissue-specific differences in antioxidant distribution and susceptibility to lipid peroxidation during development of the chick embryo. *Biochimica et Biophysica Acta*, **1304**, 1–10.
- Székely, T. (1992) Reproduction of Kentish Plover *Charadrius alexandrinus* in grassland and fishponds: the habitat mal-assessment hypothesis. *Aquila*, **99**, 59–68.
- Török, J., Hargitai, R., Hegyi, G., Matus, Z., Michl, G., Péczely, P., Rosivall, B. and Tóth, G. (2007) Carotenoids in the egg yolks of Collared Flycatchers (*Ficedula albicollis*) in relation to parental quality, environmental factors and laying order. *Behavioural Ecology and Sociobiology*, **61**, 541–550.
- Turpie, J.K. (1995) Nonbreeding territoriality: causes and consequences of individual and seasonal variation in Grey Plover *Pluvialis squatarola* behaviour. *Journal of Animal Ecology*, **64**, 429–438.
- van de Pol, M., Bruinzeel, L.W., Heg, D., van der Jeugd, H.P. and Verhulst, S. (2006) A silver spoon for a golden future: long-term effects of natal origin on fitness prospects of Oystercatchers (*Haematopus ostralegus*). *Journal of Animal Ecology*, **75**, 616–626.
- Visser, M.E., Holleman, L.J.M, and Gienapp, P. (2006) Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird. *Oecologia* **147**, 164–172.
- Von Schantz, T., Bensch, S., Grahn, M., Hasselquist, D., Wittzell, H. (1999) Good genes, oxidative stress and condition-dependent sexual signals. *Proceedings of the Royal Society B: Biological Sciences*, **266**, 1–12.
- Wiens, J.A. (1989) Spatial scaling in ecology. *Functional Ecology*, **3**, 385–397.
- Wilkin, T.A., King, L.E. and Sheldon, B.C. (2009) Habitat quality, nestling diet and provisioning behaviour in Great Tits *Parus major*. *Journal of Avian Biology*, **40**, 135–145.
- Zuur, A.F., Leno, E.N. and Elphick, C.S. (2009) A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, **1**, 3–14.

CHAPTER THREE

RELATIONSHIPS BETWEEN BREAST-BAND SIZE, INDIVIDUAL QUALITY AND TERRITORY ATTRIBUTES IN THE BAR-THROATED APALIS

Introduction

Optimal models of territoriality propose that high-quality individuals occupy resource-rich territories, with subdominant individuals being displaced into marginal habitat patches or becoming floaters (Fretwell and Lucas 1970). Correlates of individual quality may include body condition (Lozano 1994, Baydaev and Hill 2000, Whiteman and Parker 2004, Ochi and Takeyama 2009); body size (Lozano 1994); parasite load (Whiteman and Parker 2004); age (Ficken and Ficken 1966, 1967, Hill 1988, Holmes *et al.* 1996); androgen levels (e.g. testosterone concentration - Dixson 1980, Galeotti *et al.* 1997); song amplitude (Dabelsteen 1981, Todt 1981, Hyman 2003, Brumm and Todt 2004, deKort *et al.* 2009); and fighting ability (Møller 1987, Nakagawa *et al.* 2008). Sometimes, dominance is accompanied by recognisable phenotypic traits which signal quality. These may be in the form of ornaments, ranging from elaborate plumes to patches of coloured feathers (Møller 1987, Pryke *et al.* 2001, Andersson *et al.* 2002, Tarof *et al.* 2005, Dunn *et al.* 2008, Nakagawa and Burke 2008). For example, in the House Sparrow *Passer domesticus* and the Common Yellowthroat *Geothlypis trichas*, bib size reflects male fighting ability, and hence dominance (Møller 1987, McGraw *et al.* 2003, Nakagawa *et al.* 2008). Such signalling is considered 'honest' when it influences the behaviour of the receiver and confers benefits on the signaller. Ornaments such as comb size have been shown to be an honest signal of male body condition because their expression is mediated by

individual's health (e.g. in Red Junglefowl *Gallus gallus* - Zuk *et al.* 1990, Chappel *et al.* 1997).

A second ornament in House Sparrows (the extent of a black mask around the eyes of males) and bib area (raggedness) in the Black-capped Chickadee *Poecile atricapillus* both signal individual age (Otter and Ratcliffe 1999, Nakagawa and Burke 2008). A signal of age may have evolved to: (1) deter aggression from younger, subdominant individuals, or (2) enable females to assess the likely resource-holding potential of males (Otter and Ratcliffe 1999).

Cheating, or 'dishonesty' is militated against in a signalling system because the signal itself may be a 'burden' on the bearer (e.g. a long tail or excessive conspicuousness) or is occasionally tested (e.g. through direct confrontation) when cheaters are easily discovered and 'punished' (Zahavi 1975, Smith 1991, Smith and Harper 1995, Zahavi 2007).

This study has demonstrated an inverse relationship between territory size and food density in Bar-throated Apalises (Chapter 2). However, if this relationship conforms to models of optimal territoriality - which predict high-quality individuals to occupy high-quality territories - then this species should show a similar, inverse relationship between territory quality and male quality. Several studies have established a relationship between male quality and ornamentation (e.g. Møller 1987, Otter and Ratcliffe 1999, McGraw *et al.* 2003, Nakagawa and Burke 2008). However, other studies that have failed to demonstrate such a relationship despite using several putative indices of individual quality (e.g. Ferns 1978, Balph *et al.* 1979, Whitfield 1986, Korsten *et al.* 2007).

This study aims to test whether variation in breast-band size among Bar-throated Apalises is linked in any way with territory size/quality and thus address the question

of whether it is indeed an honest signal of male quality. Specifically, the study sought to determine whether breast-band size a) signals individual and/or territory quality; and/or b) is age-linked. If breast-band size is a reliable signal of individual/territory quality then it should reflect a) body condition and b) territory quality.

The age structure of the study population was largely unknown. In light of previous demonstrations that ornamentation and dominance may be age- and/or sex-linked (Watt 1986, Jackson *et al.* 1988, Wilson 1992), it was further predicted that if breast-band size is a true reflection of an individual's age, then changes in its size across years for individuals that have shown territory fidelity between years (i.e. where effect of territory quality on changes in breast-band size can be controlled) should occur independent of territory quality (otherwise breast-band size could be a *consequence* of territory quality – Otter and Ratcliffe 1999). Furthermore, because breast-band size cannot (or does not) increase indefinitely, then individuals with large breast bands should show the least absolute increment in breast-band size across years.

METHODS

Biometrics

Biometric measurements were obtained during the breeding seasons (August – October) of 2007 – 2009. Each trapping session began before sunrise (05h30 – 06h30) and lasted for 3-4 hours to minimise potential effects of variation in body mass with time of day (Korsten *et al.* 2007). For all individuals, body mass, tarsal length, and wing and tail lengths were measured (following protocols of Andersson and Andersson 1994). Body mass was measured to the nearest 0.001 g using a digital

scale (Scout[®] Pro SPU123, Ohaus Corporation USA). Tarsus length (to the nearest 0.01 mm) was recorded using a digital vernier calliper (Mitotuyo) and was measured as the length of the tarsometatarsal bone, taken from the notch of the intertarsal joint (with the foot bent through an angle of 90°) to the point where the foot bends (just anterior to the toes). Wing length (flattened wing chord to the nearest 0.5 mm) was measured from the distal end of the carpus to the tip of the longest primary feather using a stopped wing ruler. Tail length (to the nearest 0.5 mm) was measured from the base (i.e. from the calamus which is where the tail feathers emerges from the skin) to the tip of the longest pair of rectrices.

Tarsal length was used as an index of overall body size (*cf* Freeman and Jackson 1990) and body condition was expressed as the regression residual of body mass on tarsal length (Dale 2000, Török 2007), with positive residuals indicating above-average body condition.

Breast-band measurement

Breast-band sizes of territorial males during the breeding season were obtained from individuals attracted to mist nets using call play-backs. Breast-band size was determined from digital photographs (Otter and Ratcliffe 1999) taken with a Sony DSC H3 camera. Each bird was positioned on its back on a plain surface (stretching the legs and bill through an angle of 45°) alongside a millimetre ruler (Plate 3.1). Several pictures were taken, from which the three 'best shots' were selected. Using the cutout tool in Corel Graphics suite X4 (Corel Corporation USA 2008), the area of the black breast band was obtained from pixel counts calibrated against pixel counts made for a known, fixed area. An individual's breast-band size (mm² – mean of the best three pictures) was calculated as: Breast-band size (mm²) = (Bp x R)/Rp, where,

B_p = number of pixels covered by the breast-band, R = known area in mm^2 , R_p = number of pixels covered by the known area. Based on the technique of Lessells and Boag (1987), badge sizes of the same individuals measured from different photographs taken on the same day showed a repeatability of *ca* 96 % (single-factor ANOVA, $F_{79, 160} = 68.85$, $P < 0.001$).

All trapped and photographed individuals were fitted with a unique combination of one metal and three plastic colour rings. A few previously banded individuals in the study population from an earlier project were also caught. Breast-band size was determined in the same way for these retrapped individuals and could be directly related to age in four individuals, two aged two years and two aged five years. Between August and October 2009, efforts were made to retrap colour-banded individuals whose breast-band sizes had been measured in previous years (2007 and 2008) in order to determine whether breast-band size changed between successive moults (even though the ages of these birds were unknown).



Plate 3.1: A male Bar-throated Apalis photographed for breast-band size measurement.

Statistical analysis

Data were analysed using the statistical package SPSS 17 (SPSS incorporated, USA). All variables were explored for normality and equality of variance using one-sample Kolmogorov-Smirnov tests and Levene statistics. Data for body mass were pooled across all years (2007 – 2009) because there was no effect of year and/or trapping date on body mass for either males (GLM, Year: $F_{2, 45} = 2.289$, $P = 0.11$; trapping date: $F_{1, 45} = 0.196$, $P = 0.660$) or females (Year: $F_{1, 32} = 2.462$, $P = 0.10$; trapping date: $F_{1, 32} = 0.895$, $P = 0.35$). The independent-sample t-test was used to compare average differences in biometrics (breast-band size, body mass, tarsus, wing and tail lengths) between males and females. Pearson's correlation analysis was used to check for relationships between breast-band size, biometrics and body condition of individuals – a Bonferroni correction was not applied in order to avoid increasing the likelihood of type II errors to unacceptable levels (i.e. accepting a null hypothesis instead of rejecting it) and to avoid reducing statistical power. Emphasis in these analyses was thus placed on the biological implications of phenotypic variation, as advocated as appropriate for behavioural studies (Perneger 1998, Nakagawa 2004). A paired-sample t-test was used to compare changes in breast-band sizes of individuals across years. These data contained a mixture of measurements made after one year (10 individuals) and two years (6 individuals). A General Linear Mixed Model (GLMM) was used to determine whether absolute change in bib size (i.e. the difference between previous and current measures of breast-band size) was dependent on an individual's initial breast-band size (i.e. when first trapped) or territory quality (measured as prey density - Chapter 2). Results are presented as: 1) changes in breast-band size after one year ($n = 10$), and 2) changes in breast-band size after one and two

years combined ($n = 16$). Too few measurements were made at a two-year interval for these to be analysed independently.

RESULTS

Biometrics

Males were significantly larger than females in most of the variables measured, including breast-band size (averaging more than twice the size of female breast bands), and tarsus, wing and tail lengths. On average, however, females were significantly heavier than males (Table 3.1).

Table 3.1: Means, standard errors and ranges of the biometrics of male and female Bar-throated Apalises.

Trait	Male	n	Female	n	df	t	P
	Mean \pm S.E.		Mean \pm S.E.				
	(Range)		(Range)				
Breast-band size (mm ²)	148.67 \pm 6.83	49	61.81 \pm 5.17	30	76	10.131	<0.001
	(54.96 – 249.41)		(15.30 – 124.60)				
Mass (g)	11.84 \pm 0.06	48	12.31 \pm 0.16	36	44	2.684	0.010
	(11.07 – 13.00)		(10.69 – 15.00)				
Tarsus (mm)	20.77 \pm 0.07	49	20.33 \pm 0.09	36	83	3.808	<0.001
	(20.00 – 22.38)		(19.16 – 22.10)				
Wing (mm)	51.80 \pm 0.23	49	49.61 \pm 0.30	36	83	5.755	<0.001
	(48.0 – 54.50)		(45.50 – 53.00)				
Tail (mm)	53.68 \pm 0.62	22	50.41 \pm 0.73	12	32	3.244	0.003
	(49.00 – 58.00)		(46.00 – 54.00)				

Breast-band size and body condition

Males with the largest breast bands were significantly heavier and were in better body condition than were males with small breast bands (Fig. 3.1), but there was no relationship between male breast-band size and other phenotypic metrics (Table 3.2). Female breast-band size did increase significantly with female tail length, but otherwise was unrelated to phenotype (Table 3.3)

Table 3.2: Pearson's correlation matrix between breast-band size, body condition and biometrics of male Bar-throated Apalises. r = Pearson's correlation coefficient, n = sample size.

Trait	Breast- band size	Body condition	Mass	Tarsus	Wing	Tail
		r (n)	r (n)	r (n)	r (n)	r (n)
Breast-band size (mm ²)	-	0.37** (48)	0.34* (48)	- 0.02 (48)	0.16 (48)	0.36 (22)
Body condition	-	-	0.96** (48)	0.00 (48)	- 0.11 (48)	- 0.09 (22)
Mass (g)	-	-	-	0.28 (48)	- 0.09 (48)	- 0.13 (22)
Tarsus (mm)	-	-	-	-	0.04 (49)	- 0.22 (22)
Wing (mm)	-	-	-	-	-	0.04 (22)
Tail (mm)	-	-	-	-	-	-

** $P < 0.01$, * $P < 0.05$.

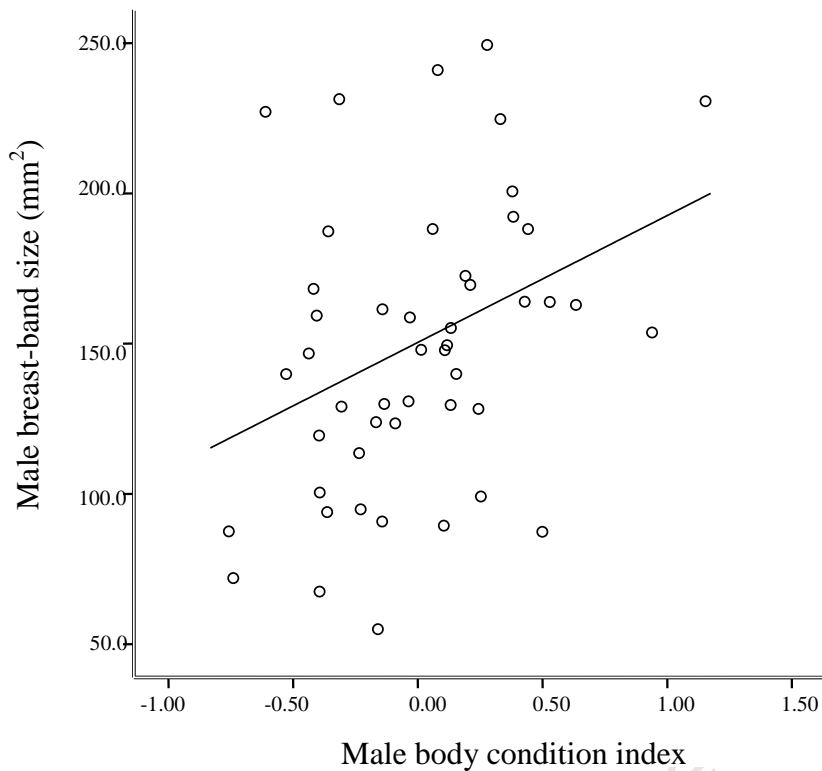


Figure 3.1: Breast-band size of male Bar-throated Apalises as a function of body condition index (residuals of a regression of body mass on tarsus length). $Y = 43.69x + 147.67$; $P < 0.05$.

Table 3.3: Pearson's correlation matrix between breast-band size, body condition and biometrics of female Bar-throated Apalises. r = Pearson's correlation coefficient, n = sample size.

Trait	Breast- band size	Body condition	Mass r (n)	Tarsus r (n)	Wing r (n)	Tail r (n)
Breast-band size (mm ²)	-	0.12 (30)	0.14 (30)	-0.15 (30)	-0.05 (30)	0.71 ^{**} (12)
Body condition	-	-	0.99 ^{**} (36)	0.00 (36)	0.38 [*] (36)	-0.20 (12)
Mass (mm)	-	-	-	-0.14 (36)	0.38 [*] (36)	0.22 (12)
Tarsus (mm)	-	-	-	-	-0.03 (36)	-0.22 (12)
Wing (mm)	-	-	-	-	-	0.01 (12)
Tail (mm)	-	-	-	-	-	-

^{**} $P < 0.01$, ^{*} $P < 0.05$.

Changes in breast-band sizes over time

Breast bands at Year₀₊₁ or Year₀₊₂ were significantly larger than they were in Year₀ (Paired sample t-test, $t = 5.046$, $df = 14$, $P < 0.001$). Absolute change in breast-band size was significantly influenced by an individual's initial (previous) breast-band size: individuals with large breast bands showed the least absolute change in breast-band size regardless or not of whether data were controlled for time since initial measurement, i.e. after one moulting season (GLMM, $B = -0.52$, $F_{1,8} = 5.901$, $P = 0.041$, Fig. 3.2) or after one- and two-year intervals combined (GLMM, $B = -0.39$, $F_{1,15} = 7.250$, $P = 0.017$). There was no effect of territory quality (prey density) on absolute change in breast-band size regardless of whether data were controlled for a single moult (GLMM, $B = 3413.79$, $df = 4$, $F = 0.129$, $P = 0.738$) or not (GLMM, $B = -3944.1$, $df = 10$, $F = 0.861$, $P = 0.375$).

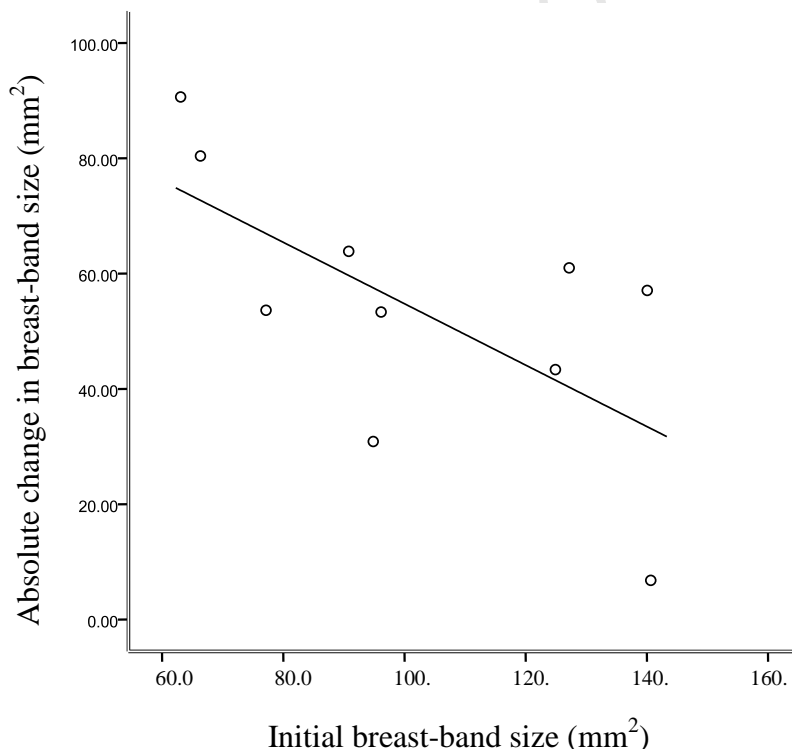


Figure 3.2: Relationship between absolute change in breast-band size and initial breast-band size of male Bar-throated Apalises after one moulting season (i.e. controlled for moult interval; $y = 108.03 - 0.528x$; $P < 0.05$).

As expected (Fig. 3.2), among four known-age individuals, breast bands of older males were larger than those of younger birds. Breast bands of two five-year-old birds measured 131.32 and 232.50 mm², and of two two-year-old birds measured 100.45 and 129.91 mm².

Breast-band size and territory quality

Breast-band size was positively correlated with territory quality: males with large breast bands defended significantly smaller, more food-rich territories (Pearson's correlation, $n = 23$, $r = 0.50$, $P = 0.015$; Fig. 3.34) than did males with small breast bands.

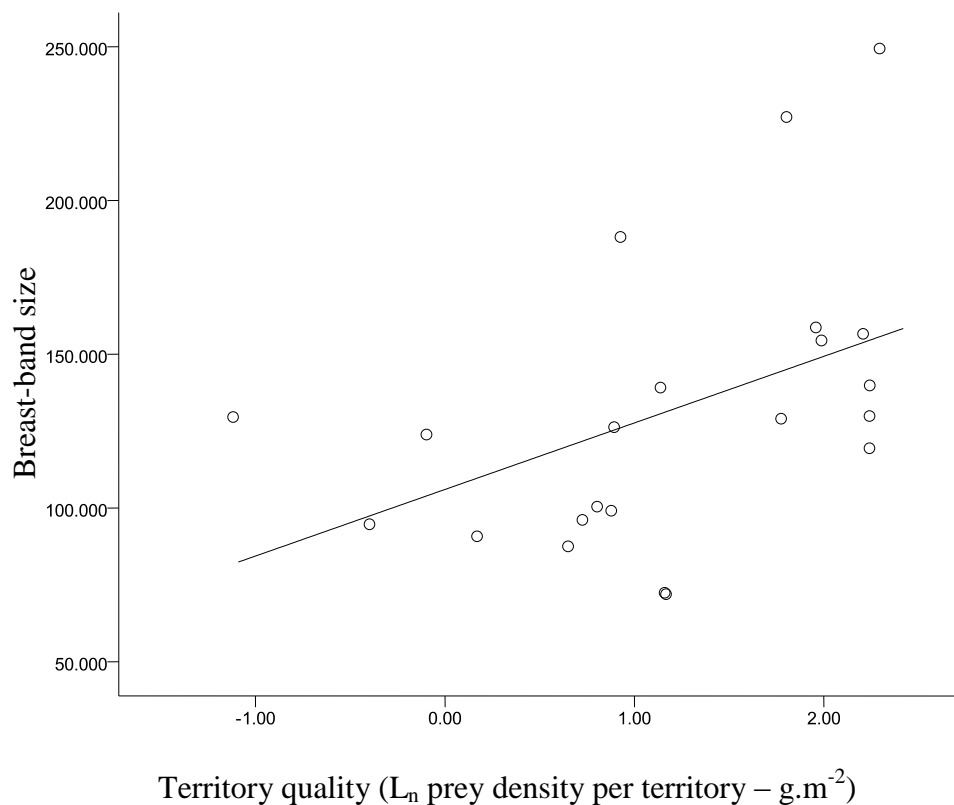


Figure 3.34: Relationship between breast-band size of male Bar-throated Apalises and food density in the territories they defended. Each male was measured once only for both variables. $Y = 1.03E4x + 113.42$, $P < 0.05$.

