

The White-crowned Black Wheatear (*Oenanthe leucopyga*)
in St. Katherine, Sinai: Age related differences in territorial
aggression and Breeding Success.

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Acknowledgements

On the plane journey to Sinai I had a few hours to consider how fortunate I was to have the opportunity to study a subject I truly enjoy in an environment that appeared so vast and exciting. However, almost five months later, whilst sat around the camp fire in Fox Camp, I understood just how utterly fantastic the experience was. I met so many people who, not only assisted me in my research, but whose sense of humour, kindness and wisdom will permanently enrich my life. Despite being the only researcher there for the first three months, I never felt alone thanks to the Fox Camp staff; Abdul, Suleman, Radwan and Hamdi Mubarak. I would like to thank Radwan and Hamdi for keeping me fed, and for all the insightful opinions shared over countless glasses of shay. I would also like to thank Faraj Fox, Salah Mahmood and Mohammed Khedr for going so far out of their way to help me, Dr Hilary Gilbert for all of the Arabic lessons and the fantastic coffee, and Hameed Hussein for the transport that made my work possible.

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Abstract

A bird's quality, measured through various factors associated with fitness, generally increases with age. Such a change in quality is often accompanied by a change in appearance that functions as a signal of status to conspecifics. An age-related change in appearance occurs in the White-crowned Black Wheatear (*Oenanthe leucopyga*), a small sedentary passerine bird (Muscipadidae) that inhabits arid habitats. In this species, young birds are black-crowned whilst older birds are white-crowned. This report studied a wild population near St. Katherine, Sinai, to test the hypothesis that white-crowned birds are of a higher quality than black crowned birds. The primary measures of quality discussed in this thesis were breeding success, body-size, levels of territorial aggression, mate-choice, survival rate and territory size. Whilst no significant difference was found in many of these measures, white-crowned birds were found to be significantly more territorially aggressive and were more successful breeders. Evidence of an age-related assortative mating system was also found in town environments. This report therefore provides evidence that a difference in quality exists between birds of different crown morphs. Should future investigations show crown-colours being used to reduce intraspecific aggressive encounters, this would suggest a signalling function for the crown.

Furthermore, general information about the Wheatear's biology is presented in order to increase our understanding of this species and of birds living in arid environments.

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1. Introduction

A bird's ability to compete with conspecifics and to reproduce successfully generally increases over time and with experience (Wooller et al. 1990; Desrochers 1992; Forslund and Pärt 1995). This boost in the ability to compete is often driven by changes in morphology, in behaviour, or both (Forslund and Pärt 1995). Changes in appearance and in behaviour are often linked, either because these changes in appearance make them physically more able to compete (Breitburg 1987), or they are used as signals to advertise their status and strength.

So-called "badges of status" have been shown to be signals of quality in many bird species, where badges help establish and maintain group structure and reduce the number of intraspecific agonistic interactions (Qvarnström 1997; Møller 1988; Pryke et al. 2002). House Sparrows (*Passer domesticus*) display a well-studied, age related badge of status in the form of a black throat patch - or "bib" - which is absent in females and that differs in size between males. Bib size increases with each successive moult as a male gets older (Nakagawa et al. 2007) and males with larger bibs obtain the better nesting sites which they defend more vigorously against other males (Møller 1990; Reyer et al. 1998). Additionally, larger bibbed birds are more desired by females when forming breeding pairs (Møller 1990). This indicates that, on average, older House Sparrows are more desirable for females, obtain better nest sites and are more aggressive than younger conspecifics.

In the Collared Flycatcher (*Ficedula albicollis*), the size of the white area on a male's forehead is considered a badge of status; males with large badges achieve greater breeding success by being more polygamous (Gustafsson et al. 1995) and by incurring fewer extra-pair young in their own nests (Sheldon et al. 1997). Larger badged males were also able to secure nesting sites more effectively (Pärt and Qvarnström 1997). Qvarnström (1997) experimented by artificially

increasing the badge size of male Collared Flycatchers: young males that had their badges enlarged beyond their ability to compete were less able to establish breeding territories in comparison to control birds and older, similarly-manipulated males. Qvarnström (1997) attributes the difference between older and younger birds to both behavioural and physiological age-related traits; older birds arrive earlier to establish territories and are more able to respond to the increased aggression experienced post-manipulation with a corresponding increase in their own testosterone levels.

In order to be an effective signalling system, mechanisms must exist that prevent subordinate birds cheating their way up the social ladder, meaning that signals must come at a cost to produce or maintain (Zahavi 1975). One possible cost was proposed as the immunohandicap hypothesis, developed from studies using house sparrows (whose bib size is dependent on testosterone levels) (Folstad and Karter 1992). Males with larger bibs possess higher levels of testosterone. As testosterone is immunosuppressive males must sacrifice their immune system potential for impressive badges. As subordinate males cannot afford this cost, they cannot cheat.