DISCUSSION

Territory sizes of Bar-throated Apalises are an inverse function of prey density (territory quality). However, if this relationship is to conform to models of optimal territoriality, it needs to be demonstrated that it is indeed high-quality individuals that occupy high-quality (small) territories. This study has shown that male breast-band size is an honest signal of individual quality: males with large breast bands are in better body condition than males with small breast bands and occupy the smallest, most resource-rich territories (Fig. 3.3). This finding bolsters conclusions of other studies (e.g. Hill 1988, Zuk *et al.* 1990, Veiga 1993, Chappel *et al.* 1997). For example, Viega (1993) reported a positive relationship between bib size and the physical condition of House Sparrows. In the same species, males with large bibs also acquired more nest sites than did males with smaller bibs. Co-variation between bib size and body condition has some social consequences, with individuals signalling high rank and/or in better condition dominating individuals with either smaller bibs and/or in poorer body condition (Dawkins and Krebs 1978, Møller 1987, Zuk *et al.* 1990, Senar *et al.* 1993, Chappel *et al.* 1997, McGraw *et al.* 2003). Thus, the honesty of individual quality as signalled by male Bar-throated Apalis breast bands reflects the resource base defended by individual males and can thus be predicted to influence mate choice by females.

Another objective of this study was to investigate whether or not breast-band size changed across years with a view to understanding its potential as an indicator of age, and thus possibly of experience. Previous studies have suggested that the relationship between bib size and dominance may be a result of age-linked plumage change (Fugle 1984, Watt 1986, Jackson *et al.* 1988, Wilson 1992). In Bar-throated Apalises, there

was a significant year (age) effect on breast-band development, independent of territory quality; i.e. the signal strength of all birds increased with age. Furthermore, males with the largest breast bands showed less absolute annual increment in breast-band size than did individuals with small breast bands, mirroring the patterns shown by (migratory) Black-capped Chickadees (Otter and Ratcliffe 1999). However, Otter and Ratcliffe's (*op. cit.*) study could not factor in the potentially confounding effect of the environment experienced by individuals during moult, which took place away from the study site. They speculatively concluded that the progressive increase in bib raggedness with time may be related to environmental conditions (food) on the moulting grounds. By contrast, this study of resident Bar-throated Apalises could account for environmental effects (territory quality) on breast-band growth and showed that breast-band growth rate reflected current breast-band size (itself age dependent) rather than territory quality, suggesting that the relationship between breast-band size and territory quality may be the result of better quality males securing better quality territories.

The ages of individual Bar-throated Apalises in this study were mostly unknown. However, the consistent pattern of increasing breast-band sizes over time, in conjunction with the observed increases in breast-band size of known-age individuals, indicate that breast-band size does increase with age and therefore has the potential to function as a signal of age: nestlings and newly fledged birds lack breast bands (Plate 3.2).



Plate 3.2: [Left to right] Adult male, newly fledged young and adult female Bar-throated Apalises – note the reduced breast band of the female and lack of a breast band in the fledgling.

The rate of increase in breast-band size slows as breast bands become larger, implying that there is an optimal breast-band size above which no additional benefit accrues to individuals. Melanin-based (black and brown) signalling badges are thought to be associated primarily with male-male conflict (Rohwer 1975, 1982, Senar 1999, McGraw *et al.* 2002, Dunn *et al.* 2008). The honesty of male Bar-throated Apalis breast bands in indicating individual quality (body condition – Fig. 3.1) and age (experience) should influence (and correlates with – Fig. 3.3) the success of individuals in securing and defending high-quality territories, attributes that are the outcomes of male-male conflict. Once a high-quality territory is established, the same (honest) signal also carries information about territory quality (Fig. 3.3). From the perspective of females, therefore, a single signal carries information about the bearer's experience, condition and the resource base of the territory. It can thus be predicted that these high-quality males will be favoured by high-quality females, or female partners should at least adjust reproductive input to take advantage of the potentially greater contribution of high-quality males to overall reproductive effort.

Conclusion

Models of optimal territoriality predict that high-quality individuals will occupy high-quality territories. This study supports this prediction: male Bar-throated Apalises with the largest breast bands, which are also the males in best body condition, occupied smaller, more resource-rich territories than did males with smaller breast bands. In addition to signalling individual and territory quality, breast-band size also signals age, although it is not possible to rank the relative honesty of these signals because it was not possible to determine the absolute link between breast-band size and age (merely that breast-band size does increase with age). Nonetheless, these findings are expected to have some implications for male reproductive fitness, because females are expected to choose males or adjust reproductive investment based on the strength of the message carried in the breast-band signal. These aspects are considered in more detail in the subsequent chapters.

REFERENCES

- Andersson, S. and Andersson, M. (1994) Tail ornamentation, size dimorphism and wing length in the genus *Euplectes* (Ploceinae). *Auk*, **111**, 80–86.
- Andersson, S., Pryke, S.R., Örnborg, J., Lawes, M.J. and Andersson, M. (2002) Multiple receivers, multiple ornaments, and a trade-off between agonistic and epigamic signaling in a widowbird. *American Naturalist*, **160**, 683–691.
- Balph, M.H., Balph, D.F. and Romesburg, H.C. (1979) Social status signalling in winter flocking birds: an examination of a current hypothesis. *Auk*, **96**, 78–83.
- Baydaev, A.V. and Hill, G.E. (2000) Evolution of sexual dichromatism: contribution of carotenoid- versus melanin-based coloration. *Biological Journal of the Linnaean Society*, **69**, 153–172.
- Brumm, H. and Todt, D. (2004) Male-male vocal interactions and the adjustment of song amplitude in a territorial bird. *Animal Behavior*, **67**, 281–286.
- Chapell, M.A., Zuk, M., Johnson, T.S. and Kwan T.H. (1997) Mate choice and aerobic capacity in Red Junglefowl. *Behaviour*, **134**, 511–529.

- Dabelsteen, T. (1981) The sound pressure level in the dawn song of the Blackbird (*Turdus merula*) and a method for adjusting the level in experimental song to the level in natural song. *Zeitschrift für Tierpsychologie*, **56**, 137–149.
- Dale, J. (2000) Ornamental plumage does not signal male quality in Red-billed Queleas. *Proceedings of the Royal SocietyB: Biological Sciences*, **267**, 2143–2149.
- Dawkins, R. and Krebs, J.R. (1978) Animal signals: information or manipulation? Pp. 282–315 in: Krebs, J. R. and Davies, N. B. (eds.) *Behavioural Ecology. An Evolutionary Approach*. Blackwell, Oxford.
- de Kort, S.R., Eldermer, E.R.B., Cramer, E.R.A. and Vehrencamp, S.L. (2009) The deterrent effect of bird song in territory defense. *Behavioral Ecology*, **20**, 200–206.
- Dixon, A.F. (1980). Androgens and aggressive behavior in primates: a review. *Aggressive Behaviour*, **6**, 37–67.
- Dunn, P.O., Whittingham, L.A., Freeman-Gallant, C.R. and DeCoste, J. (2008) Geographic variation in the function of ornaments in the Common Yellowthroat *Geothlypis trichas*. *Journal of Avian Biology*, **39**, 66–72.
- Ferns, P. N. (1978) Individual differences in the head and neck plumages of Ruddy Turnstones *Arenaria interpres* during the breeding season. *Auk*, **95**, 753–755.
- Ficken, M.S. and Ficken, R.W. (1966) Notes on mates and habitat selection in the Yellow Warbler. *Wilson Bulletin*, **78**, 232–233.
- Ficken, M.S. and Ficken, R.W. (1967) Age-specific differences in the breeding behaviour of the American Redstart. *Wilson Bulletin*, **79**, 188–199.
- Freeman, S. and Jackson, W.M. (1990) Univariate metrics are not adequate to measure avian body size. *Auk*, **107**, 69–74.
- Fretwell, S.D. and Lucas, H.J. Jr. (1970) On territorial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheoretica*, **19**, 16–36.
- Fugle, G.N., Rothstein, S.I., Osenberg, C.W. and McGinley, M.A. (1984) Signals of status in wintering White-crowned Sparrows, *Zonotrichia leucophrys gambelii*. *Animal Behavior*, **32**, 86–93.
- Galeotti, P., Saino, N., Sacchi, R. and Møller, A.P. (1997) Song correlates with social context, testosterone and body condition in male Barn Swallows. *Animal Behavior*, **53**, 687–700.
- Hill, G.E. (1988) Age, plumage brightness, territory quality, and reproductive success in the Black-headed Grosbeak. *Condor*, **90**, 379–388.

- Holmes, R.T., Marra, P.P. and Sherry, T.W.. (1996) Habitat-specific demography of Black-throated Blue Warblers *Dendroica caerulescens*: implications for population dynamics. *Journal of Animal Ecology*, **65**, 183–195.
- Hyman, J. (2003) Counter singing as a signal of aggression in a territorial songbird. *Animal Behavior*, **65**, 1179–1185.
- Jackson, W.M., Rohwer, S. and Winnegrad, R.L. (1988) Status signalling is absent within age-and-sex classes of Harris' Sparrows. *Auk*, **105**, 424–427.
- Korsten, P., Vedder, O., Szentirmai, I. and Komdeur, J. (2007) Absence of status signalling by structurally based ultraviolet plumage in wintering Blue Tits *Cyanistes caeruleus*. *Behavioral Ecology and Sociobiology*, **61**, 1933–1943.
- Lozano, G.A. (1994) Size, condition and territory ownership in male Tree Swallows *Tachycineta bicolor*. *Canadian Journal of Zoology*, **72**, 330–333.
- McGraw K.J., Mackillop E.A., Dale J. and Hauber M.E. (2002) Different colors reveal different information: how nutritional stress affects the expression of melanin- and structurally based ornamental plumage. *Journal of Experimental Biology*, **205**, 3747–3755.
- McGraw, K.J., BeeBee, M.D., Hill, G.E. and Parker, R.S. (2003) Lutein-based plumage coloration in songbirds is a consequence of selective pigment incorporation into feathers. *Comparative Biochemistry and Physiology B*, **135**, 689–696.
- Møller, A.P. (1987) Variation in badge size in male House Sparrows *Passer domesticus*: evidence for status signalling. *Animal Behavior*, **35**, 1637–1644.
- Nakagawa, S. (2004) A farewell to Bonferroni: the problems of low statistical power and publication bias. *Behavioral Ecology*, **15**, 1044–1045.
- Nakagawa, S. and Burke, T. (2008) The mask of seniority? A neglected age indicator in House Sparrows *Passer domesticus*. *Journal of Avian Biology*, **39**, 222–225.
- Ochi, H. and Takeyama, T. (2009) Increased energy investment in testes following territory acquisition in a maternal mouthbrooding cichlid. *Ichthyology Research*, **56**, 227–231.
- Otter, K. and Ratcliffe, L. (1999) Relationship of bib size to age and sex in the Black-capped Chickadee. *Journal of Field Ornithology*, **70**, 567–577.
- Perneger, T.V. (1998) What's wrong with Bonferroni adjustments. *British Medical Journal*, **316**, 1236.
- Pryke, S.R., Andersson, S. and Lawes, M.J. (2001) Sexual selection of multiple handicaps in the Red-collared Widowbird: female choice of tail length but not carotenoid display. *Evolution*, **55**, 1452–1463.
- Rohwer, S. (1975) The social significance of avian winter plumage variability. *Evolution*, **29**, 593–610.

- Rohwer, S. (1982) The evolution of reliable and unreliable badges of fighting ability. *American Zoologist*, **22**, 531–546.
- Senar, J.C., Camerino, M., Copete, J.L. and Metcalfe, N.B. (1993) Variation in black bib of the Eurasian Siskin *Carduelis spinus* and its role as a reliable badge of dominance. *Auk*, **110**, 924–927.
- Smith, J.M. (1991) Honest signaling: the Philip Sydney game. *Animal Behavior*, **42**, 1034 – 1035.
- Smith, J.M. and Harper, D. (1995) Animal signals: models and terminology. *Journal of Theoretical Biology*, **177**, 305–311.
- Tarof, S., Dunn, P.O. and Whittingham, L.A. (2005) Dual function of a melanin based ornament in the Common Yellowthroat. *Proceedings of the Royal Society B: Biological Sciences*, **272**, 1121–1127.
- Todt, D. (1981) On functions of vocal matching: effect of counter replies on song post choice and singing. *Ethology*, **57**, 73–93.
- Török, J., Hargitai, R., Hegyi, G., Matus, Z., Michl, G., Péczely, P., Rosivall, B. and Tóth, G. (2007) Carotenoids in the egg yolks of Collared Flycatchers *Ficedula albicollis* in relation to parental quality, environmental factors and laying order. *Behavioral Ecology and Sociobiology*, **61**, 541–550.
- Viega, J.P. (1993) Badge size, phenotypic quality, and reproductive success in the House Sparrow: a study of honest advertisement. *Evolution*, **47**, 1161–1170.
- Watt, D.J. (1986) Relationship of plumage variability, size and sex to social dominance in Harris' Sparrows. *Animal Behavior*, **34**, 16–27.
- Whitfield, D.P. (1986) Plumage variability and territoriality in breeding Turnstones: status signalling or individual recognition. *Animal Behavior*, **34**, 1471–1482.
- Whiteman, N.K. and Parker, P.G. (2004) Body condition and parasite load predict territory ownership in the Galápagos Hawk. *Condor*, **106**, 915–921.
- Wilson, J.D. (1992) A re-assessment of the significance of status signaling in populations of wild Great Tits *Parus major*. *Animal Behavior*, **43**, 999–1009.
- Zahavi, A. (1975) Mate selection - a selection for a handicap. *Journal of Theoretical Biology*, **53**, 205–214.
- Zahavi, A. (2007) Sexual selection, signal selection and the handicap principle. Pp.143–159 in *Reproductive Biology and Phylogeny of Birds, Part B*. (ed. B. G. M. Jamieson). Science Publishers, Plymouth.
- Zuk, M., Johnson, K., Thornhill, R. and Ligon, J.D. (1990) Parasites and male ornaments in free-ranging and captive Red Junglefowl. *Behaviour*, **114**, 232–248.

CHAPTER FOUR

CONSEQUENCES OF VARIATION IN TERRITORY AND INDIVIDUAL QUALITY ON REPRODUCTIVE PERFORMANCE AND FITNESS IN THE BAR-THROATED APALIS

Introduction

The capacity of individuals to maximize their fitness could be affected if resources critical for reproduction and survival are spatially restricted due to competitive interactions among individuals, as occurs in populations that defend territories (Fretwell 1970, Sodhi 1993, Canestrari *et al.* 2008). This is because parental reproductive performance is dependent on the environment. For example, the duration of male foraging trips during male-mate incubation feeding in Merlins *Falco columbarius* depends directly on the availability of prey within the foraging range of the male (Sodhi 1993). Such environmental constraints on male performance can have additional negative fitness consequences for males because females could adjust reproductive investment relative to male effort (Wedell and Karlsson 2003, Lyon and Montgomerie 1985). In the Snow Bunting *Plectrophenax nivalis*, the frequency with which males feed females during incubation directly influences female nest attentiveness. Regular feeding reduces the length of the incubation period, reducing attendant risks such as predation (Lyon and Montgomerie 1985). However, when there are no apparent differences in resource availability to individuals, other factors such as male quality (Jawor and Breitwisch 2006), weather (Dunn and Winkler 1999, Hussel 2003, Nooker *et al.* 2005, Whittingham *et al.* 2007) and female body condition (Gorman and Nager 2003, Hargitai *et al.* 2005, Nooker *et al.* 2005) could also influence reproductive performance. For example, under conditions of fairly uniform food availability, parental quality of Eurasian Oystercatchers *Haematopus ostralegus* affects reproductive success. In this case, the inability of poor-quality parents to

transport sufficient food to chicks results in a low fledging success relative to higher quality individuals (Ens *et al.* 1992). Because female fitness increases with male quality, females place importance on the quality of males with which they pair or mate. A consequence of selection for high-quality males could translate into an increased level of reproductive investment by females because females gain direct (e.g. increased future nestling provisioning by males) or indirect (offspring with good genes) fitness benefits from such pairings (the Differential Allocation Hypothesis – Burley 1986, De Lope and Møller 1993, Sodhi 1993, Uller *et al.* 2005, Jawor and Breitwisch 2006). Evidence for an adjustment in female reproductive effort based on male quality has been experimentally demonstrated in the monogamous Gouldian Finch *Erythrura gouldiae*. Here, females experimentally paired with high-quality males increased provisioning effort, and fledged earlier and better quality offspring than did females paired with low-quality males. Males, however, did not adjust reproductive effort (nestling provisioning) in response to female quality (Pryke and Griffith 2010).

In territorial (despotic) systems, for males to appear attractive to females and hence maximise their own reproductive success, they have to establish their status through aggressive encounters with other males in a quest to acquire resources critical for both their own survival and attempting to maximise female reproductive investment (resulting in greater fitness gains for males - Fretwell and Lucas 1970). However, because aggressive encounters are energetically costly and may result in physical injuries (Siitari and Huhta 2002), males of some species advertise their status through threat and display postures (Brown 1964, Dunn *et al.* 2004), including songs, plumage coloration and/or courtship displays (Rohwer 1975, Lyon and Montgomerie 1986, Hasselquist 1988, Searcy 1996, Gerhardt and Huber 2002, Siitari and Huhta

2002, deKort *et al.* 2009). Females are thought to exploit such advertisements by males as proximate cues to assess the quality of individual males and/or their territories. In Northern Cardinals *Cardinalis cardinalis*, for example, the bright red ventral colour of males seemingly signals territory quality and attracts high-quality females (as measured by their early nest initiation), leading to enhanced reproductive success (Wolfenbarger 1999). While this linkage has been demonstrated for carotenoid-based pigments (reds, yellows and oranges), the information signalled by melanin-based pigments (blacks and browns) remains less well understood (McGraw *et al.* 2002). Studies that have linked melanin-based badges to female reproductive behaviour have concentrated on mate choice by females (Møller 1989, Veiga 1993, Cordero *et al.* 1999, Griffith *et al.* 1999), with fewer studies exploring the fitness gains by males in terms of female reproductive investment (Cunningham and Russell 2000, Krüger and Lindström 2001, Jensen *et al.* 2004).

The present study exploited an inverse relationship between territory size and food density in the Bar-throated Apalis *Apalis thoracica* to investigate how or whether this relationship is reflected in the reproductive performance of territory occupants. The study also attempted to relate breast-band size to different aspects of the breeding ecology of the same species based on the premise of breast-band size being an honest signal of individual and territory quality (Chapter 3). Specifically, the study asked the following questions:

1. How does variation in territory quality impact on key male functions such as mate and nestling provisioning rates and the effort required to achieve these?
2. What are the consequences of variation in territory quality for female reproductive investment (i.e. timing of breeding, clutch size and mass, incubation attentiveness and rate of nestling provisioning)?

3. Do females adjust reproductive investment in response to mate quality as signalled by the breast band?

Because male territory size is inversely linked to both male and territory quality

(Chapter 2 and 3), I further predict that:

1. Male foraging efficiency will be proportional to territory quality.
2. Consequences for pairs on low-quality territories will include:
 - a. delayed nest initiation;
 - b. smaller clutches and/or smaller eggs (i.e. reduced female investment);
 - c. reduced male-mate feeding during incubation leading to reduced female nest attentiveness;
 - d. reduced nestling feeding rates; and
 - e. reduced nestling masses and fledged brood sizes (i.e. reduced reproductive performance and thus lowered fitness for both sexes).
3. Males with large breast bands should achieve the highest reproductive performance and enjoy proportionally high fitness benefits.

METHODS

Detailed descriptions of the study site, territory size measurement, food density calculation, and measurements of breast-band size and body condition are provided in Chapters 2 and 3.

Nest location and monitoring protocol

Nests were located using well-established techniques based on parental behaviours, primarily the carrying of nest material (Martin and Guepel 1993). Relative to making direct searches for nests, this approach minimises biases in nest detectability (Martin 1998). Once located, nests were monitored at two-day intervals during the nest-building phase but, when the nest structure was completed, nests were monitored daily to determine clutch initiation date (but for analysis of determinants of initiation date only the initiation dates of the first clutches of each female in each year were used). Daily monitoring of nests continued throughout the egg-laying stage in order to determine clutch size with accuracy. Once clutches were completed, monitoring reverted to two-day intervals.

Newly laid eggs were weighed to an accuracy of 0.001 g using a digital balance (Scout[®] Pro SPU123, Ohaus Corporation USA). Pairs of Bar-throated Apalises re-nest when nests fail due to predation or other factors, such that multiple egg and clutch weights were recorded for several pairs both within and between breeding seasons (August – October, 2005 and 2007 – 2008). Egg data from an earlier study using similar protocols in 2005 (19 clutches) were obtained (C. Eising *in litt.*) to achieve statistically adequate sample sizes. Data were only used for individuals that remained on the same territories since 2005. The effect of year was retained in all models involving this set of data (see statistics section below).

Once hatched, nestlings were weighed (to the nearest 0.001 g) at two-day intervals starting on the day of hatching (day 0) until pin break of the primary feathers (standardised at day 9). Chicks were not handled after this point in order to obviate possible early fledging (Safina and Burger 1983), but nest contents were monitored

daily until fledglings left the nest. Number of fledged young per territory was thus recorded in each study year.

Measurements of parental reproductive effort

Foraging path distance

Individual birds could be distinguished during foraging trips by unique colour-ring combinations (Chapter 3). The nest locations and positions of individual plants from which territory occupants obtained food were recorded onto a GPS (Garmin® Etrex H). Foraging-path distance (to the nearest 1 m) was then calculated from GPS records and an average foraging-path distance was determined for each individual's collective provisioning trips. Foraging-path distances of male Bar-throated Apalises during the incubation (mate-feeding) period were measured during a weekly, one-hour observation period to ascertain territory boundaries (Chapter 2). Foraging-path distances of both males and females when provisioning nestlings were measured within the first three days after eggs hatched.

Male-mate incubation feeding, female nest attentiveness and nestling feeding

Data on the rates at which males fed incubating females, nestling feeding rates, female nest attentiveness and prey size were obtained from video recordings made during the breeding seasons of 2007 and 2008. A nest camera (SW211-SPY, Swann Communication Pty. Ltd., Australia) attached to a video recorder (Archos™ 604 series) was camouflaged in vegetation near the nest and video recordings started at sunrise (05h30 – 07h30). Data were obtained from 35 breeding attempts, 13 of which survived to the point of hatching. Individual video recordings ran for maximum of six hours, but sequences were not analysed beyond 13h00 to minimise time-of-day effects

on foraging activity. In addition, the first and last 15 minutes of data were disregarded because the birds' behaviour may have been influenced by observer presence when positioning and dismantling the cameras. For incubation feeding, video recordings were made within three days of clutch completion and, in order to avoid problems arising from pseudoreplication, no pair was filmed on more than one occasion. During nestling feeding, two video records were obtained if a nest survived long enough for nestlings to reach the age at which pin break of primary feathers occurred (to account for effects of nestling growth on parental provisioning effort). The first video was obtained 24 h after nestlings hatched (day 1) and the second after pin break of the primary feathers, standardized at day 9. The following data were transcribed from video records:

1. Average time spent between provisioning visits (i.e. time elapsed between provisioning visits – min).
2. Average male-mate incubation feeding rate (expressed as number of male-mate feedings per hour of female incubation).
3. Average incubation nest attentiveness per hour (the proportion of time that females spent incubating).
4. Average nestling feeding rate (number of feeds per nest per hour).
5. Prey size: scored on a scale of 1 – 3 (1= prey items < 1/3 of bill length, 2= prey items 1/3 – 2/3 of bill length and 3= prey items > 2/3 of bill length).

Statistical analysis

The following questions were subjected to statistical analysis:

1. How does variation in territory and individual quality influence male incubation and nestling feeding effort? Variables considered in the analyses were foraging path distance (m), feeding rate (visits per hour) and prey size.
2. How do variation in territory quality and male quality (breast-band size) influence female reproductive investment? Variables considered were clutch initiation date, clutch size, mean egg mass, nest attentiveness and, for nestling feeding, foraging path distance (m), feeding rate (visits per hour) and prey size.
3. How do the sexes differ in reproductive investment?
4. How is the reproductive performance of males and females affected by territory size?

All dependent variables were tested for normality and equality of variance using the One-Sample Kolmogorov-Smirnov test and Levene Statistic. After these analyses were performed, graphical exploration was used to assess the fit of the various data to a normal distribution (Zuur *et al.* 2009). The SPSS 17 Statistical package was used for analysis (SPSS Corporation USA).

Analysis of male reproductive effort during incubation and chick feeding

A General Linear Model (GLM) was used to assess the significant predictors of male reproductive effort. The following dependent variables were assessed, both when feeding the incubating female and when provisioning nestlings: foraging path distance; provisioning rate; and prey size. Each dependent factor was pooled across years (2007 and 2008) after an independent t-test showed no significant difference

between years ($P > 0.05$). Year did have a mildly significant effect on the sizes of prey brought to the incubating female ($df = 17$, $t = 2.158$, $P = 0.05$), but small sample sizes made it necessary to combine these data across years. Because of the large number of independent (predictor) variables and confounding effects of multicollinearity (Gerard 2001), a principal components analysis was performed to reduce the independent factors into non-correlating components (Pearson 1901, Jolliffe 2002, Budaev 2010). These non-correlating components were selected based on the rotation technique of Varimax with Kaiser Normalization (Jolliffe 2002, Budaev 2010). Bartlett's sphericity test and the Kaiser-Meyer-Olkin (KMO) test were used to analyse sampling adequacy of the correlation matrix: use of the correlation matrix is appropriate if the hypothesis of all zero correlations is rejected (i.e. if the P -value of Bartlett's sphericity test is < 0.05) and when $KMO > 0.6$ (Budaev 2010). Variables retained for the interpretation of each principal component are those whose loadings are > 0.5 or < -0.5 as is appropriate for small sample size (i.e. where $n < 100$ – Budaev 2010). Factors included in the analysis included prey density per territory ($\text{g}\cdot\text{m}^{-2}$); male tarsus and wing lengths (mm); male breast-band size; and clutch size. Male breast band-size positively correlates with indices of male quality (male body condition and mass – Chapter 3) and thus was used in lieu of these two variables such that the inclusion of many variables does not complicate interpretation of the principal components. Two principal components (PC) were eventually selected which accounted for 72.5% of the variance in the five variables above (Table 4.1a).

Table 4.1: Principal components used as independent factors in the analysis of Bar-throated Apalis male reproductive effort. Variables included in the interpretation of each principal component (i.e. those with loadings > 0.5 or < -0.5) are identified in bold.

Variables	PC1 (Male body size)	PC2 (Clutch size, territory and male quality)
Clutch size	- 0.17	0.81
Breast-band size	0.30	0.71
Average prey biomass density	0.59	0.68
Male tarsus length (mm)	0.88	- 0.13
Male wing length (mm)	0.76	0.42

KMO = 0.681; Bartlett's sphericity test $df = 10$, $\chi^2 = 18.95$, $P = 0.041$.

For the dependent variables of male foraging path distance, male-mate incubation feeding rate and average prey size delivered to the incubating female, a separate GLM analysis was carried out involving PC1 and PC2 as predictors. At the outset of each model, all main effects and all possible interactions between predictors were included. If interacting terms had no significant effect in the model, they were removed and only main effects were considered. The minimum model accounting for most of the variation in any dependent variable was selected based on F -values after serial backward elimination of non-significant predictors with the highest P -values.

Female reproductive effort: incubation attentiveness

Determinants of female nest attentiveness were analysed using General Linear Models. There was no significant effect of year on female incubation attentiveness

(Independent sample t-test, $df = 24$, $t = 0.220$, $P = 0.828$), so data for the two study years were pooled. The model included the following predictors: male-mate incubation feeding rate; average prey size delivered to the incubating female; female body mass and tarsus length; and clutch size. Average male-mate incubation feeding rate per hour of female incubation decreased significantly with time spent between provisioning visits (Pearson's correlation $n = 26$ $r = -0.49$ $P = 0.011$), similarly, male breast-band size positively correlates with female body mass and male-mate feeding rate ($P < 0.05$) hence these variables were never included in the same model. In similar vein, prey density per territory correlated negatively with time spent between male provisioning visits ($n = 22$, $r = -0.45$, $P = 0.035$) and positively with average male-mate incubation feeding rate ($n = 22$, $r = 0.50$, $P = 0.017$) and clutch size ($n = 27$, $r = 0.45$, $P = 0.017$). Prey density was thus excluded from the model. Thus, variables used as predictors here and in other analysis were based on their biological importance. Model selection criteria were the same as those detailed above for male reproductive effort.

Female reproductive effort: clutch initiation date, clutch size and egg mass

Some females laid clutches in both study years and multiple clutches within seasons. To account for such pseudoreplication, a Linear Mixed Model (LMM) was used to assess predictors of female nest initiation dates, clutch sizes and egg masses per clutch. In the analysis of female nest initiation date, only the first nests of the season for each female were included. Female identity was included as a random factor in the model because several females bred in the same territories over more than one year. In addition, the nested effect of clutches within individual females was included as a random effect in analyses involving female clutch size and egg mass. The variables

included as predictors for the dependent variables; clutch initiation date, clutch size and mean clutch mass are summarised in Table 4.2.

Table 4.2: Predictors used in the analysis of female clutch initiation date, clutch size and mean clutch mass in the Bar-throated Apalis.

Clutch initiation date	Clutch size	Mean clutch mass
Year	Year	Year
Female body mass	Female body mass	Female body mass
Female tarsus length	Female tarsus length	Female tarsus length
Male breast-band size	Male breast-band size	Male breast-band size
Clutch size	–	Clutch size
	Clutch initiation date	Clutch initiation date

When analysing mean clutch mass, clutch initiation date and clutch size were controlled for. The effect of year was controlled for in all analysis as a fixed factor. Prey density correlates positively with both male breast-band size and female body mass (Chapters 2 and 3). Similarly, female wing length correlates positively with female body mass (Chapter 3). Thus, neither prey density nor female wing length was included in the models; male tarsus length was also not included because it was considered biologically unimportant. The backward elimination approach was adopted in which the predictors with the largest non-significant P -values (or smallest F -values) were eliminated sequentially. Model performances were compared based on their Akaike's Information Criteria (AICs); the model with the smallest AIC was selected as the best-fit model explaining variation in the dependent variable.

Reproductive effort by both parents: nestling feeding effort

General linear mixed models were used to assess the effects of sex, nestling stage (at 1 and 9 days), food density and body size (male and female tarsus length) on three dependent variables - foraging path distance, nestling feeding rate per hour and prey size delivered to nestlings. Each dependent variable was assessed separately using the same predictors. Nest identity was used as a random factor in the analysis. The effect of nestling stage was not controlled for in the analysis of distances travelled to obtain food for nestlings. Also, due to small sample sizes, the possible effect of brood-size variation could not be controlled for in all models. All possible interactions between biologically meaningful predictors were also assessed. The backward elimination approach based on *F*-values (as detailed previously) was used.

Nestling mass

A General Linear Mixed Model was used to analyse nestling mass because of the nested effect of multiple nestling masses within pairs. Average nestling mass (calculated from multiple measures of each nestling from day 1 to day 9) was used as the dependent variable. Nestling mass was pooled across two years (2007 – 2008) because there were no significant differences in average nestling growth rates between the two years (Independent t-test, $df = 114$, $t = -1.821$, $P = 0.071$). The effect of nestlings nested within pairs was accounted for as a random factor. Predictors in the model included:

- i. Male body condition;
- ii. Female body condition;

iii. Average parental feeding effort per hour =

$$\frac{AvMF_1 + AvMF_2}{2} + \frac{AvFF_1 + AvFF_2}{2}$$

Where AvMF= average male feeding rate per hour and AvFF= average female feeding rate per hour. Subscript 1= at day 1; subscript 2= at day 9;

iv. Average time spent between provisioning trips by both parents =

$$\frac{AvMT_1 + AvMT_2}{2} + \frac{AvFT_1 + AvFT_2}{2}$$

Where AvMT = average time spent between male provisioning visits (min) and AvFT = average time spent between female provisioning visits (min). Subscripts 1 = at day 1; Subscript 2 = at day 9;

v. Average prey size delivered to nestlings (by males and females separately).

Predictors iii and iv were calculated for both males and females combined because there was a positive correlation between average male and female provisioning rates (Pearson's correlation, $n = 7$ pairs, $r = 0.721$, $P < 0.001$). There was also a positive correlation between time spent between provisioning visits of both male and female parents ($n = 7$ pairs, $r = 0.349$, $P < 0.001$). Male and female body condition were not included in the model simultaneously because these variables were also positively correlated ($r = 0.335$, $P = 0.001$). Due to the small sample size ($n = 7$ pairs), the effect of brood size was not controlled for in the analysis. The best-fit model was selected as detailed under analysis of female clutch initiation date, clutch size and egg mass above.

Annual productivity across territories

Determinants of annual fledgling production per territory were modelled using a Multiple Binomial Logistic Regression. Productivity per year was used as the dependent variable (productivity was classified binomially according to the success (1) or failure (0) in fledging at least one youngster in a given year). Year (2007 and 2008) and territory sizes for each territory were used as predictors in the model (random and covariate variables respectively). The effect of predictors were tested both collectively (i.e. retaining the effects of the two predictors in the model) and separately (i.e. treating each predictor one at a time) and the best fit-model was selected based on Nagelkerke's r^2 (an modified version of the Cox and Snell's r^2 that adjusts the scale of the statistic to cover the full range from 0 – 1, Nagelkerke 1991).

RESULTS

Male incubation feeding

Foraging path distance

Average distances travelled by individual males to obtain food for incubating females ranged from 10.50 – 61.67 m, averaging 26.06 ± 2.38 S.E. m ($n = 30$ males). The principal component related to clutch size, male and territory quality (PC2) was the most significant predictor of these travel distances, accounting for 29.8% of the variation between males (GLM, $B = -4.229$, $F_{1, 13} = 6.943$, $P = 0.021$; Fig. 4.1).

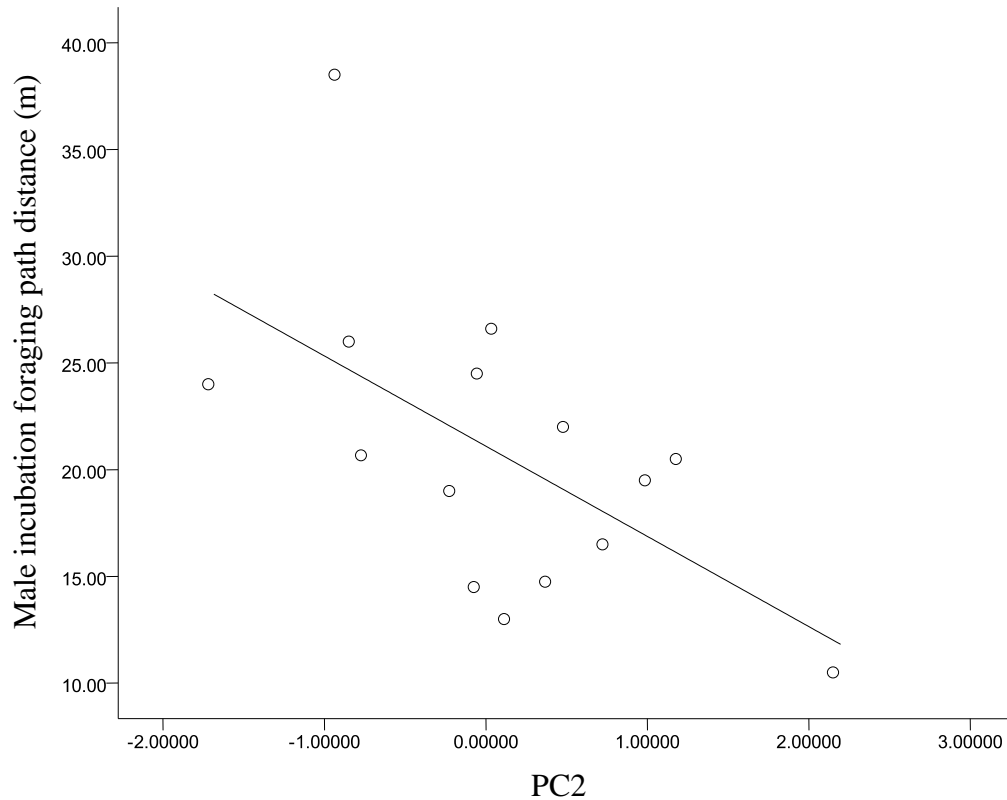


Figure 4.1: Relationship ($y = 21.091 - 4.229x$) between foraging path distances travelled by male Bar-throated Apalises during incubation feeding of females and PC2 (clutch size, male and territory quality): increasing values of PC2 indicate increasing clutch size, and male and territory quality.

Male-mate incubation feeding rate

The rate at which males provisioned incubating females ranged from 0.20 – 3.20 deliveries per hour (1.14 ± 0.16 S.E., $n = 23$). Most (34.3%) of the variation in this provisioning rate was also accounted for by the significant effect of PC2 (clutch size, and male and territory quality – Table 4.3, Fig. 4.2).

Table 4.3: The minimum model explaining variations in the rate at which male Bar-throated Apalises provisioned incubating females. Dependent variable: male-mate incubation feeding rate.

Predictors	<i>df</i>	<i>B</i>	<i>F</i>	<i>P</i>
Intercept	1, 14	0.726	17.351	0.001
PC2	1, 14	0.486	0 7.295	0.017

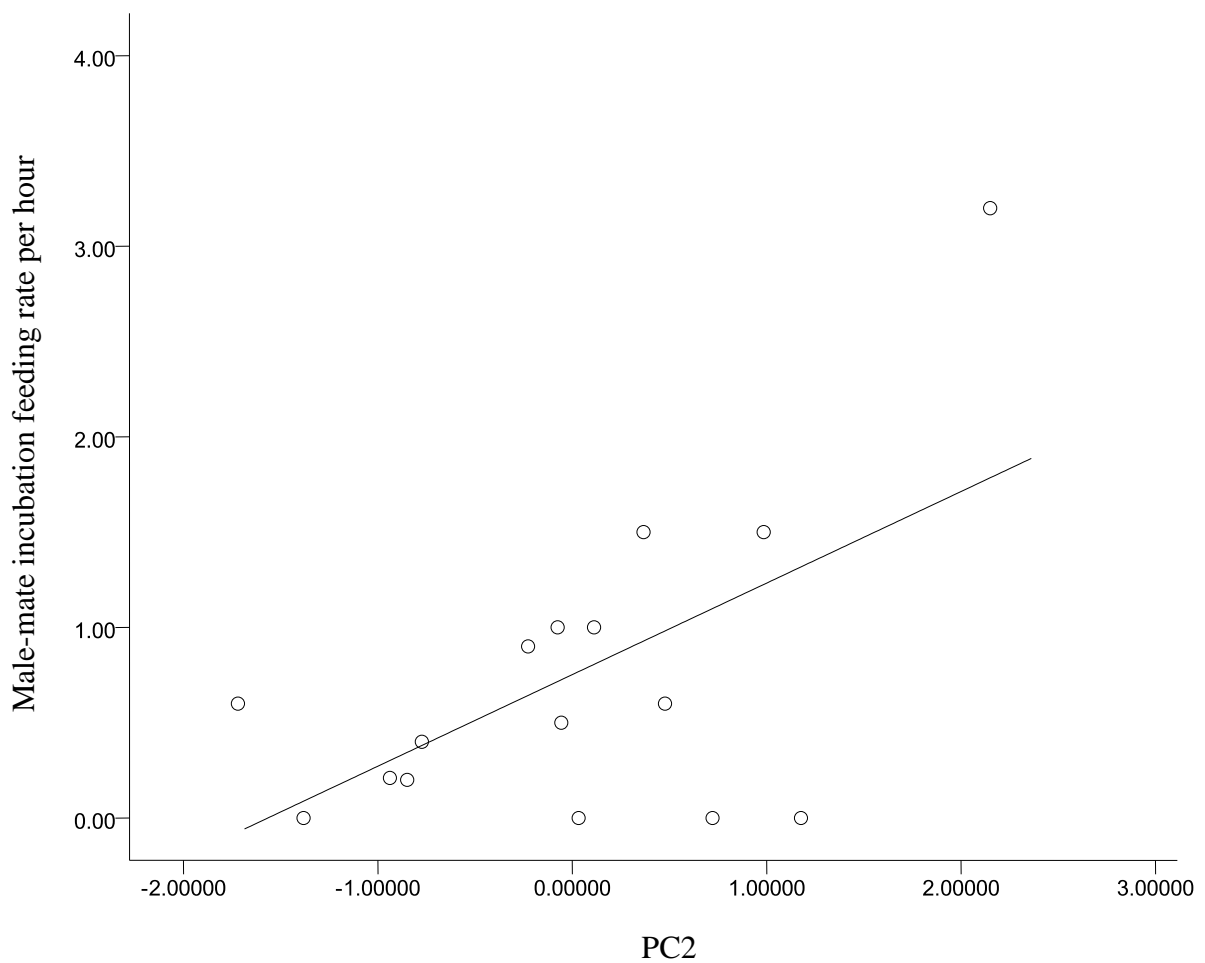


Figure 4.2: Relationship ($y = 0.486x - 0.726$; $P < 0.05$) between male-mate incubation feeding rate in Bar-throated Apalises and PC2: increasing values of PC2 indicate increasing clutch size, and male and territory quality.

Prey size brought to females by males during incubation

Prey sizes brought to females by males during incubation provisioning were not significantly explained by any of the predictors used in the model, viz PC1 ($B = 0.035$, $F_{1, 8} = 0.138$, $P = 0.720$) or PC2 ($B = -0.006$, $F_{1, 8} = 0.003$, $P = 0.958$).

Female reproductive investment

Clutch initiation date

The earliest and latest dates of clutch initiation by individual females were 28 July (2005) and 23 October (2008). Female body mass was the only significant predictor in the best-fit model explaining this variation (Table 4.4).

Table 4.4: LMM exploring determinants of female clutch initiation date in Bar-throated Apalises. Dependent variable: female clutch initiation date. AIC = 176.493.

Predictors	<i>df</i>	<i>B</i>	<i>F</i>	<i>P</i>
Intercept	1, 22	12.405	0.051	0.824
Female body mass	1, 21	-20.971	21.818	< 0.001

Clutch size, mean clutch mass and brood sizes

Females laid 2-4 eggs per clutch ($n = 66$ clutches, 12 females). Female body mass was the only significant predictor of clutch size (LMM, $B = 0.204$, $F_{1, 21} = 9.095$, $P = 0.007$, AIC = 21.069). None of the other predictors tested had a significant effect on female clutch size, viz female tarsus length ($P = 0.424$); clutch initiation date ($P = 0.386$); year ($P = 0.308$); or male breast-band size ($P = 0.141$).