A further type of age-related variation in appearance associated with a change in behaviour is delayed plumage maturation. In this phenomenon, yearling birds capable of breeding retain the appearance either of a bird in its first year, or of a female bird, until a time when they are able to compete more effectively (Rohwer and Niles 1979; Hill 1996; Delhey and Kempenaers 2006). Many explanations have been proposed for the selective advantage of delayed plumage maturation (reviewed in Lyon and Montgomerie 1986); the initial explanation, termed the *cryptic hypothesis*, suggests that the increased risk of predation associated with conspicuous adult plumage outweighs the benefits, because even with adult plumage, yearling birds would still have a very low chance of breeding successfully (Procter-Gray and Holmes 1981). The *winter adaptation hypothesis* suggests that yearlings cannot afford the cost of the moult after their difficult first

winter (Rohwer et al. 1983). The *female mimicry hypothesis* argues that yearlings attempt to deceive older males into believing that they are females in an effort to reduce the amount of aggression that they incur. Whilst yearling males showing delayed plumage maturation do suffer less aggression than older birds in Red-winged Blackbirds (*Agelaius phoeniceus*) and Northern Orioles (*Icterus galbula*) (Rohwer 1978; Flood 1984), this hypothesis implies that deceit is the motivating factor, and is only applicable to polygamous, sexually dimorphic species (Lyon and Montgomerie 1986). As an alternative, Lyon and Montgomerie (1986) proposed the *status signalling hypothesis*, which shares many features with the more recently described badge of status. These authors suggest that rather than attempting to deceive older birds, yearlings are signalling their status as a subordinate at the cost of decreased sexual attractiveness. Unlike the *female mimicry hypothesis*, the *status signalling hypothesis* can be applied to monogamous, sexually monomorphic birds (Lyon and Montgomerie 1986).

Compared to birds living in temperate environments, our understanding of desert species is poor in both breadth and depth. Not only are records for survival and breeding success scarce for sedentary desert birds, many behavioural and social ecological phenomena, well understood in temperate-living species, are poorly described (if at all) in their cousins from arid environments. Compared to temperate environments, the difficulties associated with living in an arid region include high temperatures, low rainfall and limited food sources (Anava *et al.* 2001; Rotenberry and Wiens 1991; Patten and Rotenberry 1999; Bolger *et al.* 2005; Dingle and Khamala 1972; Sinclair 1978; Delinger 1980). The selective pressures faced by birds in these two environments will therefore be very different. Consequently, one would expect desert birds to differ from those from temperate habitats, both physically and behaviourally (Anava *et al.* 2001; Ghalambor and Martin 2001). To assume that birds living in these two very differing environments display the same behavioural and ecological traits could be a large oversimplification, or just plain incorrect. Closing the gap in

knowledge between two unequally understood environments would not only increase our understanding of desert species, but also that of temperate birds and the field of ornithology as a whole.

As discussed above, status signalling through age-related plumage variation/dimorphism is well documented in temperate-living birds. As a consequence of the lack of studies, neither badges of status, nor delayed plumage maturation have been documented in sedentary birds living in arid environments. Sedentary arid-living species have been described as having age-related plumage dimorphisms, yet no studies have attempted to understand the function (if any) of such dimorphisms as a potential status signalling system.

Study site and study species

The White-crowned Black Wheatear (*Oenanthe leucopyga*: Muscicapidae) is a monogamous, sexually monomorphic (Panov 2005) with a geographical range that spans across North Africa into the southern half of the Arabian Peninsula via Sinai (Svensson *et al.* 2010). This thesis presents and discusses data collected during the 2012 field season in St. Katherine, Sinai (Egypt) (28°33'44.97" N, 33°56'56.66" E). Following Pio (2011), this is the second year of a proposed long-term study into the biology of the White-crowned Black Wheatear. The study is itself a component of a larger project investigating desert species in Sinai – particularly within the St. Katherine Protectorate.

The Protectorate occupies almost half of the area of south Sinai. The terrain is high and mountainous, and the climate fluctuates between August averages of 36 °C (highs > 40 °C) and cool winters (February mean of 7.8 °C) (White *et al.* 2001). Because of its unique biodiversity (Zalat *et al.* 2001) and placement between the continents of Africa and Asia, the St. Katherine Protectorate is an important habitat for sedentary and migratory birds; in recognition, it has been given Important Bird Area (IBA) status by Birdlife International. (Baha El Din 1999).

St. Katherine city is the administrative centre of the protectorate. It is here and the surrounding wadis where the majority of fieldwork was performed. Despite currently possessing a relatively small human population, this number is increasing rapidly. Consequentially, urban development is encroaching further into the surrounding wadi systems. Furthermore, the nearby culturally significant areas such as the Monastery of St. Katherine and Mount Sinai attract large numbers of tourists leading to further human intrusion into the protectorate. The South Sinai project is uniquely positioned to study this situation as it develops and monitor the effect this has on the local species (Grainger and Gilbert 2008).