Mean clutch mass ranged from 1.336 – 1.792 g (1.552 ± 0.012 S.E. g, $n = 66$ clutches, 12 females). The best-fit model explaining variation in female clutch mass retained

the significant effects of male breast-band size, female body mass and clutch initiation date. Mean clutch mass increased significantly with all the above predictors (Table 4.5). Year was retained in the model as a marginally non-significant predictor of mean clutch mass.

Table 4.5: LMM exploring determinants of mean clutch mass in Bar-throated Apalises. Dependent variable: mean female egg mass per clutch. AIC = 50.781.

Predictors	<i>df</i>	<i>B</i>	<i>F</i>	<i>P</i>
Intercept	1, 9	- 1.069	3.480	0.094
Year	1, 8	- 0.069	3.667	0.089
Male breast-band size (mm ²)	1, 9	0.001	7.515	0.022
Female body mass	1, 8	0.090	7.397	0.024
Clutch initiation date	1, 10	- 0.005	15.164	0.003

Brood size ranged from 2-4 nestlings ($n = 13$ pairs), but because of the small sample size resulting from high predation rates, predictors of brood-size variation could not be tested.

Female nest attentiveness during incubation

Average female nest attentiveness ranged from 12.30 – 45.20 min.h⁻¹ (Mean 25.74 ± 1.62 S.E. min; $n = 26$ females). The minimum model that best accounted for this variation (27.1%) included only a significant effect of male provisioning rate: female nest attentiveness increased with male provisioning rate ($B= 5.003$, $F_{1, 17} = 7.685$, $P= 0.013$, Fig. 4.3).

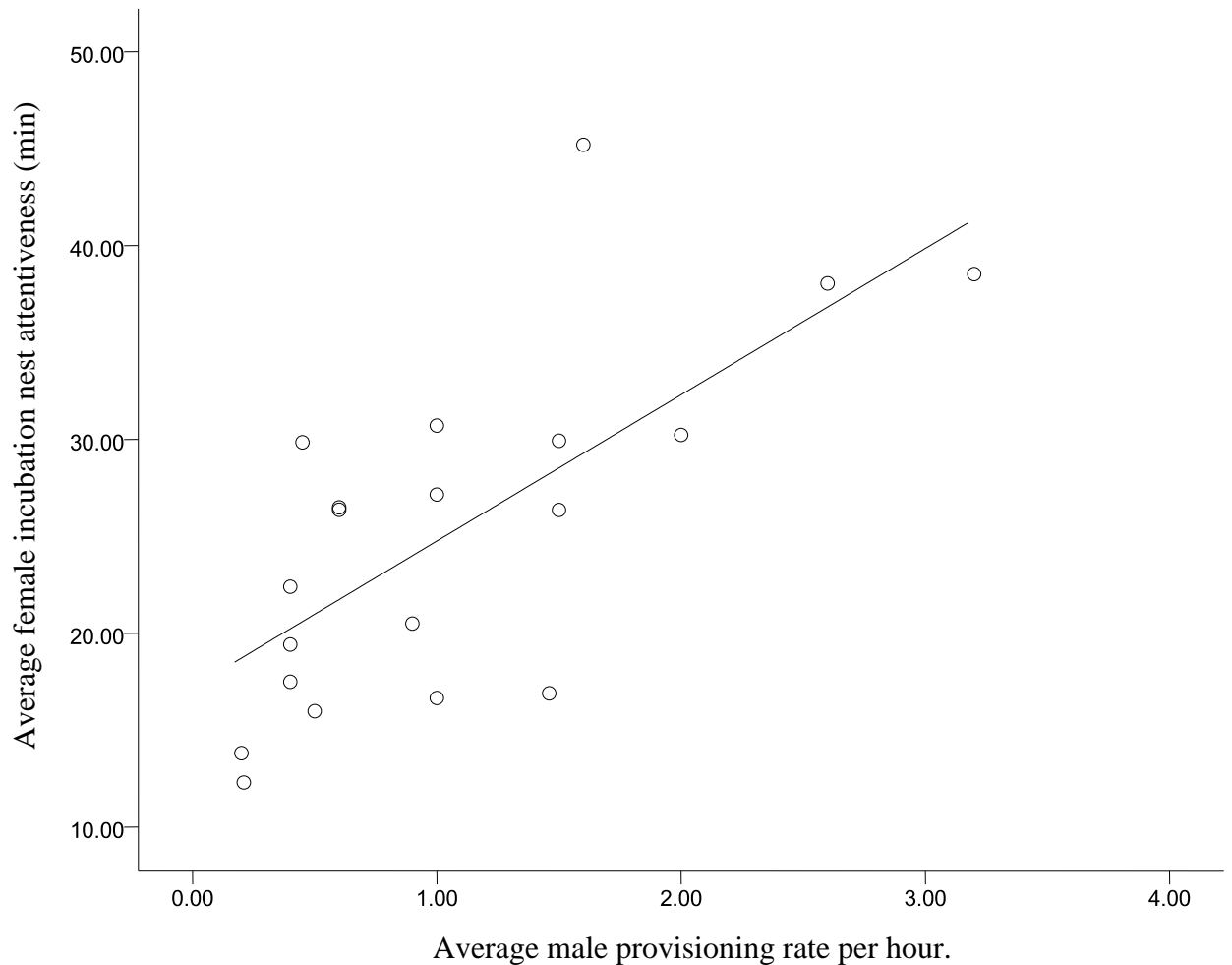


Figure 4.3: Relationship ($Y = 5.003x + 22.016$) between female incubation nest attentiveness and average provisioning rate by male Bar-throated Apalises.

Nestling feeding

Foraging path distances

The distances that individuals travelled to obtain food for nestlings differed significantly between males and females; males travelled shorter distances (mean foraging path distance $31.53 \text{ m} \pm 4.51 \text{ S.E.}$) than females ($34.58 \text{ m} \pm 5.09$).

Additionally, individuals in high-quality territories travelled significantly shorter distances to obtain food for nestlings compared to those in poorer territories (Table 4.6). This was irrespective of sex (sex by prey density interaction; $P > 0.05$) or individual body size (tarsus length and all its interactions; $P > 0.05$).

Table 4.6: Effects of sex and prey density on distances travelled to obtain food for nestlings by parent Bar-throated Apalises. Dependent variable: foraging path distance. AIC = 6.756 (LMM).

Model	<i>B</i>	<i>df</i>	<i>F</i>	<i>P</i>
Intercept	1.247	1, 20	281.738	< 0.001
Sex	0.319	1, 20	10.220	0.005
Prey density per territory	-0.045	1, 20	7.918	0.011

Feeding rates

There was a significant difference between the sexes in nestling feeding rates; male feeding rate was significantly twice (6.150 ± 0.498 S.E. feeds per hour) that of females (3.137 ± 0.513 feeds per hour). Older nestlings were provisioned more often than younger nestlings by both parents (6.586 ± 0.760 vs 2.607 ± 0.493 feeds per hour; Table 4.7).

Territory quality was the only significant predictor of the rate at which nestlings were provisioned (Table 4.7): nestling feeding rate increased with increasing territory quality ($B = 0.236$) for both sexes (sex by prey density interaction; $P > 0.05$) irrespective of variation in individual body size (tarsus length and all its interactions; $P > 0.05$).

Females did not adjust provisioning rate relative to male nestling feeding either when provisioning either 1-day old nestlings (Pearson correlation: $n = 13$ pairs, $r = 0.298$, $P = 0.473$) or 9-day old nestlings ($n = 13$ pairs, $r = 0.209$, $P = 0.653$).

Table 4.7: Effects of sex, nestling stage and prey density on nestling provisioning rate in the Bar-throated Apalis. Dependent variable: nestling provisioning rate. AIC = 170.051 (LMM).

Model	df	<i>F</i>	<i>P</i>
Intercept	1, 37	39.758	< 0.001
Sex	1, 37	19.984	< 0.001
Nestling stage (day 1 and 9)	1, 37	34.750	< 0.001
Prey density	1, 37	4.968	0.032

Prey size delivered to nestlings

The sizes of prey delivered to nestlings by their parents differed significantly between males and females: males provisioned younger nestlings with larger prey (mean prey size as a proportion of beak length 1.755 ± 0.080 S.E.) than did females (1.436 ± 0.080). Older nestlings were provisioned with larger prey by both sexes (males 2.087 ± 0.084 ; females 2.038 ± 0.089 ; Table 4.8). However, none of the independent variables investigated (sex, tarsus length and prey density) significantly predicted the sizes of prey delivered to nestlings by both males and females either as main effects or as interactions. Females also did not adjust the sizes of prey brought to nestlings relative to sizes of prey delivered by males either when feeding young (Spearman's rho correlation: $n = 13$ pairs, $r = 0.167$, $P = 0.693$) or older nestlings ($n = 13$ pairs, $r = 0.198$, $P = 0.670$).

Table 4.8: Effect of sex and nestling stage on prey sizes delivered to nestlings. Dependent variable: prey size. AIC = 10.984 (LMM).

Model	<i>df</i>	<i>F</i>	<i>P</i>
Intercept	1, 37	2154.169	< 0.001
Sex*nestling stage (day 1 and 9)	3, 37	14.824	< 0.001

Nestling mass

The best-fit model explaining variation in nestling growth rates included the significant effect of hatching date and average parental provisioning rate per hour (Table 4.9).

Table 4.9: LMM analysis of predictors of nestling mass in Bar-throated Apalises. Dependent variable: nestling mass. AIC=460.759.

Predictors	<i>df</i>	<i>B</i>	<i>F</i>	<i>P</i>
Intercept	1, 98	- 13.668	4.138	0.045
Nestling hatch date	1, 98	0.055	5.979	0.016
Average parental feeding rate per hour	1, 98	43.725	12.730	0.001

Annual production of young across territories

The best-fit model explaining variation in breeding performance combined effects of year and territory size ($r^2 = 0.092$). However, neither of these two variables significantly predicted annual productivity across territories (Year: $B = - 1.255$, $df = 1$, $\chi^2 = 2.405$, $P = 0.121$, Territory size: $B = 9.0E-5$, $df = 1$, $\chi^2 = 0.812$, $P = 0.367$). On average, however, more pairs fledged young in 2007 than in 2008 and more offspring were fledged from small territories than from large ones. Indeed, no territory >7500 m² produced a single fledgling in either year (Figs. 4.4a, b).

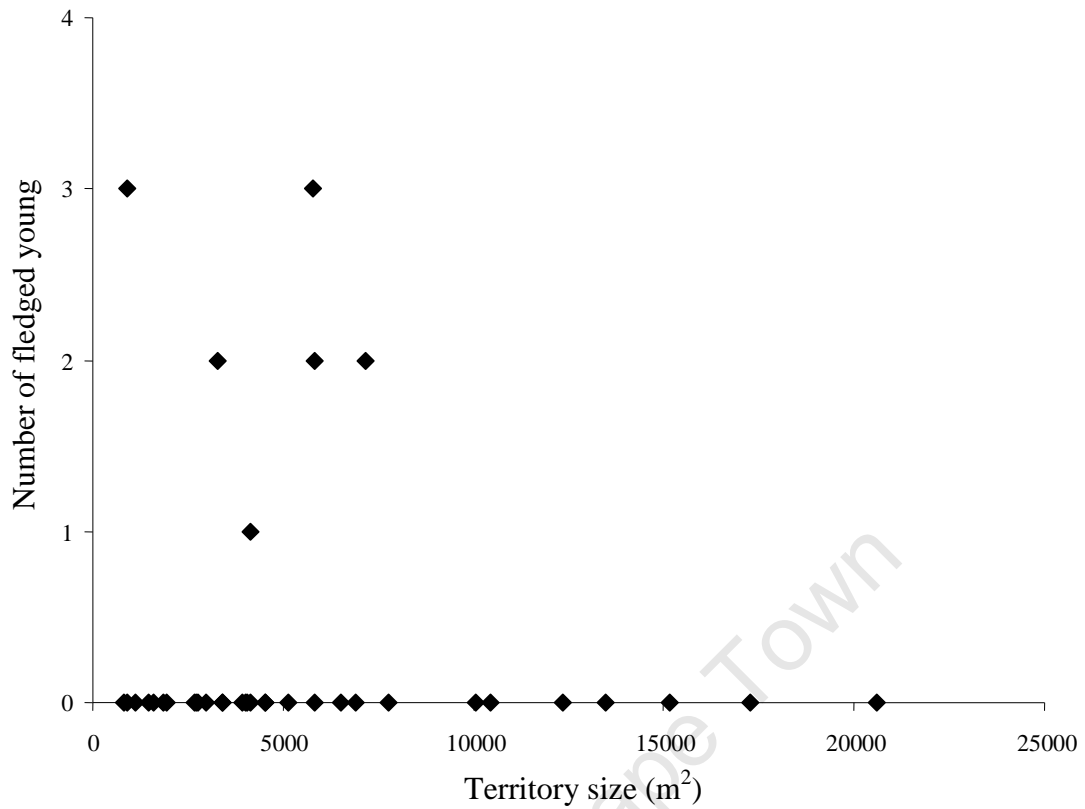


Figure 4.4a: Relationship between fledgling production and territory size in the Bar-throated Apalis during the breeding season of 2007 ($n = 37$ territories)

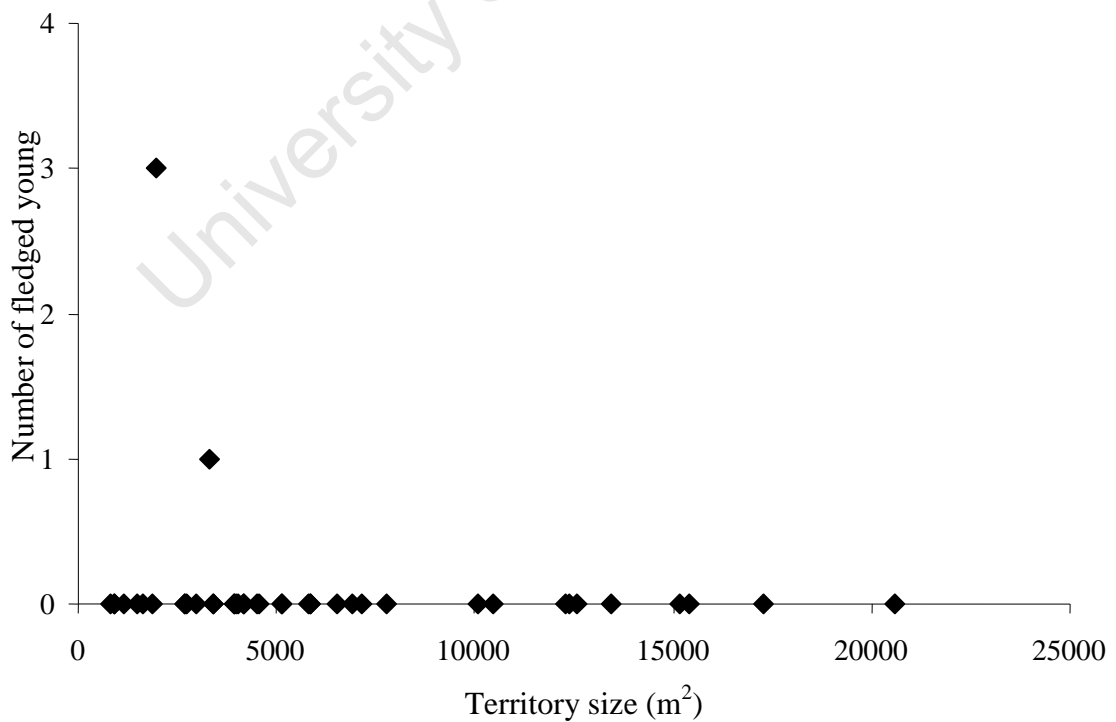


Figure 4.4b: Relationship between number of fledged young per territory and territory size during the breeding season of 2008 ($n = 42$ territories)

DISCUSSION

Male reproductive performance

Male reproductive effort is expected to be constrained by both territory and individual quality (Lyon and Montgomerie 1985, Sodhi 1993, Nooker *et al.* 2005). In this study, the index (principal component) related to territory and male quality was the only significant predictor of the distances males travelled to obtain food for incubating females and subsequently for nestlings. In both situations, males in high-quality territories travelled less far than their counterparts in poorer territories.

Unsurprisingly, territory quality therefore influenced male provisioning rate during incubation and nestling feeding, with males in high-quality territories making more frequent provisioning visits to the nest than males in poorer territories. These relationships between territory quality and indices of male reproductive performance are presumably related to variation in prey density (Chapter 2). The same effect was demonstrated experimentally in a study of Whinchats *Saxicola rubetra*. When foraging patches were artificially enriched with insect prey (mealworms), breeding birds travelled less far from nests to acquire food (Andersson 1981). Likewise, the duration of male foraging trips during incubation feeding by Merlins *F. columbarius* depends on prey abundance: males encountering low prey abundance in their foraging ranges spend more time foraging than do birds in areas with richer food resources (Sodhi 1993). This relationship is mediated by prey encounter rates. For example, in both Great *Parus major* and Blue Tits *P. caeruleus*, search time per prey item increases exponentially with decreasing prey (caterpillar) biomass density (Naef-Daenzer and Keller 1999).

In Bar-throated Apalises, there is an inverse relationship between prey density and territory size (Chapter 2), supporting the hypothesis that prey availability determines the distances that males travel (and hence the time that they spend travelling) to provision their mates and nestlings. However, aside from territory quality, individual quality also seems to play a role in male reproductive effort in this species. Male quality, as signalled by breast-band size, was closely related to the principal component that predicted the rate at which males provisioned incubating females. It has been proposed previously that elements of plumage coloration serve as honest signals of male provisioning ability (Hill 1991). For example, male Eastern Bluebirds *Sialia sialis* with large chestnut breast patches provision nestlings more often than do males with smaller breast patches (Siefferman and Hill 2003). Brighter UV/blue coloration in the same species also signals male incubation-feeding potential, with brighter males provisioning incubating females more often than drabber males (Siefferman and Hill 2005). Similarly, the intensity of blue colour in male Blue Grosbeaks *Guiraca caerulea* signals both male body condition and the contribution made to feeding nestlings (Keyser and Hill 2000). The strong association between male breast-band size and provisioning effort in Bar-throated Apalises may be linked with male experience (age) and/or body condition, both of which are signalled by the breast-band (Chapter 3). Such attributes have been closely tied to male ornamentation and/or breeding performance in several species (Newton and Marquiss 1982, Perrins and McCleery 1985, Myrberget 1986, Wilson 1992, Otter and Ratcliffe 1999, Keyser and Hill 2000, Nakagawa and Burke 2008). The provisioning of large prey to younger apalis nestlings by males as compared to females may be suboptimal for nestlings and possibly reflect the inexperience of males in nestling care. This effect has been shown in Common Terns *Sterna hirundo*, with males with breeding experience (≥ 2 years)

delivering smaller and more easily manageable prey to nestlings than those brought by first-time breeders (Limmer and Becker 2009). However, this might also be an optimal foraging strategy to maximise the value of individual prey items in order to counter the energetic costs of increased travelling distances (Houston 1987, McNamara and Houston 2008). In this study, males in food-poor territories travelled further to obtain food for their young.

Female reproductive performance

Incubation nest attentiveness

Early studies suggested that mate feeding may function to strengthen the pair bond (Lack 1940, Kluyver 1950, Andrew 1961), but subsequent research indicates that its functions are probably considerably more complex and far-reaching. Female reproductive effort is suggested to be proximately influenced by male quality, with females investing more when paired with high-quality mates (Burley 1986, Pryke and Griffith 2010). In species that exhibit male-mate incubation feeding, it has been proposed that female nest attentiveness is regulated by male provisioning effort (Royama 1966, Lyon and Montgomerie 1985, Nilsson and Smith 1988). For example, there is a positive correlation between male incubation feeding frequency and female nest attentiveness in Meadow Pipits *Anthus pratensis* (Hałupka 1994). Male provisioning is perceived (logically) to contribute significantly to the female's energy budget (the Female Nutrition Hypothesis – Royama 1966), a saving which females in turn channel into improving their body condition (Lyon and Montgomerie 1985, Slagsvold 1986, Moore *et al.* 2000). The results of this study concur with previous models (Nilsson and Smith 1988, Hałupka 1994): as male provisioning frequency increases (in tandem with increasing territory quality), so too does female nest

attentiveness. This relationship has consequences for offspring fitness because increased nest attendance by females can a) reduce risk of lethal egg chilling, and b) decrease the length of incubation period (Lyon and Montgomerie 1985, Nilsson and Smith 1988), which may itself confer benefits in terms of reduced risk of nest predation. It has been suggested that mate-feeding performance may be used by females as a proximate cue to male quality thereby helping a female to adjust future reproductive investment to reflect her mate's input to the joint reproductive effort (Nisbet 1973, 1977, Donazar *et al.* 1992, Green and Krebs 1995, Jawor and Breitwisch 2006).

Clutch initiation date

The significant determinant of first clutch initiation dates of female Bar-throated Apalises was female body mass. This finding accords with other studies that have found early breeding to be strongly associated with female quality (e.g. Wolfenbarger 1999). Among apalises, female body mass correlates positively with prey density on the territory (Pearson correlation, $n = 19$ females, $r = 0.512$, $P = 0.025$), with birds in good condition being paired with high-quality mates (as signalled by breast-band size) occupying small, resource-rich territories (Chapter 2). Early clutch initiation by such females could be a response to mate and/or territory quality.

Studies that have shaped our understanding of male ornamentation in socially monogamous species have shown that highly ornamented males attract early breeding females (Møller 1988, 1990, Hill 1990, Norris 1990, Wolfenbarger 1999). This relationship has potential fitness implications, not least because early breeding in several bird species has been linked to high reproductive success (Hill 1990, Wolfenbarger 1999). This may also be the case in this study because prey density

decreased as the breeding season progressed (Chapter 2). Although not significant (possibly because of sample sizes), it also appears that both males and females gain higher reproductive fitness on high-quality territories, fledging more young per annum than their counterparts on small, food-poor territories. Indeed, over the two seasons when productivity was documented, not one pair on a territory $> 7500 \text{ m}^2$ successfully reared a chick.

Mean clutch mass

Clutch initiation date, male breast-band size and female body condition were collectively the major determinants of variation in egg masses of Bar-throated Apalises. Mean clutch mass was positively related to male ornamentation and female body condition, and decreased as the season progressed (and as food became progressively more scarce – Chapter 2). The links between clutch initiation date and female body condition support previous theories that female investment in eggs is limited by a trade-off between the physiological condition of egg-laying females and the added nutritional costs of egg-laying (Jarvinen and Ylimaunu 1986, Meathrel and Ryder 1987, Viñuela 1997). In this study, female body condition was inversely correlated with territory size (Pearson's correlation, $n = 25$, $r = -0.44$, $P = 0.027$), with females in small, food-rich territories laying the heaviest eggs. This supports the contention that females in high-quality territories have less precarious energy budgets than females in larger, food-poor territories.

Heavier eggs produce structurally larger chicks with larger fat reserves that could confer survival advantages during periods of resource scarcity (Bolton *et al.* 1992, 1993, Moore *et al.* 2000). On the other hand, the positive correlation between egg mass and male breast-band size could be due to the strong association between male

breast-band size and territory quality (prey density). However, females could also adjust reproductive investment relative to the quality of their partner (the Differential Allocation Hypothesis – Burley 1986, Uller *et al.* 2005, Pryke and Griffith 2010). Experimentally manipulated male ornaments (tail length) in monogamous Barn Swallows *Hirundo rustica* resulted in females adjusting their reproductive effort (nestling feeding rate) both within breeding attempts and in the number of clutches produced per season: this adjustment was based solely on perceived male quality as signalled by (manipulated) tail length (De Lope and Møller 1993). A similar effect, although it could not be tested experimentally because of sample-size constraints, may be operating among Bar-throated Apalises.

Female nestling feeding effort

Overall, females put less effort into provisioning chicks than did males. Whether this reflects female inexperience or an optimal foraging response to increased male effort cannot as yet be resolved, although within pairs there was no evidence for compensatory effort by females in response to the male's contribution to chick-rearing.

Nestling mass

The significant effects of hatching date and combined parental provisioning rate provided the best explanation for variation in nestling growth, with nestling mass being positively correlated with these two predictors. The seemingly contradictory positive relationship between nestling mass and hatching date may be related to a combination of parental and territory quality. Closer examination of the data showed that nestlings that were monitored later in the season were mostly hatched on high-

quality territories where parental provisioning rates are high. By comparison, late in the season very few pairs on poor-quality territories reached the hatching stage. Similar relationships between nestling mass and combined parental provisioning effort have been reported elsewhere (Naef-Daenzer and Keller 1999, Dawson and Bidwell 2005). For example, both the growth rates and fledging weights of nestling Great and Blue Tits correlate positively with the rate of food delivery (Naef-Daenzer and Keller 1999). This pattern can be confidently predicted for altricial birds, such as apalises, because nestlings are wholly reliant on their parents to provide food (Starck and Ricklefs 1998), with provisioning rates varying with individual and territory quality.

Annual breeding success across territories

The number of young fledged per territory was low (an average of 0.20 chicks fledged per territory per year), given the number of nests monitored during the study (Fig. 4.4a, b). This low productivity is comparable to other passerines at the same site (only 20 of 98 Karoo Prinia *Prinia maculosa* nests fledged young - Nalwanga *et al.* 2004a). Elsewhere, Woodchat Shrikes *Lanius senator* in Western Bulgaria fledged an average of 0.246 young per pair per year (Nikolov 2005), and Three-striped Warblers *Basileuterus tristriatus* in northern Venezuela which fledged only 0.22 young per pair per year (Cox and Martin 2009). The low fledging rate in the Bar-throated Apalis is a result of high nest predation rates at the study site: daily predation is estimated to be as high as 10.7%, with some pairs renesting as many as 10 times within a three-month breeding season (Nalwanga *et al.* 2004b). Suspected predators include snakes and moongose: on one occasion an apalis nest was observed to be torn apart and its content eaten by a Small Grey Moongose *Galerella pulverulenta*.

Conclusion

Early proponents of the Ideal Despotism theory contended that high-quality individuals defend high-quality territories which in turn help them maximise both their survival and their reproductive fitness (Fretwell and Lucas 1970). Based on this premise, theories explaining female mate choice propose that high-quality females choose high-quality males and that females will adjust their reproductive investment according to mate quality (Burley 1986). Such choice may be based on the male phenotypic and/or behavioural traits that signal individual and/or territory quality (Wolfenbarger 1999). In this study, pattern of territory occupancy were strongly asymmetric. High-quality males (signalled by large breast bands) occupied high-quality, small but food-rich territories which in turn influenced their reproductive performance relative to the performance of birds on poor-quality territories. Specifically, territory quality determined the distances that males travelled to obtain food for both their incubating mates and their nestlings. By the same token, however, male breast-band size was also a good indicator of the rates at which males provisioned mates. As a consequence, males on high-quality territories received fitness benefits that included early nest initiation by females, increased clutch mass, increased female nest attentiveness, faster nestling growth and higher nestling survivorship.

REFERENCES

- Andersson, M. (1981) Central place foraging in the Whinchat, *Saxicola rubetra*. *Ecology*, **62**, 538–544.
- Andrew, R.J. (1961) The displays given by passerines in courtship and reproductive fighting: a review, *Ibis*, **103**, 315–348.

- Bolton, M., Houston, D. and Monaghan, P. (1992) Nutritional constraints on egg formation in the Lesser Black-backed Gull: an experimental study. *Journal of Animal Ecology*, **61**, 521–532.
- Bolton, M., Monaghan, P. and Houston, D. (1993) Proximate determination of clutch size in Lesser Black-backed Gulls: the roles of food supply and body condition. *Canadian Journal of Zoology*, **71**, 273–279.
- Brown, J.L. (1964) The evolution of diversity in avian territorial systems. *Wilson Bulletin*, **76**, 160–169.
- Budaev, S.V. (2010) Using principal components and factor analysis in animal behaviour research: caveats and guidelines. *Ethology*, **116**, 472–480.
- Burley, N. (1986) Sexual selection for aesthetic traits in species with biparental care. *American Naturalist*, **127**, 415–445.
- Canestrari, D., Chiarati, E., Marcos, J.M., Ekman, J. and Baglione, V. (2008) Helpers but not breeders adjust provisioning effort to year-round territory resource availability in Carrion Crows. *Animal Behaviour*, **76**, 943–949.
- Cordero, P.J., Wetton, J.H. and Parkin, D.T. (1999) Extra-pair paternity and male badge size in the House Sparrow. *Journal of Avian Biology*, **30**, 97–102.
- Cox, W.A. and Martin, T.E. (2009) Breeding biology of the Three-Striped Warbler in Venezuela: a contrast between Tropical and Temperate Parulids. *The Wilson Journal of Ornithology*, **121**, 667–678.
- Cunningham, E.J.A. and Russel A.F. (2000) Egg investment is influenced by male attractiveness in the Mallard. *Nature*, **404**, 74–77.
- Dawson, R.D. and Bidwell, M.T. (2005) Dietary calcium limits size and growth of nestling Tree Swallows *Tachycineta bicolor* in a non-acidified landscape. *Journal of Avian Biology*, **36**, 127–134.
- deKort, S.R., Eldermer, E.R.B., Cramer, E.R.A., Vehrencamp, S.L. (2009) The deterrent effect of bird song in territory defense. *Behavioural Ecology*, **20**, 200–206.
- De Lope, F., and Møller, A.P. (1993) Female reproductive effort depends on the degree of ornamentation of their mates. *Evolution*, **47**, 1152–1160.
- Donázar, J.A., Negro, J.J. and Hiraldo, F. (1992) Functional analysis of mate-feeding in the Lesser Kestrel *Falco naumanni*. *Ornis Scandinavica* **23**, 190–194.
- Dunn, M., Copelston, M. and Workman, L. (2004) Trade-offs and seasonal variation in territorial defence and predator evasion in the European Robin *Erithacus rubecula*. *Ibis*, **146**, 77–84.

- Dunn, P.O. and Winkler, D.W. (1999) Climate change has affected the breeding date of Tree Swallows throughout North America. *Proceedings of the Royal Society B: Biological Sciences*, **266**, 2487–2490.
- Ens, B.J., Kersten, M., Brenninkmeijer, A. and Hulscher, J.B. (1992) Territory quality, parental effort and reproductive success of Oystercatchers *Haematopus ostralegus*. *Journal of Animal Ecology*, **61**, 703–715.
- Fretwell, S.D. and Lucas, H.L. (1970) On territorial behaviour and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheoretica*, **19**, 16–36.
- Gerard, E.D. (2001) <http://www.jerrydallal.com/LHSP/collin.htm>.
- Gerhardt, H.C and Huber, F. (2002) Acoustic communication in insects and anurans. University of Chicago, Chicago.
- Gorman, H.E. and Nager, R.G. (2003) State-dependent incubation behaviour in the Zebra Finch. *Animal Behaviour*, **65**, 745–754.
- Green, D.J. and Krebs, E.A. (1995). Courtship feeding in Ospreys *Pandion haliaetus*: a criterion for mate assessment? *Ibis*, **137**, 35–43.
- Griffith, S. C., Owens, I.P.F. and Burke, T. (1999) Female choice and annual reproductive success favour less-ornamented male House Sparrows. *Proceedings of the Royal Society B: Biological Sciences*, **266**, 765–770.
- Hałupka, K. (1994) Incubation feeding in Meadow Pipit *Anthus pratensis* affects female time budget. *Oikos*, **25**, 251–253.
- Hargitai, R., Török J., Tóth, L., Hegyi, G., Rosival B., Szigeti, B. and Szöllös, E. (2005) Effects of environmental conditions and parental quality on inter- and intraclutch egg-size variation in the Collared Flycatcher *Ficedula albicollis*. *Auk*, **122**, 509–522.
- Hasselquist, D. (1988) Polygyny in Great Reed Warblers: a long-term study of factors contributing to male fitness. *Ecology*, **79**, 2376–2390.
- Hill, G.E. (1990) Female House Finches prefer colourful males: sexual selection for a condition-dependent trait. *Animal Behavior*, **40**, 563–572.
- Hill, G.E. (1991) Plumage coloration is a sexually selected indicator of male quality. *Nature*, **350**, 337–339.
- Houston, A.I. (1987) Optimal foraging by parent bird feeding dependent young. *Journal of Theoretical Biology*, **124**, 251–274.
- Hussell, D.J.T. (2003) Climate change, spring temperatures, and timing of breeding of Tree Swallows (*Tachycineta bicolor*) in southern Ontario. *Auk*, **120**, 607–618.

- Jarvinen, A. and Ylimaunu, J. (1986) Intraclutch egg-size variation in birds: physiological responses of individuals to fluctuations in environmental conditions. *Auk*, **103**, 235–237.
- Jawor, J.M. and Breitwisch, R. (2006) Is mate provisioning predicted by ornamentation? A test with Northern Cardinals (*Cardinalis cardinalis*). *Ethology*, **112**, 888–895.
- Jensen, H., Sæther, B., Ringsby, T.H., Tufto, J., Griffith, S.C. and Ellegren, H. (2004) Lifetime reproductive success in relation to morphology in the House Sparrow *Passer domesticus*. *Journal of Animal Ecology*, **73**, 599–611.
- Jolliffe, I.T. (2002) *Principal Component Analysis*. 2nd ed., pp. 28. Springer, New York.
- Keyser, A.J. and Hill, G.E. (2000) Structurally based plumage coloration is an honest signal of quality in male Blue Grosbeaks. *Behavioral Ecology*, **11**, 202–209.
- Kluyver, H.N. (1950) Daily routines of the Great Tit *Parus m. major* L. *Ardea*, **38**, 99–135.
- Krüger, O. and Lindström, J. (2001) Lifetime reproductive success in Common Buzzard, *Buteo buteo*: from individual variation to population demography. *Oikos*, **93**, 260–273.
- Lack, D. (1940) Courtship feeding in birds. *Auk*, **57**, 169–178.
- Limmer, B. and Becker, P.H. (2009) Improvement in chick provisioning with parental experience in a seabird. *Animal Behavior*, **77**, 1095–1101.
- Lyon, B.E. and Montgomerie, R.D. (1985) Incubation feeding in Snow Buntings: female manipulation or indirect male parental care? *Behavioral Ecology and Sociobiology*, **17**, 279–284.
- Martin, T.E. (1998) Are microhabitat preferences of coexisting species under selection and adaptive? *Ecology*, **79**, 656–670.
- Martin, T.E. and Guepel, G.R. (1993) Nest-monitoring plots: methods for locating nests and monitoring success. *Journal of Field Ornithology*, **64**, 507–519.
- McGraw K.J, Mackillop E.A., Dale J. and Hauber M.E. (2002) Different colors reveal different information: how nutritional stress affects the expression of melanin- and structurally based ornamental plumage. *Journal of Experimental Biology*, **205**, 3747–3755.
- McNamara, J.M. and Houston, A.I. (2008) Optimal annual routines: behaviour in the context of physiology and ecology. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **363**, 301–319.

- Meathrel, C.E. and Ryder, J.P. (1987) Intraclutch variation in the size, mass and composition of Ring-billed Gull eggs. *Condor*, **89**, 364–368.
- Møller, A.P. (1988) Badge size in the House Sparrow *Passer domesticus*. Effects of intra- and intersexual selection. *Behavioral Ecology and Sociobiology*, **22**, 373–378.
- Møller, A.P. (1989) Natural and sexual selection on a plumage signal of status and on morphology in House Sparrows, *Passer domesticus*. *Journal of Evolutionary Biology*, **2**, 125–140.
- Møller, A.P. (1990) Sexual behavior is related to badge size in the House Sparrow *Passer domesticus*. *Behavioral Ecology and Sociobiology*, **27**, 23–29.
- Moore, D.J., Williams, T.D. and Morris, R.D. (2000) Mate provisioning, nutritional requirements for egg production, and primary reproductive effort of female Common Terns *Sterna hirundo*. *Journal of Avian Biology*, **31**, 183–196.
- Myrberget, S. (1986) Age and breeding of Willow Grouse *Lagopus lagopus*. *Ibis*, **128**, 282–285.
- Naef-Daenzer, B. and Keller, L.K. (1999) The foraging performance of Great and Blue Tits (*Parus major* and *P. caeruleus*) in relation to caterpillar development, and its consequences for nestling growth and fledging weight. *Journal of Animal Ecology*, **68**, 708–718.
- Nagelkerke, N. (1991) A note on a general definition of the coefficient of determination. *Biometrika*, **78**, 691–692.
- Nakagawa, S. and Burke, T. (2008) The mask of seniority? A neglected age indicator in House Sparrows *Passer domesticus*. *Journal of Avian Biology*, **39**, 222–225.
- Nalwanga, D., Lloyd, P., du Plessis, M.A. and Martin, T.E. (2004a) The influence of nest-site characteristics on the nesting success of the Karoo Prinia *Prinia maculosa*. *Ostrich*, **75**, 269–274.
- Nalwanga, D., Lloyd, P., du Plessis, M.A. and Martin, T.E. (2004b) Nest-site partitioning in a strandveld shrubland bird community. *Ostrich*, **75**, 250–258.
- Newton, I. and Marquiss, M. (1982) Eye colour, age and breeding performance in Sparrowhawks *Accipiter nisus*. *Bird Study*, **29**, 195–200.
- Nikolov, B.P. (2005) Reproductive success of the Woodchat Shrike *Lanius senator* in Western Bulgaria. *Ornis Fennica*, **82**, 73–80.
- Nilsson, J. and Smith, H.G. (1988) Incubation feeding as a male tactic for early hatching. *Animal Behavior*, **36**, 641–647.
- Nisbet, I.C.T. (1973) Courtship-feeding, egg-size and breeding success in Common Terns. *Nature*, **241**, 141–142.

- Nisbet, I.C.T. (1977) Courtship-feeding and clutch size in Common Terns *Sterna hirundo*. In *Evolutionary Ecology* (Eds Stonehouse, B and Perrins, C), pp. 101–109. Macmillan, London.
- Nooker, J.K., Dunn, P.O. and Whittingham, L.A. (2005) Effects of food abundance, weather and female body condition on reproduction in Tree Swallows (*Tachycineta bicolor*). *Auk*, **122**, 1225–1238.
- Norris, K.J. (1990) Female choice and the evolution of the conspicuous plumage coloration of monogamous Great Tits. *Behavioral Ecology and Sociobiology*, **26**, 129–138.
- Otter, K. and Ratcliffe, L. (1999) Relationship of bib size to age and sex in the Black-capped Chickadee. *Journal of Field Ornithology*, **70**, 567–577.
- Pearson, K. (1901) On lines and planes of closest fit to systems of points in space. *Philosophical Magazine*, **2**, 559–572.
- Perrins, C.M. and McCleery, R.H. (1985) The effect of age and pair bond on the breeding success of Great Tits *Parus major*. *Ibis*, **127**, 306–315.
- Pryke, S.R. and Griffith, S.C. (2010) Maternal adjustment of parental effort in relation to mate compatibility affects offspring development. *Behavioral Ecology*, **21**, 226–232.
- Rohwer, S. (1975) The social significance of avian winter plumage variability. *Evolution*, **29**, 593–610.
- Royama, T. (1966) A re-interpretation of courtship feeding. *Bird Study*, **13**, 116–129.
- Safina, C. and Burger, J. (1983) Effects of human disturbance on reproductive success in the Black Skimmer. *Condor*, **85**, 164–171.
- Searcy, W. A. (1996) Sound-pressure levels and song preferences in female Red-winged Blackbirds *Aegelaius phoeniceus* (Aves, Emberizidae). *Ethology*, **102**, 187–196.
- Siefferman, L. and Hill, G. E. (2003) Structural and melanin plumage coloration indicate parental effort and reproductive success in male eastern bluebirds. *Behavioral Ecology*, **14**, 855–861.
- Siefferman, L. and Hill, G.E. (2005) Blue structural coloration of male Eastern Blue birds *Sialia sialis* predicts incubation provisioning to females. *Journal of Avian Biology*, **36**, 488–493.
- Siitari H. and Huhta E. (2002) Individual color variation and male quality in Pied Flycatchers (*Ficedula hypoleuca*): a role of ultraviolet reflectance. *Behavioral Ecology*, **13**, 737–741.

- Slagsvold, T. (1986) Asynchronous versus synchronous hatching in birds: experiments with the Pied Flycatcher. *Journal of Animal Ecology*, **55**, 1115–1134.
- Sodhi, N.S. (1993) Proximate determinants of foraging effort in breeding male Merlins. *Wilson Bulletin*, **105**, 68–76.
- Starcks, J.M. and Ricklefs, R.E. (1998) Patterns of development: the altricial-precocial spectrum. In Avian growth and development. Evolution within the altricial-precocial spectrum (Eds Starck, J.M, and Ricklefs, R.E.). Oxford University Press, Oxford. Pp.3–30.
- Uller, T., Eklöf, J. and Andersson, S. (2005) Female egg investment in relation to male sexual traits and the potential for transgenerational effects in sexual selection. *Behavioral Ecology and Sociobiology*, **57**, 584–590.
- Veiga, J.P. (1993) Badge size, phenotypic quality and reproductive success in the House Sparrow: a study on honest advertisement. *Evolution*, **47**, 1161–1170.
- Viñuela, J. (1997) Adaptation vs constraint: intraclutch egg-mass variation in birds. *Ecology*, **66**, 781–792.
- Wedell, N. and Karlsson, B. (2003) Paternal investment directly affects female reproductive effort in an insect. *Proceedings of the Royal Society B: Biological Sciences*, **270**, 2065–2071.
- Whittingham, L.A., Dunn, P.O. and Lifjeld J.T. (2007) Egg mass influences nestling quality in Tree Swallows, but there is no differential allocation in relation to laying order or sex. *Condor*, **109**, 585–594.
- Wilson, J.D. (1992) A re-assessment of the significance of status signaling in populations of wild Great Tits *Parus major*. *Animal Behaviour*, **43**, 999–1009.
- Wolfenbarger, L.L. (1999) Red coloration of male Northern Cardinals correlates with mate quality and territory quality. *Behavioral Ecology*, **10**, 80–90.
- Zuur, A.F., Leno, E.N. and Elphick, C.S. (2009) A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, **1**, 3–14.

CHAPTER FIVE

MATE FIDELITY, TERRITORY FIDELITY AND ADULT SURVIVAL IN THE BAR-THROATED APALIS

Introduction

Levels of survivorship, and mate and territory retention, vary considerably within several bird species (Wickler and Seibt 1983, Nakamura and Kubota 1998, Cézilly *et al.* 2000, Pyle *et al.* 2001, Sedinger *et al.* 2008). Factors regulating such variation are wide ranging and may involve both environmental and individual attributes.