Fieldwork was completed from the 22nd January 2012 until 25th March and between the 9th April and the 30th May 2012. Locations were selected within 6 km of the field accommodation based upon last year's study and access permissions; Fox Camp, St. Katherine Tourist Village, Wadi Raha, Abu Sila, Wadi Tlah, Wadi Sreig, Wadi Ferrah, Safsaffah and Wadi Arbaeen (Figure 1).

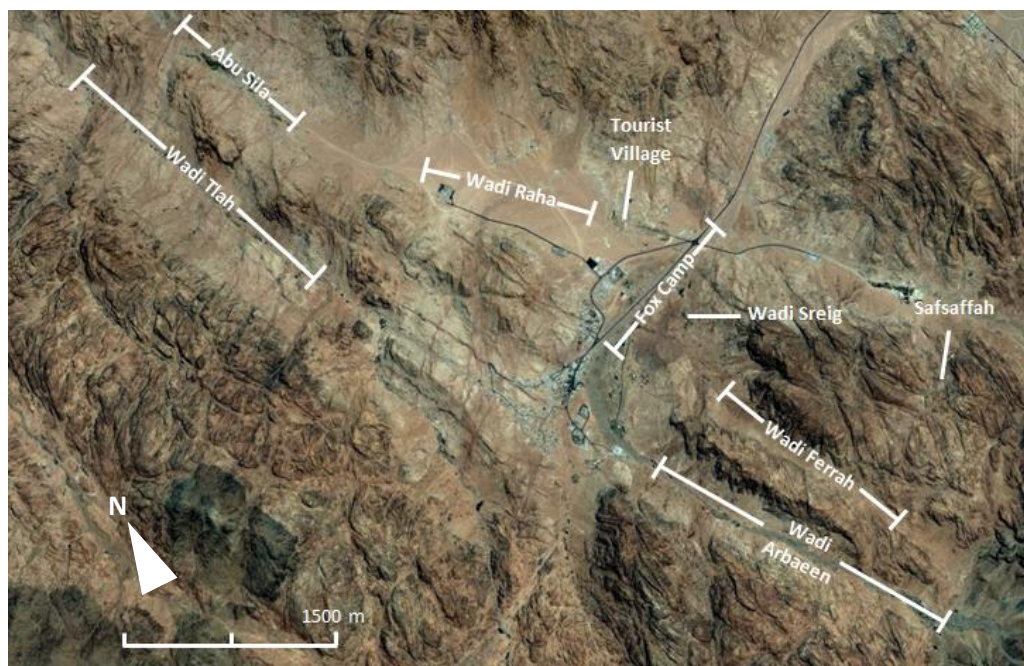


Figure 1: Map of all study sites radiating from St. Katherine city in the centre.

The White-crowned Black Wheatear has a large yet apparently declining population in the St. Katherine Protectorate (White *et al.* 2001; Pio 2011). Despite its abundance (White *et al.* 2001; Svensson *et al.* 2010), the species has rarely been studied and consequentially its biology is poorly understood - especially in relation to wheatears that do not live in arid environments, such as the Northern Wheatear (*Oenanthe oenanthe*).

The majority of what we know about this species comes from two relatively old studies (Fischman 1977; Palfrey 1988) together with information by Pio (2011). The following notes combine literature information with my own observations from 2012.



Figure 2: Variation in crown-moult stages in territory holding wheatears. From left to right; fully moulted, white crown area non-fragmented - categorised as "white-crowned"; moult not begun, no white feathers in crown - categorised as "black-crowned"; small, fragmented areas of white feathers, majority of crown area black - categorised as "black-crowned"

The White-crowned Black Wheatear is sexually monomorphic in a typically strongly dimorphic genus (Panov 2005). It is named for its large crown of white feathers in adult birds (Figure 2), the function of which is currently unknown. Born black-crowned, they moult into white crowns sometime between their first autumn (Palfrey 1988) and two years of age (Panov 2005). Mid-moult birds were common in St. Katherine, recognizable because the white area was less than 10% of the size of the crown in adults and was also frequently fragmented. Excluding the crown, the bird is glossy black, with a white rump, tail and vent - the tail has the usual wheatear pattern, here with a thick central black bar and a black speck in each corner of the tail.

Of 32 home ranges observed, 31 encompassed one or more permanent or semi-permanent human residences. In the wider wadis and towns, a home range typically incorporated a segment of the valley floor area or town and the majority of the wall of one side of the wadi. Many home ranges radiated out from a flat, wide central area of human settlement. In narrower, longer wadis, home ranges spanned the entire width and height of the wadi and were arranged in series, in most cases with large unoccupied areas between territories. Two females were replaced as quickly as three days after their disappearance.