Survivorship may be influenced by food (Lahti *et al.* 1998, Davis *et al.* 2005), age (Greenberg and Gradwohl 1997, Lahti *et al.* 1998, Brown and Roth 2009), vegetation structure (Oro and Furness 2002, Davis *et al.* 2005, Maguire 2006), territory quality (Switzer 1997), predators (Maguire 2006) and temperature (Lahti *et al.* 1994). For instance, survival of adult Southern Emu-Wrens *Stipiturus malachurus* is determined primarily by the density of predatory snakes (Maguire 2006). Territory fidelity, by contrast, may be regulated by conspecific density: as density increases, the chance of encountering suitable vacant breeding sites decreases which may lead to increased territory fidelity (Fretwell and Lucas 1970, Pulliam 1988, Caughley 1994). Territory fidelity may also be influenced by the predictability of habitat quality, assessed by neighbour success or area familiarity (Eason and Hannon 1994, Desrochers and Magrath 1996; Boulinier and Danchin 1997). Mate fidelity could be influenced by the costs associated with changing mates or by familiarity with an existing mate and breeding site (Ens *et al.* 1993, 1996, Orell *et al.* 1994, Choudhury 1995, Croxall and Davis 1999, Bried and Jouventin 2002). Costs incurred in mate switching can include lowered reproductive success (e.g. due to inbreeding - Ens *et al.* 1996); increased time and energy costs of searching for and 'sampling' a new mate (Lifjeld and Slagsvold

1988, Real 1990 Choudhury 1995); or a delay in the initiation of breeding (Pampus *et al.* 2005, Nisbet and Dann 2009). Mate fidelity may also be influenced by skewed sex ratios, with less fidelity expected by the under-represented sex (Jones *et al.* 2004, 2005, Maness and Andersson 2007, Mills *et al.* 2007). In several species there is a link between mate fidelity and longevity (Coulson 1966, Mills 1973, Richdale and Warham 1973, Ollason and Dunnet 1978, Dhont and Andriaensen 1994, Choudhury 1995, Ens *et al.* 1996, Dubois and Cézilly 2002), but there have also been suggestions that mate fidelity may be a consequence of territory fidelity rather than its cause (Cézilly *et al.* 2000). In some species, mate fidelity is related to traits associated with individual quality. In the Least Auklet *Aethia pusilla*, for example, male ornamentation (facial plumes) is correlated with mate fidelity: males with large facial plumes are more likely to re-unite with their current mates in the following year than are males with smaller facial plumes (Jones and Montgomerie 1991). Regardless of the factors regulating these life-history variables, variations in any of the above parameters may have significant consequences for individual reproductive success (Rowley 1983). For instance, individuals mating with the same partners over consecutive seasons may be better able to synchronize their breeding activities than birds which switch mates (and hence achieve higher fitness - Coulson 1966, Cooke *et al.* 1981, Williams and Rodwell 1992, Choudhury and Black 1994, Bried and Jouventin 2002, Nisbet and Dann 2009).

On the other hand, retention of breeding sites may be beneficial because individuals can learn the location of important resources such as food, nest sites and nesting materials, thereby saving them the energetic costs associated with searching for these resources on a new territory (Part 1995, Murphy 1996). Territory fidelity in combination with mate fidelity may further influence the number of young produced

annually (Newton and Marquiss 1982). And if such fidelity translates into enhanced survivorship, this in turn may result in enhanced lifetime reproductive success. If these putative benefits linked to mate- or territory fidelity are not realised, individuals may desert their partner and/or territory in search of better options that may enhance their fitness (the Better Option Hypothesis – Ens *et al.* 1993).

Bar-throated Apalises at Koeberg Nature Reserve breed under varying range of environmental constraints (particularly varying food densities). They also differ in their physical condition and reproductive output. Potentially, these factors could, together or independently, influence pair-bond stability, territory fidelity and adult survival (Nakamura and Kubota 1998, Pyle *et al.* 2001, Pampus *et al.* 2005, Sedinger *et al.* 2008). The Best Options Hypothesis (Ens *et al.* 1993) identifies a suite of situations and scenarios under which an individual may make fitness-related decisions about the retention or otherwise of a mate or territory. To explore whether there is evidence for such decisions being made by Bar-throated Apalises, this study examined:

1. Mate fidelity, territory fidelity and apparent adult survival of Bar-throated Apalises at Koeberg Nature Reserve; and
2. Environmental factors (e.g. prey density, abundance of foraging substrata, vegetation structure) and individual attributes (e.g. body mass, biometrics and breast-band size) that may influence these variables.

Based on the wide ranges of territory sizes and individual qualities of birds in the study area, the study further tested the predictions that:

- i. Individuals that switch mates and/or territories will do so in such a way that their new mate/territory is/are of higher quality than their previous mate/territory; and

- ii. Adult survival will be highest on high-quality territories.

METHODS

Pair-bond stability and territory fidelity

Pairs were monitored at the study area over the breeding seasons of 2007 - 2009 (August – October each year). All birds were trapped and ringed with a unique combination of a numbered aluminium band and three plastic coloured bands (Chapter 2), making individual recognition possible within and between years. Pairs were monitored to determine the extent to which individuals retained their mates and territories between breeding seasons. Territory fidelity was expressed as the percentage of individuals (males and females) from year j remaining on the same territory in year $j+1$. Mate fidelity was expressed as the number of individuals retaining the same mate on the same *or* a new territory from year j to year $j+1$: the latter was calculated only for those individuals whose partner was still alive in year $j+1$. The chi-squared test of independence was used to test for significant differences in mate and territory fidelity between years (2007 – 2008 and 2008 – 2009) and sexes. The 30th of September, when most apalises at Koeberg have ceased breeding, was used as a standard to adjudge whether an individual had a) survived and b) remained faithful to mate or territory throughout the breeding season. Any bird present on a territory in the study area in year j that was not relocated anywhere in the study area in year $j+1$ was assumed to have died during the non-breeding season. There are some problems with this assumption as it cannot be categorically proven that some of these birds did not disperse away from the study area.

Differences in territory and individual attributes for territory-switching individuals and for current and previous territory occupants

For individuals that switched territories between years, differences in territory attributes (prey density, cover of foraging substrata, overall vegetation cover and vegetation height) were compared between their previous and current territories. Similarly, biometrics (body weight, tarsus and wing lengths, and breast-band sizes) of new mates of territory-switching individuals were compared with the same biometrics of previous mates. In instances where territory ownership changed, the biometrics of the current territory holders were compared with those of the occupants of the same territory in the previous breeding season. Independent sample t-tests were used to test the significance of all two-way comparisons using the package SPSS version 17.0. Measurements of territory and individual attributes are detailed in Chapters 2 and 3. Displacement distances (m) from previous territories by territory-switching individuals were estimated (from territory centre to territory centre - Chapter 2) with GPS Software (Garmin® Etrex H).

Adult survival

To estimate annual survival, observations of ringed individuals were reduced to the presence or absence of an individual during the breeding season of each study year. Cormack-Jolly-Seber (CJS) open-population, capture-recapture models (Cormack 1964, Jolly 1965, Seber 1965) in the Programme Mark were used to estimate survival. The CJS yields two parameters, *viz.* apparent survival (Φ) and resighting/recapture (p) rates. Apparent survival is the product of 'true' survival rate (S – the probability that an individual survives across the sampling interval) and site-fidelity rate (F – the probability that an individual returns to the same site if it survives).

Resighting/recapture rates are the product of site propensity rate (γ^* – the probability that an individual returns the following year, if it survives and returns to the same site i.e. does not emigrate) and true encounter rate (p^* – the probability that an individual is detected by the observer if present on the study area). The information theoretic approach as described by Burnham and Anderson (1998) was followed in selecting the best-fit model explaining variation in survival and recapture rates of territorial individuals. First a general model (i.e. $\Phi_{(g^*t)}$, $p_{(g^*t)}$, where g = all grouping levels and t = yearly variation) was fitted to separate survival and recapture parameters for all independent variables and times (Lebreton *et al.* 1992, Burnham and Anderson 1998, Doherty and Grubb 2002, Fernández 2003). In addition to the general model, in order to model survivorship and resighting rates a set of models that included the effects of sex and territory size were developed. In these models, territory size (Tsize) was used as a surrogate for territory quality because of its inverse relationship to prey density across territories and its stability between years (Chapter 2). Models were developed that included all possible combinations of the two factors (sex and territory size), either as constants ($\Phi_{(constant)}$, $p_{(constant)}$), additive effects ($\Phi_{sex+Tsize}$, $p_{sex+Tsize}$), individual effects (Φ_{Tsize} , p_{Tsize}), (Φ_{sex} , p_{sex}), (Φ_{Tsize} , p_{sex}), and (Φ_{sex} , p_{Tsize}), or interactions ($\Phi_{sex*Tsize}$, $p_{sex*Tsize}$). All models were constructed using a Logit-Link function. The best-fit model was adjudged the one with the smallest Akaike Information Criterion (AIC) after correcting for small sample size (AICc - Burnham and Anderson 1998). Models were considered equivalent when their AICc values differed from the best-fit model by a margin of ≤ 2 : in such cases, the model with the fewest parameters was considered the most parsimonious (Doherty *et al.* 2002). Estimates of apparent annual survival and recapture/resighting rates, as well as unconditional variance that includes

model uncertainty (Burnham and Anderson 1998), were calculated through model averaging based on Akaike weights (w) (Doherty *et al.* 2002, Fernández 2003).

RESULTS

Mate fidelity, territory fidelity and territory switching

Mate fidelity:

There was no significant difference in mate fidelity between study years ($\chi^2 = 0.071$, $df = 1$, $P = 0.789$). Twenty-seven of the 34 pairs (79.4%) monitored in 2007 retained the same mate in the 2008 breeding season. Of the 46 pairs monitored in 2008, 29 pairs (63.0%) remained together in 2009 (Table 5.1).

Territory fidelity:

Territory fidelity did not vary between the two study years – Males: $\chi^2 = 0.397$, $df = 1$, $P = 0.528$; Females: $\chi^2 = 0.065$, $df = 1$, $P = 0.798$) or between sexes ($\chi^2 = 0.069$, $df = 1$, $P = 0.792$). Thirty of 34 females (88.2%) remained on the same territory between 2007 and 2008: 29 of 34 males (85.3%) remained territory faithful over the same period. Between 2008 and 2009, 32 of 46 females (69.6%), and 34 of 46 males (73.9%) remained on the same territories (Table 5.1).

Territory switching and displacement distance:

In 2008, only one of the 34 pairs monitored in the previous year switched territory while remaining together. In 2009, one pair, and a single male and female, switched territories (Table 5.1). The previous mates of the latter two individuals were never relocated and were presumed dead. Average displacement distance from the previous

territory by males was 346 ± 156 S.D. m (range: 140 – 566 m, $n = 3$) and for females was 216 ± 102 m (range: 140 – 332 m, $n = 3$). These differences were not significant (Independent sample t-test, $df = 4$, $t = 0.95$, $P = 0.39$). Males skipped between one and four territories to reach new territories while females (whether moving alone or with their mate) skipped a maximum of one territory.

Table 5.1: Annual rates of mate and territory fidelity among Bar-throated Apalises. Apparent mismatches between mate fidelity and the number of territory-switching individuals are due to birds that had either left the study area or had died between the two years.

Years	Mate fidelity % (number of pairs)	Territory switching individuals		Territory fidelity % (number of pairs)	
		Male	Female	Male	Female
2007 – 2008	79.4 (27/34)	1	1	85.3 (29/34)	88.2 (30/34)
2008 – 2009	63.0 (29/46)	2	2	73.9 (34/46)	69.6 (32/46)
Mean \pm SD	70.0 \pm 11.6			78.8 \pm 8.1	77.5 \pm 13.2

Differences in territory attributes between previous and current territories of switching individuals

Due to small sample sizes, differences in mate and territory attributes between current and previous territory occupants could not be statistically tested. However, current territories were, on average, improvements over previous territories in terms of prey density, cover of foraging substrata and overall vegetation cover. For females that switched mates, replacement males on average were heavier, larger and had larger breast bands than did the original males (Table 5.2). There are no data for the new female partner of the single male that switched both territory and mate.

Table 5.2: Differences in territory and mate attributes for territory-switching male and female Bar-throated Apalises.

Sex (n)		Previous territory/mate (Mean)	Current territory/mate (Mean)
Male (2)	Prey density (g.m ⁻²)	1.45 E-03	1.48 E-03
	Average vegetation height (m)*	1.01	0.95
	Overall vegetation cover (%)	71.85	73.85
	Cover of foraging substrata (%)	22.00	28.55
Female (2)	Prey density (g.m ⁻²)	4.0 E-05	1.3 E-04
	Average vegetation height (m)*	0.91	0.89
	Overall vegetation cover (%)	67.63	68.70
	Cover of foraging substrata (%)	6.23	13.55
	Male body mass (g)	11.49	11.56
	Male tarsus length (mm)	20.41	20.80
	Male wing length (mm)	51.00	53.00
	Male breast-band size (mm ²)	118.603	127.337

*high-quality territories have lower-than-average vegetation height (Chapter 2).

Differences in biometrics between previous and current territory occupants

When the male on a territory was replaced, the new occupant was significantly heavier and had a significantly larger breast band than the male he replaced, although the new males also had significantly shorter wings than their predecessors (Table 5.3). On the other hand, females on new territories differed from their predecessors only in having significantly shorter wings (Table 5.3).

Table 5.3: Differences in biometrics of Bar-throated Apalises between current and previous territory occupants (Independent sample t-test).

Sex	Variable	Previous territory occupant (i.e. displaced or dead individual) Mean \pm S.E.	Current territory occupant Mean \pm S.E.	<i>df</i>	<i>t</i>	<i>P</i>
Male (<i>n</i> = 10)	Breast-band size (mm ²)	113.71 \pm 8.97	164.73 \pm 14.16	18	3.043	0.007
	Body mass (g)	11.47 \pm 0.09	12.21 \pm 0.18	18	3.602	0.002
	Tarsal length (mm)	20.89 \pm 0.12	21.10 \pm 0.22	18	0.813	0.427
	Wing length (mm)	52.94 \pm 0.32	50.80 \pm 0.46	18	3.755	0.001
Female (<i>n</i> = 9)	Breast-band size (mm ²) (<i>n</i> = 10)	57.34 \pm 9.33	69.69 \pm 6.04	15	1.111	0.284
	Body mass (g)	12.51 \pm 0.31	12.87 \pm 0.48	16	0.624	0.541
	Tarsal length (mm)	20.21 \pm 0.15	20.36 \pm 0.12	16	0.783	0.445
	Wing length (mm)	50.72 \pm 0.14	49.06 \pm 0.68	8	2.381	0.042

Adult survival

The best-fit model explaining variations in apparent survival and resighting rates indicated that survival was influenced by territory size and resighting rate was influenced by either territory size or sex (Table 5.4a), with survival and territory size being negatively correlated ($B = -0.190$). Estimates for apparent survival were lower between 2007 and 2008 than between 2008 and 2009 despite resighting rates being higher from 2007 to 2008 than from 2008 to 2009. Apparent survival and resighting rates were also slightly higher for males than for between 2008 and 2009 (Table 5.4b).

Table 5.4a: Akaike Information Criterion (AICc) values for maximum-likelihood models of apparent survival (Φ) and detection probability (p) of territorial male and female Bar-throated Apalises (n= 38 males, 37 females). AICc values are expressed as deviations from the best fit models, i.e. ΔAICc . In instances where $\Delta\text{AICc} \leq 2$, the best approximating models are indicated in bold.

Model for apparent survival	Model for resightings				
	$P_{\text{sex}*\text{Tsize}}$	$P_{\text{sex}+\text{Tsize}}$	P_{sex}	P_{Tsize}	P_{constant}
$\Phi_{\text{sex}*\text{Tsize}}$	3.844	6.021	3.844	3.844	3.844
$\Phi_{\text{sex}+\text{Tsize}}$	6.021	3.844	1.859	6.420	6.021
Φ_{sex}	3.844	3.844	1.427	1.944	3.844
Φ_{Tsize}	1.704	1.704	0.00	0.00	1.704
Φ_{constant}	3.844	6.021	3.844	3.844	3.844

* =model with interaction; + = model with additive or main effects

Table 5.4b: Apparent survival (Φ) and resighting rates (p) between years and sexes for Bar-throated Apalises at Koeberg Nature Reserve. Annual estimates are calculated using model averaging.

Parameters	Year	Estimate \pm unconditional S.E.	
		Males	Females
Apparent survival (Φ)	2007 – 2008	0.821 \pm 0.061	0.814 \pm 0.063
	2008 – 2009	0.896 \pm 0.425	0.880 \pm 1.430
Resighting (p)	2007 – 2008	1.00 \pm 1.74E-05	1.00 \pm 2.26E-05
	2008 - 2009	0.849 \pm 0.335	0.820 \pm 1.015

DISCUSSION

Mate and territory fidelity

More than 70% of Bar-throated Apalises remained on the same territory or with the same mate between years. Statistically, both males and females had similar levels of territory and mate fidelity between years, but on average both territory and mate fidelity were higher between 2007 and 2008 than between 2008 and 2009. These levels of mate and territory fidelity are similar to those reported for other socially monogamous, territorial birds. For example, site fidelity is approximately 70% for the

Piping Plover *Charadrius melodus* Haig and Oring (1988), and Black Turnstones *Arenaria melanocephala* have territory fidelity of up to 88% and an average mate fidelity of 89% (Handel and Gill 2000). Among passerines, the Buff-breasted Wren *Thryothorus leucotis* has average territory fidelity of up to 93.3% for males and 87.2% for females and mate fidelity averaging 80.8% (Gill and Stutchbury 2006).

Such high territory fidelity may be a response to high population density and lack of vacant breeding territories (Fretwell and Lucas 1970, Weatherhead and Boak 1986, Pulliam 1988, Caughley 1994). There is almost certainly a shortage of territories for the apalis population at Koeberg. All known territories within the limits of the study area remained occupied year-round throughout the three-year study period and floaters were trapped within the study area each year. These patterns suggest that density dependence is operating (Fretwell and Lucas 1970), with a surplus of non-breeding birds being present (cf Hockey *et al.* 2011). In further support of this conclusion, territory quality and male quality are closely coupled (Chapters 2, 3). With respect to habitat/territory quality, previous studies have proposed that site fidelity should prevail when a bird's immediate environment is predictable, based for example on the success of neighbours or its own reproductive success (Eason and Hannon 1994, Desrochers and Magrath 1996, Boulinier and Danchin 1997). Similarly, if there is strong asymmetry in male quality (as signalled by breast-band size in the case of the Bar-throated Apalis), and the 'best' males occupy the 'best' territories, this may serve to suppress the frequency of territorial contests (because the outcome of such contests is largely predetermined - Rohwer 1975, 1982, Senar 1993, McGraw *et al.* 2002, Dunn *et al.* 2008). The same reasoning may explain the high levels of mate fidelity in the study population. In support of this, a comparative study

of 42 species in the Order Ciconiiformes reported a significant inverse correlation between divorce rate and site fidelity (Cézilly *et al.* 2000).

It cannot be ruled out, however, that the survivorship of apalises recorded here does not influence mate fidelity. Several studies have shown a positive relationship between mate fidelity and survival which has been attributed to low reproductive rates of long-lived species (Coulson 1966, Mills 1973, Richdale and Warham 1973, Ollason and Dunnet 1978, Bried *et al.* 2003). However, exceptions to this generalisation do occur. For example, in both Flightless Cormorants *Nannopterum harrisi* and Greater Flamingos *Phoenicopterus ruber*, divorce occurs predictably and immediately after breeding (Harris 1979, Cézilly and Johnson 1995).

High levels of mate- and territory retention by apalises may confer some significant benefits to territory holders. Territory fidelity in particular may enable individuals to learn the 'geography' of critical resources such as the locations of nest sites, food and predators, saving individuals the cost of searching for these key resources on a new territory (Part 1995, Murphy 1996). Mate fidelity further reduces costs associated with pair formation (Croxall and Davis 1999, Bried and Jouventin 2002) and mate retention may improve reproductive success due to better coordination of breeding activities as a result of mate familiarity (Coulson 1966, Williams and Rodwell 1992, Bried and Jouventin 2002, Setiawan *et al.* 2005).

Territory switching: territory and mate attributes

Although differences in territory and mate attributes between new and old territories or between new and old mates of territory-switching individuals could not be tested statistically because of small sample sizes. However, new territories of switching individuals had, on average, higher prey densities and more vegetation cover. More

convincingly, even though sample sizes were again small, in instances where females abandoned an existing territory to join a new mate elsewhere, the new males had, on average, larger breast bands and were larger and heavier than the female's previous mate (i.e. the new male was of better quality – *cf.* Diamond 1987, Harris *et al.* 1987). This conforms to predictions of the Better Option Strategy (Ens *et al.* 1993) and may reflect a bid to improve reproductive success (Coulson and Thomas 1983, Rowley 1983). There are, however, other possible explanations for mate switching. Territory or mate desertion, rather than being adaptive, could be forced on an individual through the action of competing conspecifics (the Salvage Strategy or Non-adaptive Divorce – Choudhury 1995, Taborsky and Taborsky 1999) or by accidental separation (Owen *et al.* 1988, Forsuland and Larsson 1992). However, if these non-adaptive processes are driving mate switching by female apalises, it is difficult to explain away the observation that female apalises which did switch mates ended up with higher quality males than they had before. More compelling however, is that high-quality male apalises were better at provisioning both mate and nestlings (Chapter 4), implying that a 'mate upgrade' has the potential to translate into improved fitness. Whilst the findings of this study provide some qualitative support to the conclusion that female apalises are adopting the Better Option Strategy, mate-switching is nonetheless infrequent and the conclusions cannot be tested statistically.

Biometrics: old and new territory occupants

When males were replaced on a territory, the new males were of higher quality (heavier and with larger breast bands) than their predecessors. New females on territories differed from their predecessors only in being longer winged (long-winged females being those in the best body condition – Chapter 3). The pattern shown by

males in particular suggests that individual quality is key in the acquisition of a new territory. What could not be determined in this study was/were the cause/s of territorial males leaving their territories. They could have been displaced as losers of territorial contests, or they could have died. After disappearing from their territories, most males were never resighted within the boundaries of the study area, suggesting emigration or death. However, the observations that a) new incumbents were higher quality males than the original occupants, and b) floaters were present in the study area, strongly suggest that competition for territories is intense and its resolution is dependent on individual quality (Dawkins and Krebs 1978, Senar *et al.* 1993, Chappel *et al.* 1997, McGraw *et al.* 2003, Nakagawa *et al.* 2007).

Apparent survival and resighting

In the best-fit models explaining variation in apparent survival and resighting/recapture rates, adult survival varied with territory size (a surrogate for territory quality) and resighting rate varied with either territory size or sex. In both instances, however, the retention of territory size as a key variable in the best-fit model underscores the importance of this factor on survival, with birds on highest quality territories having the highest survivorship. Among Bar-throated Apalises, territory size correlates inversely with both prey density and vegetation structural diversity (Chapter 2), factors that have been linked to individual survival (Oro and Furness 2002, Davis *et al.* 2005, Maguire 2006). For example, vegetation structural complexity may help confound predators' search images which in turn increase the chances of an individual's survival (Martin 1988, Nias and Ford 1992, Candolin and Voigt 2001, Maguire 2006). On the other hand, in Bar-throated Apalises territory size is also inversely correlated with a potential age indicator (breast-band size – Chapter

3): this could confound the effects of territory size/quality on survival because it raises the possibility of age-specific effects on survival, which may operate independently of environmental effects. For example (and intuitively unexpectedly) among Checker-throated Antwrens *Myrmotherula fulviventris*, young birds (1 year old) have higher survivorship (85 – 90%) than older birds (50 – 76%) (Greenberg and Gradwohl 1997). Conversely, among Willow Tits *Parus montanus* survival of adults (96.3 – 99.2%) is higher than that of yearlings (71.4 – 89.3% - Lahti *et al.* 1998). Based on a 31-year study of individually marked Wood Thrushes *Hylocichla mustelina*, survival is highest for middle-aged birds (4 – 6 years old), decreasing later in life (Brown and Roth 2009).

The best-fit models in this study indicated that year-to-year survival was independent of sex (as reported for juvenile Western Slaty-Antshrikes *Thamnophilus atrinucha* – Tarwater *et al.* 2011) , but that sex did influence recapture/resighting rates. Sex-independent survivorship suggests that both males and females may occupy very similar niches (e.g. feeding on same prey type and size, relying on same habitat attributes for cover) and thus experience very similar environmental constraints. This is supported by the fact that year-to-year survivorship of both sexes followed similar trajectories. Between 2007 and 2008, survivorship of both sexes was lower (males 0.821; females 0.814) than between 2008 and 2009 (males 0.896; females 0.880). Vegetation structure remained stable between years with no modification by fire or human intervention, suggesting that inter-annual differences in survivorship were driven by either variation in prey availability and/or variation in predator densities and that this variability affected both sexes in the same way. However, this study could not rule out the potentially confounding effect of differential dispersal on survival estimates, whereby birds assumed to be dead had dispersed beyond the limits of the

study area, resulting in an under-estimate of survivorship (Powell *et al.* 2000, Cilimburg *et al.* 2002). For example, a study of Yellow Warblers *Dendroica petechia* that could account for effect of dispersal on survival probabilities reported an increase of 6.5 – 22.9% in survival estimates when dispersal was taken into account (Cilimburg *et al.* 2002). The average annual survival rates of apalises estimated in this study (0.85, range 0.81 – 0.90) are high. If these are indeed under-estimates of survivorship because of a failure to be able to factor in the effect of dispersal, then survivorship of these apalises would be extraordinarily high on a global scale. In Europe, 31 passerine species have an average survivorship of 0.52 (0.32-0.71). Equivalent values for 30 North American passerines are 0.53 (0.29-0.63) and for 17 Trinidadian passerines are 0.65 (0.45-0.85 – Johnston *et al.* 1997). Nine Puerto Rican species have an average annual survivorship of 0.68 (0.51-0.79 – Faaborg & Arend 1995), and equivalent values for 25 Panamanian species are 0.56 (0.33-0.73 – Karr *et al.* 1990). These comparisons strongly suggest that dispersal beyond the boundaries of the study area by Bar-throated Apalis occurs very rarely. Of the 112 species documented in the above studies, only the 8.4 g White-flanked Antwren *Myrmotherula axillaris* of Trinidad has an equivalently high survivorship (0.845 – Johnston *et al.* 1997).

Conclusion

Mate fidelity, territory fidelity and adult survival in the Bar-throated Apalis, especially in relation to territory quality, have not previously been quantified. Both mate and territory fidelity were high, suggestive of high population numbers translating into density-dependent effects, further evidenced by the presence of floaters in the study area. Territory replacements, although infrequent, corresponded

to the predictions of an Ideal Despotic Distribution whereby it is high-quality individuals that gain access to the most food-rich territories. This is further supported by the fact that when territory replacements did occur, the new occupants were of higher quality than their predecessors. In this species, it also appears that high survivorship among territory holders (among the highest recorded for any passerine anywhere in the world) is a direct fitness benefit stemming from occupancy of a small, high-quality territory.

REFERENCES

- Anu, A., Sabu, T.K. and Vineesh, P.J. (2009) Seasonality of litter insects and relationship with rainfall in a wet evergreen forest in South Western Ghats. *Journal of Insect Science*, **9**, 1–10.
- Bried, J. and Jouventin, P. (2002) Site and mate choice in seabirds: an evolutionary approach. In *Biology of Marine Birds* (Eds Schreiber, E.A. and Burger, J.), pp. 263–305. CRC Press, Boca Raton, Florida.
- Bried, J., Dominique, P. and Jouventin, P. (2003) Mate fidelity in monogamous birds: a re-examination of the Procellariiformes. *Animal Behavior*, **65**, 235–246.
- Brown, W.P. and Roth, R.R. (2009) Age-specific reproduction and survival of individually marked Wood Thrushes, *Hylocichla mustelina*. *Ecology*, **90**, 218–229.
- Boinski, S. and Fowler, N.L. (1989) Seasonal patterns in tropical lowland forest. *Biotropica*, **21**, 223–233.
- Candolin, U. and Voigt, H.R. (2001) Correlation between size and territory quality: consequences of male competition or predation susceptibility. *Oikos*, **95**, 225–230.
- Caughley, G. (1994) Directions in conservation biology. *Journal of Animal Ecology*, **63**, 215–244.
- Cézilly, F., Dubois, F. and Pagel, M. (2000) Is mate fidelity related to site fidelity? A comparative analysis in Ciconiiformes. *Animal Behavior*, **59**, 1143–1153.
- Cézilly, F. and Johnson, A.R. (1995) Re-mating between and within breeding seasons in the Greater Flamingo *Phoenicopterus ruber*. *Ibis*, **137**, 543–546.
- Chapell, M.A., Zuk, M., Johnson, T.S. and Kwan T.H. (1997) Mate choice and aerobic capacity in Red Junglefowl. *Behaviour*, **134**, 511–529.

- Choudhury, S. (1995) Divorce in birds: a review of the hypotheses. *Animal Behavior*, **50**, 413–429.
- Choudhury, S. and Black, J.M. (1994) Barnacle geese preferentially pair with familiar associates from early life. *Animal Behavior*, **48**, 81–88.
- Cilimburg, A.B., Lindberg, M.S., Tewksbury, J.J. and Hejl, S.J. (2002) Effects of dispersal on survival probability of adult Yellow Warblers *Dendroica petechia*. *Auk*, **119**, 778–789.
- Cooke, F., Bousfield, M.A. and Sadura, A. (1981) Mate change and reproductive success in the Lesser Snow Goose. *Condor*, **83**, 322–327.
- Coulson, J.C. (1966) The influence of the pair-bond and age on the breeding biology of the Kittiwake Gull *Rissa tridactyla*. *Journal of Animal Ecology*, **35**, 269–279.
- Coulson, J.C. and Thomas, C.S. (1983) Mate choice in the Kittiwake Gull. Mate choice (Ed Bateson, P.), pp 361–376. Cambridge University Press, Cambridge.
- Croxall, J.P. and Davis, L.S. (1999) Penguins: paradoxes and patterns. *Marine Ornithology*, **27**, 1–27.
- Davis, S.E., Nager, R.G. and Furness, R.W. (2005) Food availability affects adult survival as well as breeding success of Parasitic Jaegers. *Ecology*, **86**, 1047–1056.
- Dawkins, R. and Krebs, J.R. (1978) Animal signals: information or manipulation? In Behavioural ecology. An Evolutionary Approach (Eds Krebs, J.R. and Davies, N.B.). Blackwell, Oxford. Pp. 282–315.
- Dhondt, A.A. and Adriaensen, F. (1994) Causes and effects of divorce in the Blue Tit *Parus caeruleus*. *Journal of Animal Ecology*, **63**, 979–987.
- Diamond, J.M. (1987) A Darwinian theory of divorce. *Nature*, **329**, 765–766.
- Dubois, F. and Cézilly, F. (2002) Breeding success and mate retention in birds: a meta-analysis. *Behavioral Ecology and Sociobiology*, **52**, 357–364.
- Dunn, P.O., Whittingham, L.A., Freeman-Gallant, C.R. and DeCoste, J. (2008) Geographic variation in the function of ornaments in the Common Yellowthroat *Geothlypis trichas*. *Journal of Avian Biology*, **39**, 66–72.
- Ens, B.J., Safriel, U.N. and Harris, M.P. (1993) Divorce in the long-lived and monogamous Oystercatcher, *Haematopus ostralegus*: incompatibility or choosing the better option? *Animal Behavior*, **45**, 1199–1217.
- Ens, B.J., Choudhury, S. and Black, J.M. (1996) Mate fidelity and divorce in monogamous birds. Partnerships in birds: In *The Study of Monogamy* (Ed J.M. Black), pp 344–401. Oxford University Press, Oxford.

- Faaborg, J. And Arendt, W. (1995) Survival rates of Puerto Rican birds: are islands really that different? *Auk*, **112**, 503-507.
- Forslund, P. and Larsson, K. (1992) The effect of mate change and new partner's age on reproductive success in the Barnacle Goose, *Branta leucopsis*. *Behavioral Ecology*, **2**, 116–122.
- Fretwell, S. D. and Lucas, H. L. (1970) On territorial behaviour and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheoretica*, **19**, 16–36.
- Gill, S.A. and Stutchbury, B.J.M. (2006) Long-term mate and territory fidelity in Neotropical Buff-breasted Wren *Thryothorus leucotis*. *Behavioral Ecology and Sociobiology*, **61**, 245–253.
- Greenberg, R. and Gradwohl, J. (1997) Territoriality, adult survival and dispersal in the Checker-throated Antwren in Panama. *Journal of Avian Biology*, **28**, 103–110.
- Handel, C.M. and Gill Jr., R.E. (2000) Mate fidelity and breeding site tenacity in a monogamous sandpiper, the Black Turnstone. *Animal Behavior*, **60**, 471–481.
- Harris, M.P. (1979) Population dynamics of the flightless Cormorant *Nannopterum harrisi*. *Ibis*, **121**, 135–146.
- Harris, M.P., Safriel, U.N., Brooke, M., de, L. and Britton, C.K. (1987) The pair bond and divorce among Oystercatchers *Haematopus ostralegus* on Skokholm Island, Wales. *Ibis*, **129**, 45–57.
- Hockey, P.A.R., Wanless, R.M. and von Brandis, R. (2011) Demographic resilience of territorial island birds to extinction: the flightless Aldabra Rail (*Dryolimnas [cuvieri] aldabranus*) as an example. *Ostrich* **82**, 1-9.
- Johnston, J.P., Peach, W.T., Gregory, R.D. and White, S.A. (1997) Survival rates of tropical and temperate passerines: a Trinidadian perspective. *American Naturalist* **150**, 771-789.
- Jones, I.L. and Montgomerie, R. (1991) Mating and remating of Least Auklets *Aethia pusilla* relative to ornamental traits. *Behavioral Ecology*, **2**, 249–257.
- Jones, A. G., Arguello, J. R. and Arnold, S. J. (2004) Molecular parentage analysis in experimental newt populations: the response of mating system measures to variation in the operational sex ratio. *American Naturalist*, **164**, 444–456.
- Jones, A.G., Rosenqvist, G., Berglund, A. and Avise, J.C. (2005) The measurement of sexual selection using Bateman's principles: an experimental test in the sex-role-reversed Pipefish *Syngnathus typhle*. *Integrative Comparative Biology*, **45**, 874–884.
- Karr, J.R., Nichols, J.D., Klimkiewicz, M.K. and Brawn, J.D. 1990. Survival rates of birds of tropical and temperate forests: will the dogma survive? *American Naturalist* **136**, 277-291.

- Lahti, K., Orell, M., Rytönen, S. and Koivula, K. (1998) Time and food dependence in Willow Tit winter survival. *Ecology*, **78**, 2904–2916.
- Lifjeld, J. T. and Slagsvold, T. (1988) Mate fidelity of renesting Pied Flycatchers *Ficedula hypoleuca* in relation to characteristics of the pair mates. *Behavioral Ecology and Sociobiology*, **22**, 117–123.
- Maguire, G.S. (2006) Territory quality, survival and reproductive success in Southern Emu-Wrens *Stipiturus malachurus*. *Journal of Avian Biology*, **37**, 579–593.
- Maness, T.J. and Anderson, D.J. (2007) Serial monogamy and sex ratio bias in Nazca Boobies. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 2047–2054.
- Martin, T.E. (1988) Area and habitat effects on structure of forest bird assemblages: is nest predation an underlying influence? *Ecology*, **69**, 74–84.
- McGraw, K.J., Mackillop, E.A., Dale, J. and Hauber, M.E. (2002) Different colors reveal different information: how nutritional stress affects the expression of melanin- and structurally-based ornamental plumage. *Journal of Experimental Biology*, **205**, 3747–3755.
- McGraw, K.J., BeeBee, M.D., Hill, G.E. and Parker, R.S. (2003) Lutein-based plumage coloration in songbirds is a consequence of selective pigment incorporation into feathers. *Comparative Biochemistry and Physiology B*, **135**, 689–696.
- Mills, J.A. (1973) The influence of age and pair bond on the breeding biology of the Red-billed Gull *Larus novaehollandiae scopulinus*. *Journal of Animal Ecology*, **42**, 147–162.
- Mills, S.C., Grapputo, A., Koskela, E. and Mappes, T. (2007) Quantitative measure of sexual selection with respect to the operational sex ratio: a comparison of selection indices. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 143–150.
- Murphy, M.T. (1996) Survivorship, breeding dispersal and mate fidelity in Eastern Kingbirds. *Condor*, **98**, 82–92.
- Nakagawa, S. and Burke, T. (2008) The mask of seniority? A neglected age indicator in House Sparrows *Passer domesticus*. *Journal of Avian Biology*, **39**, 222–225.
- Nakamura, M. and Kubota, H. (1998) Food supply in early spring and the stability of pair bonds in the Varied Tit *Parus varius*. *Journal of Avian Biology*, **29**, 201–205.
- Newton, I. and Marquiss, M. (1982) Fidelity to breeding area and mate in Sparrowhawks *Accipiter nisus*. *Journal of Animal Ecology*, **51**, 327–341.
- Nias, R.C. and Ford, H.A. (1992) The influence of group size and habitat on reproductive success in the Superb Fairy-Wren *Malurus cyaneus*. *Emu*, **92**, 238–243.

- Nisbet, I.C.T. and Dann, P. (2009) Reproductive performance of Little Penguins *Eudyptula minor* in relation to year, age, pair-bond duration, breeding date and individual quality. *Journal of Avian Biology*, **40**, 296–308.
- Ollason, J.C. and Dunnet, G.M. (1978) Age, experience and factors affecting the breeding success of the Fulmar *Fulmarus glacialis* in Orkney. *Journal of Animal Ecology*, **47**, 961–976.
- Orell, M., Rytönen, S. and Koivula, K. (1994) Causes of divorce in the monogamous Willow Tit, *Parus montanus*, and consequences for reproductive success. *Animal Behaviour*, **48**, 1143–1154.
- Oro, D. and Furness, R.W. (2002) Influences of food availability and predation on survival of Kittiwakes. *Ecology*, **83**, 2516–2528.
- Owen, M., Black, J. M. and Liber, H. (1988) Pair bond duration and timing of its formation in Barnacle Geese *Branta leucopsis*. Waterfowl winter ecology (Ed M.W. Weller), pp. 23–38. University of Minnesota Press, Minnesota.
- Part, T. (1995) The importance of local familiarity and search costs for age- and sex-biased philopatry in the Collared Flycatcher. *Animal Behavior*, **49**, 1029–1038.
- Pampus, M., Schmidt, K. and Wiltschko, W. (2005) Pair bond and breeding success in Blue Tits *Parus caeruleus* and Great Tits *Parus major*. *Ibis*, **147**, 92–108.
- Powell, L.A., Conroy, M.J., Hines, J.E., Nichols, J.D. and Kremenetz, D.G. (2000) Simultaneous use of mark–recapture and radiotelemetry to estimate survival, movement, and capture rates. *Journal of Wildlife Management*, **64**, 302–313.
- Pulliam, H.R. (1988) Sources, sinks and population regulation. *American Naturalist*, **132**, 652–661.
- Pyle, P., Sydeman, W.J. and Hester, M. (2001) Effects of age, breeding experience, mate fidelity and site fidelity on breeding performance in a declining population of Cassin's Auklets. *Journal of Animal Ecology*, **70**, 1088–1097.
- Real, L. (1990) Search theory and mate choice. I. Models of single-sex discrimination. *American Naturalist*, **136**, 376–405.
- Richards, L.A. and Windsor, D.M. (2007) Seasonal variation of arthropod abundance in gaps and the understorey of a lowland moist forest in Panama. *Journal of Tropical Biology*, **23**, 169–176.
- Richdale, L.E. and Warham, J. (1973) Survival, pair-bond retention and nest-site tenacity in Buller's Mollymawk. *Ibis*, **115**, 257–263.
- Rohwer, S. (1975) The social significance of avian winter plumage variability. *Evolution*, **29**, 593–610.
- Rohwer, S. (1982) The evolution of reliable and unreliable badges of fighting ability. *American Zoologist*, **22**, 531–546.

- Rowley, I. (1983) Re-mating in birds. In *Mate Choice* (Ed. P. Bateson), pp. 331–360. Cambridge University Press, Cambridge.
- Salamolard, M., Butet, A., Leroux, A. and Bretagnolle, V. (2000) Responses of an avian predator to variations in prey density at a temperate latitude. *Ecology*, **81**, 2428–2441.
- Sedinger, J.S., Chelgren, N.D., Ward, D.H. and Lindberg, M.S. (2008) Fidelity and breeding probability related to population density and individual quality in Black Brent Geese *Branta bernicla nigrans*. *Journal of Animal Ecology*, **77**, 702–712.
- Senar, J.C., Camerino, M., Copete, J.L. and Metcalfe, N.B. (1993) Variation in black bib of the Eurasian Siskin *Carduelis spinus* and its role as a reliable badge of dominance. *Auk*, **110**, 924–927.
- Setiawan, A.N., Massaro, M., Darby, J.T. and Davis, L.S. (2005) Mate and territory retention in the Yellow-eyed Penguin. *Condor*, **107**, 703–709.
- Switzer, P.V. (1997) Factors affecting site fidelity in a territorial animal *Perithemis tenera*. *Animal Behaviour*, **53**, 865–877.
- Taborsky, B. and Taborsky, M. (1999) The mating system and stability of pairs in kiwi *Apteryx* spp. *Journal of Avian Biology*, **30**, 143–151.
- Tarwater, C.E., Ricklefs, R.E., Maddox, J.D. and Brawn, J.D. (2011) Pre-reproductive survival in a tropical bird and its implications for avian life histories. *Ecology*, **92**, 1271–1281.
- Wickler, W. and Seibt, U. (1983) Monogamy: an ambiguous concept. In *Mate Choice* (Ed P. Bateson), pp. 33–50. Cambridge University Press, Cambridge.
- Williams, T. D. and Rodwell, S. (1992) Annual variation in return rate, mate and nest-site fidelity in breeding Gentoo and Macaroni Penguins. *Condor*, **94**, 636–645.
- Wolda, H. (1988) Insect seasonality: why? *Annual Review of Ecology and Systematics*, **19**, 1–18.

CHAPTER SIX

SYNTHESIS

The underlying principles of territoriality propose that high population density precipitates competition for resources. This in turn compels individuals to defend areas (territories) that give them exclusive access to critical resource(s), enabling them to maximise their reproductive success and/or chances of survival (Fretwell and Lucas 1970). The theory suggests that only high-quality individuals succeed in occupying areas rich in resources that are limiting at the landscape level. Subsequent studies have demonstrated that the areas defended vary in size between individual territory holders (Nice 1941, Wortman-Wunder 1997, Adams 2001, Marshall and Cooper 2004). The factors that determine this variation have also been shown to vary widely from one species to another and may vary geographically within species (Stenger, 1958, MacLean and Seastedt 1979, Smith and Shugart 1987, Turpie 1995, Finck 1990, Marshall and Cooper 2004). This implies that any unifying theory will ultimately be based on species-specific studies of territoriality, its determinants and its consequences. With this in mind, the main aim of this study, focussing on socially monogamous Bar-throated Apalises, was to determine the ecological factors that influence variation in territory size and their consequences for reproduction (effort and reward), pair stability and survival. Linked to this, the study also investigated the signalling properties of the species' black breast-band (a prominent 'badge' emblazoned across the white underparts) in relation to male and territory quality.

Specifically, the study had the following objectives:

1. To investigate variations in breeding territory size in Bar-throated Apalises and the roles that vegetation and food density play in influencing this variability.

2. To determine the consequences of variation in territory size/quality for:
 - a. Key male functions such as mate and nestling provisioning rate and the effort required to achieve these.
 - b. Female reproductive investment (i.e. initiation of breeding, clutch size and mass, incubation attentiveness, rate of nestling provisioning and breeding productivity).
 - c. Pair stability and adult survival.
3. To determine whether badge size is an 'honest' signal of territory quality and/or male quality and fitness.

Variation in breeding territory size and quality

Bar-throated Apalis territories varied considerably in size within the study site. Most of this variation was explained by food density, which was inversely correlated with territory size. Food density was also a secondary correlate of vegetation structure, with territories rich in food also containing taller shrubs and greater vegetation cover. It has been hypothesised that territory size is determined by food availability (the Food Value Hypothesis – Stenger 1958, Gill and Wolf 1975), specific habitat features that are linked to (and thus indicate) food (the Structural Cues Hypothesis – Marshall and Cooper 2004), intruder pressure (the Intra-specific Competition Hypothesis – Hinde 1956) or a combination of several factors (Marshall and Cooper 2004). These are discussed in detail in Chapters 1 and 2. This study did not seek to make comparisons between these hypotheses. Rather, the approach to quantifying food density followed the premises of the Structural Cue Hypothesis (Marshall and Cooper 2004) and the approach of Komdeur *et al.* (1997). The results support the notion that a quantification of food density based on specific habitat features (that themselves

determine food density) is a) possible and b) can explain variations in territory size. Positive correlations between food density and vegetation structure adequately encapsulate most of the factors that are synonymous with the concept of territory quality (*sensu* MacLean and Seastedt 1979, Smith and Shugart 1987, Turpie 1995, Sergio and Newton 2003, Marshall and Cooper 2004). High food density assures nutrient provision to both territorial adults and their offspring (Schowalter and Crossley, 1983, Hagar *et al.* 2007, Wilkin *et al.* 2009), while the associated vegetation cover enhances protection against predators (Bowman and Harris 1980, Martin and Roper 1988, Kolada *et al.* 2009). Clearly, both of these benefits have the potential to translate into differences in individual fitness.

Breast-band size and male quality

One of the key assumptions in Fretwell and Lucas's (1970) model of territoriality is that high-quality territories are occupied by high-quality individuals. This study strongly supports the validity of this assumption. Breast-band (badge) size is positively correlated with male body condition and males with large breast bands occupy small, food-rich territories. This pattern persisted even when territory ownership changed. Further investigation of this index of male quality identified an age signal associated with breast-band size, with badge size increasing with age irrespective of territory quality. Male ornaments have been previously shown to signal multiple components of male quality, including dominance/fighting ability (Møller 1987, McGraw *et al.* 2002, Nakagawa *et al.* 2007), body condition (Zuk *et al.* 1990, Chapple *et al.* 1997) and age (Otter and Ratcliffe 1999, Nakagawa and Burke 2008). The pattern of badge growth observed here showed similarities to the bib growth pattern of Black-capped Chickadees *Poecile atricapillus* where bib raggedness

increases with age (Otter and Ratcliffe 1999). However, reasons for the age-related changes in badge sizes of Black-capped Chickadees and Bar-throated Apalises may be subtly different. Otter and Ratcliffe (1999) speculatively linked changes in bib areas of chickadees to environmental conditions (food) at the time of moult. Among apalises, however, it was possible to account for and exclude the potential influence of environmental conditions (territory quality/food density) experienced by individuals thereby allowing conclusions to be based solely on age. The honesty of the breast band in signalling individual body condition in males, and the lack of such a relationship in females, suggests that its primary role relates to male-male interactions. Melanin-based ornaments have been linked to male aggression (Rohwer 1975, 1982, Senar 1993, McGraw *et al.* 2002, Dunn *et al.* 2008) and, theoretically, such ornamentation acts as a status signal which could save individuals energetically costly fights because its honesty unambiguously predicts the outcome of a fight (Brown 1964, Rohwer 1975, Lyon and Montgomerie 1985, Dunn *et al.* 2004). Territorial interactions mostly involve males perching on tall vegetation at a territory boundary and calling aggressively at each other. This form of ritualised aggression was almost always sufficient to secure an outcome: physical fights involving territorial apalises were very rare.

Territory quality, individual quality and parental reproductive performance

Where access to resources is spatially restricted due to competitive interactions and territoriality, this is predicted to set the stage for constraints on reproductive performance and hence fitness (Fretwell and Lucas 1970, Sodhi 1993, Canestrari *et al.* 2008). Among apalises, the reproductive performance and fitness of individuals does indeed vary as a function of territory quality. For example, the duration and

distance of foraging trips made by males feeding incubating females and chicks are shorter on high-quality (small) than on low-quality (large) territories. Similarly, provisioning rates on high-quality territories are higher. Demonstration of these differences in food delivery rates as a function of prey density is not new (Andersson 1981, Sodhi 1993, Naef-Daenzer and Keller 1999). However, independently of the effects of territory quality, individual experience can also influence the foraging efficiency of males (e.g. Newton and Marquiss 1982, Perrins and McCleery 1985, Myrberget 1986, Wilson 1992, Otter and Ratcliffe 1999, Keyser and Hill 2000, Nakagawa and Burke 2008). Among apalises, male breast-band size is not only positively correlated with body condition, but also increases with age. This implies that the high-quality males occupying high-quality territories are among the older males in the population: influences of experience on foraging efficiency thus cannot be ruled out. However, if body condition, age and experience are all positively correlated with breast-band size, then regardless of their *relative* contributions to individual performance, breast-band size remains an honest signal of male quality.

This study also provided evidence that females respond positively to the breast-band signal. High-quality males on high-quality territories pair with high-quality females. This high female quality reflects in early nest initiation, laying of heavier eggs, enhanced nestling provisioning rates and relatively high breeding success. In some instances, female effort is a direct response to male effort. During incubation, for example, female nest attentiveness is positively correlated with male provisioning rate during incubation feeding. This decreases female energy expenditure and increases the degree of protection she can provide for the clutch while at the same time shortening the incubation period. Similar adjustments in female reproductive effort have been reported for Snow Buntings *Plectrophenax nivalis* (Lyon and

Montmerie 1985) and Northern Cardinals *Cardinalis cardinalis* (Jawor and Breitwisch 2006). Once eggs have hatched, the combined provisioning efforts of both male and female parents are highest on high-quality territories. In combination with the influence of hatching date (early hatched nests are the most successful) this has a positive influence on offspring fitness: chicks in high-quality territories grow the fastest, minimising the duration of the risk to which they are exposed while confined to the nest. Such constraints imposed on offspring by parental effort are typical of altricial birds in which nestlings rely on parental effort to meet all their nutritional needs (Starck and Ricklefs 1998, Naef-Daenzer and Keller 1999). Thus, ultimately, birds on high-quality territories on average achieve greater direct fitness benefits through number of fledged young per annum than do birds on larger, low-quality territories: none of the territories $> 7500 \text{ m}^2$ ever fledged any young (Chapter 4).

Pair stability, territory fidelity and adult survival

Territory quality is highly variable between individuals and appears highly predictable (due to positive correlations between food density and vegetation structure). If territory quality is easy to assess, it is predicted that territory usurpation should occur regularly, with individuals on poorer territories deserting to contest for higher quality positions (Fretwell and Lucas 1970, Ens *et al.* 1993, Wauters *et al.* 1995). Contrary to this prediction, however, Bar-throated Apalises exhibit high territory fidelity, implying strong stability in the system. This is likely explained by a combination of a) high survivorship (leading to 'natural' vacancies on territories occurring infrequently - Coulson 1966, Mills 1973, Richdale and Warham 1973, Ollason and Dunnet 1978); territory size being adjusted to food density; slow vegetation turnover (leading to inter-annual food predictability and stable territory boundaries); and a male

‘dominance hierarchy’ that is established by signalling rather than by overt aggression. The latter in particular (which advertises a combination of age and body condition) should make it very difficult for a young/poor-condition bird to ‘cheat’ the system and acquire a disproportionately food-rich territory.

Furthermore, because individuals on high-quality territories enjoy the greatest fitness benefits, not least because their mates are also of high quality (Chapter 4) there is little incentive for these birds to abandon their high-quality territories (Fretwell and Lucas 1970, Wauters *et al* 1995). The spatial stability of territories between years may also be influenced by a) the fact that the study area was saturated with territories, themselves adjusted to food density, and b) the presence of floaters in the population (indicative of a population at high density - Fretwell and Lucas 1970, Pulliam 1988, Caughley 1994) who would have acted as competitors both for birds attempting to switch territories and for the vacant positions left behind by such dispersers. This set of conditions makes territory abandonment (in an attempt to improve status - the Better Option Hypothesis – Ens *et al.* 1993) a risky prospect, presumably with a measurable probability of a previous territory owner becoming a floater. There is evidence for assortative mating among apalises dependent on body condition. High-quality females are paired with high-quality males, although female quality is not signalled by the breast band. Theoretically, this sets the stage for female dishonesty whereby low-quality females could attempt to pair with high-quality males. The fact that mate fidelity is so high suggests that this is not happening, possibly (but untestably) as a result of mate familiarity (Coulson 1966, Williams and Rodwell 1992, Bried and Jouventin 2002, Setiawan *et al.* 2005). The benefits of such mate familiarity are presumably greatest on high-quality territories where both pair members tend to be of high quality and making high reproductive investment (chapter 4). Separation of

such pairs may only occur through non-adaptive means (e.g. through accidental separation of death – Owen *et al.* 1988, Forsuland and Larsson 1992).

In further support of the mate-fidelity argument for high-quality territories, the best model explaining individual survival among Bar-throated Apalises retained only the effect of territory size as a significant predictor, with survival being highest on high-quality territories, as reported for several other species (Greenberg and Gradwohl 1997, Lahti *et al.* 1998, Oro and Furness 2002, Davis *et al.* 2005, Maguire 2006, Brown and Roth 2009).

Summary

Food density is a major determinant of territory quality in the Bar-throated Apalis. Food density in turn correlated with both vegetation structure and floristics. High-quality males occupied high-quality territories and were paired with high-quality females. Differences in territory and individual quality influenced the reproductive performance and fitness of individuals, ranging from the capacity of parents to meet nutritional demands, to nestling growth rates and the number of fledged young per annum. Territory quality, coupled with the influences of other factors such as individual quality and population density, also appear to influence levels of mate fidelity, territory fidelity and adult survival. There is thus substantial asymmetry in the fitness of individuals within the population. This fitness asymmetry is not, however, maintained through overt, territorial aggression. Rather, male breast-band size was shown to be an honest signal of individual quality, age and territory quality. The honesty of this signal is interpreted as the underlying factor accounting for both mate and territory stability in the population.

Limitations of the study

This study set out to establish the major factors that may determine territory and individual quality in a resident African passerine and determine how variation in these qualities affects reproductive performance and fitness. The study was able to show that the size of the breast band of male apalises was an honest signal of quality to which females respond in terms of both mate choice and reproductive investment: male breast-band size correlates positively with male quality, male age and territory quality. What this study could not distinguish however is which, or which combination of these attributes is the one to which females are responding the most strongly. Obviously, this requires an experimental approach based on manipulation of male breast-band sizes. The size of the apalis population at Koeberg precluded such an experiment, which would require independent and combined manipulation of both breast-band sizes and territory quality (age cannot be manipulated), while still allowing adequate controls for all treatments. This would require a *very* much larger population of birds than was available at Koeberg (as well as requiring life-history data for all experimental pairs prior to manipulation). Alternatively, it would require several different study sites, each subjected to different experimental treatments (but with the same backdrop of unmanipulated life-history data). Before such an experiment is contemplated, it may be more fruitful to carry out field studies of other African passerines that may be using comparable signalling badges to explore the degree of fitness asymmetry that they exhibit relative to local environmental variability. Potential candidates for such studies include the shrubland-dwelling Black-chested Prinia *Prinia flavicans* and Rufous-eared Warbler *Malcorus pectoralis*.

REFERENCES

- Adams E.S. (2001) Approaches to the study of territory size and shape. *Annual Review of Ecology and Systematics*, **32**, 277–303.
- Andersson, M. (1981) Central place foraging in the Whinchat, *Saxicola rubetra*. *Ecology*, **62**, 538–544.
- Bowman, G.B. and Harris, L.D. (1980) Effect of spatial heterogeneity on ground-nest depredation. *Journal of Wildlife Management*, **44**, 806–813.
- Bried, J. and Jouventin, P. (2002) Site and mate choice in seabirds: an evolutionary approach. *Biology of marine birds* (Eds Schreiber, E.A. and Burger, J.), pp. 263–305. CRC Press, Boca Raton, Florida.
- Brown, J.L. (1964) The evolution of diversity in avian territorial systems. *Wilson Bulletin*, **76**, 160–169.
- Brown, W.P. and Roth, R.R. (2009) Age-specific reproduction and survival of individually marked Wood Thrushes, *Hylocichla mustelina*. *Ecology*, **90**, 218–229.
- Canestrari, D., Chiarati, E., Marcos, J.M., Ekman, J. And Baglione, V. (2008) Helpers but not breeders adjust provisioning effort to year-round territory resource availability in carrion crows. *Animal Behavior*, **76**, 943–949.
- Caughley, G. (1994) Directions in conservation biology. *Journal of Animal Ecology*, **63**, 215–244.
- Chapple, I.L.C. (1997) Reactive oxygen species and antioxidants in inflammatory diseases. *Journal of Clinical Periodontology*, **24**, 287–296.
- Coulson, J.C. (1966) The influence of the pair-bond and age on the breeding biology of the Kittiwake Gull *Rissa trydactyla*. *Journal of Animal Ecology*, **35**, 269–279.
- Davis, S.E., Nager, R.G. and Furness, R.W. (2005) Food availability affects adult survival as well as breeding success of Parasitic Jaegers. *Ecology*, **86**, 1047–1056.
- Dunn, M., Copelston, M. and Workman, L. (2004) Trade-offs and seasonal variation in territorial defence and predator evasion in the European Robin *Erithacus rubecula*. *Ibis*, **146**, 77–84.
- Dunn, P.O., Whittingham, L.A., Freeman-Gallant, C.R. and DeCoste, J. (2008) Geographic variation in the function of ornaments in the Common Yellowthroat *Geothlypis trichas*. *Journal of Avian Biology*, **39**, 66–72.
- Ens, B.J., Safriel, U.N. and Harris, M.P. (1993) Divorce in the long-lived and monogamous Oystercatcher *Haematopus ostralegus*: incompatibility or choosing the better option? *Animal Behavior*, **45**, 1199–1217.

- Finck, P. (1990) Seasonal variation of territory size with the Little Owl *Athene noctua*. *Oecologia*, **83**, 68–75.
- Forslund, P. and Larsson, K. (1992) The effect of mate change and new partner's age on reproductive success in the Barnacle Goose *Branta leucopsis*. *Behavioral Ecology*, **2**, 116–122.
- Fretwell, S.D. and Lucas, H.J., Jr. (1970) On territorial behaviour and other factors influencing habitat distribution in birds. *Acta biotheoretica*, **19**, 16–36.
- Gill, F.B. and Wolf, L.L. (1975) Economics of feeding territoriality in the golden-winged sunbird. *Ecology*, **56**, 333–345.
- Greenberg, R. and Gradwohl, J. (1997) Territoriality, adult survival and dispersal in the Checker-throated Antwren in Panama. *Journal of Avian Biology*, **28**, 103–110.
- Hagar, J.C., Dugger, K.M. and Starkey, E.E. (2007) Arthropod prey of Wilson's Warblers in the understory of douglas-fir forests. *The Wilson Journal of Ornithology*, **119**, 533–546.
- Hinde, R.A. (1956) The biological significance of the territories of birds. *Ibis*, **98**, 340–369.
- Jawor, J.M. and Breitwisch, R. (2006) Is mate provisioning predicted by ornamentation? A test with Northern Cardinals *Cardinalis cardinalis*. *Ethology*, **112**, 888–895.
- Keyser, A.J. and Hill, G.E. (2000) Structurally based plumage coloration is an honest signal of quality in male Blue Grosbeaks. *Behavioral Ecology*, **11**, 202–209.
- Kolada, E.J., Casazza, M.L. and Sedinger, J.S. (2009) Ecological factors influencing nest survival of Greater Sage-Grouse in Mono County, California. *Journal of Wildlife Management*, **73**, 1341–1347.
- Komdeur, J., Daan, S., Tinbergen, J. and Mateman, C. (1997) Extreme adaptive modification in sex ratio of the Seychelles Warbler's eggs. *Nature*, **385**, 522–525.
- Lahti, K., Orell, M., Rytönen, S. and Koivula, K. (1998) Time and food dependence in Willow Tit winter survival. *Ecology*, **78**, 2904–2916.
- Lyon, B.E. and Montgomerie, R.D. (1985) Incubation feeding in Snow Buntings: female manipulation or indirect male parental care? *Behavioral Ecology and Sociobiology*, **17**, 279–284.
- McGraw K.J, Mackillop E.A., Dale J. and Hauber M.E. (2002) Different colors reveal different information: how nutritional stress affects the expression of melanin- and structurally-based ornamental plumage. *Journal of Experimental Biology*, **205**, 3747–3755.

- MacLean, S.F. and Seastedt, T.R. (1979) Avian territoriality: sufficient resources or interference competition. *American Naturalist*, **114**, 308–312.
- Maguire, G.S. (2006) Territory quality, survival and reproductive success in Southern Emu Wrens *Stipiturus malachurus*. *Journal of Avian Biology*, **37**, 579–593.
- Marshall, M. R. and Cooper, R.J. (2004) Territory size of a migratory songbird in response to caterpillar density and foliage structure. *Ecology*, **85**, 432–445.
- Martin, T.E. and Roper, J.J. (1988) Nest predation and nest-site selection of a western population of hermit thrush. *Condor*, **90**, 51–57.
- Mills, J.A. (1973) The influence of age and pair bond on the breeding biology of the Red-billed Gull *Larus novaehollandiae scopulinus*. *Journal of Animal Ecology*, **42**, 147–162.
- Møller, A.P. (1987). Variation in badge size in male house sparrows *Passer domesticus*: evidence for status signalling. *Animal Behaviour*, **35**: 1637 – 1644.
- Myrberget, S. (1986) Age and breeding of Willow Grouse *Lagopus lagopus*. *Ibis*, **128**, 282–285.
- Naef-Daenzer, B. and Keller, L.K. (1999) The foraging performance of Great and Blue Tits *Parus major* and *P. caeruleus* in relation to caterpillar development, and its consequences for nestling growth and fledging weight. *Journal of Animal Ecology*, **68**, 708–718.
- Nakagawa, S. and Burke, T. (2008) The mask of seniority? A neglected age indicator in House Sparrows *Passer domesticus*. *Journal of Avian Biology*, **39**, 222–225.
- Newton, I. and Marquiss, M. (1982) Eye colour, age and breeding performance in Sparrowhawks *Accipiter nisus*. *Bird Study*, **29**, 195–200.
- Nice, M.M. (1941) The role of territory in bird life. *American Midland Naturalist*, **26**, 441–487.
- Ollason, J.C. and Dunnet, G.M. (1978) Age, experience and factors affecting the breeding success of the Fulmar *Fulmarus glacialis* in Orkney. *Journal of Animal Ecology*, **47**, 961–976.
- Oro, D. and Furness, R.W. (2002) Influences of food availability and predation on survival of Kittiwakes. *Ecology*, **83**, 2516–2528.
- Otter, K. and Ratcliffe, L. (1999) Relationship of bib size to age and sex in the black-capped chickadee. *Journal of Field Ornithology*, **70**, 567–577.
- Owen, M., Black, J. M. and Liber, H. (1988) Pair bond duration and timing of its formation in Barnacle Geese *Branta leucopsis*. *Waterfowl in winter* (eds M.W. Weller), pp. 23–38. University of Minnesota Press, Minnesota.
- Perrins, C.M. and McCleery, R.H. (1985) The effect of age and pair bond on the breeding success of Great Tits *Parus major*. *Ibis*, **127**, 306–315.

- Pulliam, H.R. (1988) Sources, sinks and population regulation. *American Naturalist*, **132**, 652–661.
- Richdale, L.E. and Warham, J. (1973) Survival, pair-bond retention and nest-site tenacity in Buller's Mollymawk. *Ibis*, **115**, 257–263.
- Rohwer, S. (1975) The social significance of avian winter plumage variability. *Evolution*, **29**, 593–610.
- Rohwer, S. (1982) The evolution of reliable and un-reliable badges of fighting ability. *American Zoologist*, **22**, 531–546.
- Schowalter, T.D. and Crossley Jr., D.A. (1983) Forest canopy arthropods as sodium, potassium, magnesium and calcium pools in forests. *Forest Ecology and Management*, **7**, 143–148.
- Senar, J.C., Camerino, M., Copete, J.L. and Metcalfe, N.B. (1993) Variation in black bib of the Eurasian Siskin *Carduelis spinus* and its role as a reliable badge of dominance. *Auk*, **110**, 924–927.
- Sergio, F. and Newton, I. (2003) Occupancy as a measure of territory quality. *Journal of Animal Ecology*, **72**, 857–865.
- Setiawan, A.N., Massaro, M., Darby, J.T. and Davis, L.S. (2005) Mate and territory retention in the Yellow-eyed Penguin. *Condor*, **107**, 703–709.
- Smith, T.M. and Shugart, H.H. (1987) Territory size variation in the Ovenbird: the role of habitat structure. *Ecology*, **68**, 695–704.
- Sodhi, N.S. (1993) Proximate determinants of foraging effort in breeding male Merlins. *Wilson Bulletin*, **105**, 68–76.
- Starcks, J.M. and Ricklefs, R.E. (1998) Patterns of development: the altricial-precocial spectrum. In Avian growth and development. Evolution within the altricial-precocial spectrum (Eds Starck, J.M. and Ricklefs, R.E.). Oxford University Press, Oxford. pp.3–30.
- Stenger, J. (1958) Food habits and available food of ovenbirds in relation to territory size. *Auk*, **75**, 335–346.
- Turpie, J.K. (1995) Nonbreeding territoriality: causes and consequences of individual and seasonal variation in Grey Plover *Pluvialis squatarola* behaviour. *Journal of Animal Ecology*, **64**, 429–438.
- Wauters, L.A., Lens, L. and Dhondt, A.A. (1995) Variation in territory fidelity and territory shifts among Red Squirrel *Sciurus vulgaris* females. *Animal Behavior*, **49**, 187–193.
- Wilkin, T.A., King, L.E. and Sheldon, B.C. (2009) Habitat quality, nestling diet and provisioning behaviour in Great Tits *Parus major*. *Journal of Avian Biology*, **40**, 135–145.

- Williams, T.D. and Rodwell, S. (1992) Annual variation in return rate, mate and nest-site fidelity in breeding Gentoo and Macaroni Penguins. *Condor*, **94**, 636–645.
- Wilson, J.D. (1992) A re-assessment of the significance of status signaling in populations of wild Great Tits *Parus major*. *Animal Behavior*, **43**, 999–1009.
- Wortman-Wunder, E. (1997) Territory size in Lincoln's Sparrow *Melospiza lincolnii*. *The Southwestern Naturalist*, **42**, 446–453.
- Zuk, M., Thornhill, R., Ligon, C., Johnson, K., Austad, S., Ligon, S.H., Thornhill, N.W. and Costin, C. (1990) The role of male ornaments and courtship behavior in female mate choice of Red Jungle Fowl. *American Naturalist*, **136**, 459–473.

University of Cape Town