Wheatear diets are varied (Palfrey 1988), and birds in St. Katherine were no exception. The majority of feeding was done on the ground or in vegetation, but also prey were also frequently taken on the wing: invertebrates such as flies (Diptera), ants (Formicidae), honey-bees (*Apis mellifera*), and adult and larval butterflies and moths (Lepdoptera) appear to form the major part of the diet. Birds also foraged for seeds amongst dung and groomed larger animals (such as camel) for parasites. Fruits such as olives (*Olea europaea*) were taken from trees cultivated in Bedouin gardens when available, along with seeds (e.g. poppy *Papaver somniferum*). As noted by Fischman (1977), human settlements seem to have an important role in shaping diets in the study area; many families put out large quantities of food specifically for wheatears, typically cooked rice, fruit and vegetables such as aubergines and tomatoes, as well as processed foods such as bread - none of which are available in the natural environment in Sinai.

Wheatears were often seen foraging with other birds, particularly Desert Larks (*Ammonanes deserti*), but also Scrub Warblers (*Scotocerca inquieta*), Tristram's Starlings (*Onychognathus tristramii*), Laughing Doves (*Streptopelia senegalensis*) and, less frequently, Sand Partridges (*Ammoperdix heyi*) and Sinai Rosefinches (*Carpodacus synoicus*). Wheatears sporadically chased the smaller larks and warblers from food sources, and in turn were regularly chased away by Tristram's Starlings. The Starred Agama (*Laudakia stellio*) was twice observed pushing adult wheatears from feeding sites (Figure 3).



Figure 3: Chronologically, clockwise from top left; A white-crowned bird being chased from a baited trap by a Starred Agama Lizard. Photographs taken by in Andrew Power, Nottingham University.

Birds were most territorial after dawn and before dusk. Both sexes sang, the male considerably more frequently. The territorial song was highly variable (samples, see Appendix), and mimicry of other sounds played a major role, such as the song of the Scrub Warbler, the wolf-whistle of Tristram's Starling, feral cats and even vehicles.

In the males, singing was often accompanied by the displays described by Palfrey (1988). The most frequent was the “crouch posture” performed on song posts in conjunction with singing or a low pitched “buzz”. This display was characterised by the hunched posture of the male, with both head and tail lowered almost to touch the song post, tail spread and rump feathers raised to reveal the extent of the white area beneath. On wide song posts such as roofs and boulders, the bird would then scuttle forward to the apex or the corner; on song posts where there was no room to move forward, fence posts or trees, birds could rotate on the spot whilst displaying. The “song flight” display was also regularly observed in males (Figure 4) when flying between two crouch-posture displays: probably it is an extension of that behaviour: the tail was held low and fanned, the white rump feathers were visible and puffed up, and primary wing feathers were also fanned and upturned.



Figure 4: Song flight of a white-crowned bird from front and rear. Note spread tail and raised white area on the lower back. Flight feathers fanned and pointing upwards.

Town birds used the corners of houses, fence posts, lampposts and masts, typically the highest points in their territories. Outside the towns, mainly they used rocky outcrops, boulders, bushes and trees. When birds had territories on opposing sides of a ridge between parallel wadis, they would frequently sing at the peak of the dividing ridge.

Overwhelmingly, agonistic behaviour was limited to singing and displaying: occasionally, both sexes would pursue invading birds if they

encroached too far. Pursuits were usually performed in short intense bursts, one following the other closely. Both birds would then land a few metres apart to sing and display before beginning another round of pursuit. On one occasion, four birds from three different territories did this. Only on one occasion did aggression escalate further and an actual fight ensued: after a few pursuits, two black-crowned birds from neighbouring territories landed on the same roof - the fight appeared to consist of males leaping a metre into the air and attempting to land on top of the other.

Aggression was not just focussed towards conspecifics; both sexes of the White-crowned Black Wheatears pursued Hooded Wheatears (*Oenanthe monacha*) and Black Redstarts (*Phoenicurus ochruros*) from a territory. Palfrey (1988) observed the same reaction to Mourning (*Oenanthe lugens*) and Pied Wheatears (*Oenanthe pleschanka*).

No predation attempts on adult wheatears were witnessed during the field season, but many potential predators exist in the area; mammals such as red foxes (*Vulpes vulpes*) and feral house cats (*Felis catus*), reptiles including venomous and non-venomous snakes, and birds including shrikes (Laniidae), Peregrine Falcons (*Falco peregrinus*) and Sooty Falcons (*Falco concolor*) also occur and are known to feed on similar small passerine birds. Wheatears reacted to the presence of a threat in their territory with a continuous alarm call, a trill chirp followed by one or two guttural barks: whilst producing this call, birds would repeatedly bow down and flick their closed tail forward. (See appendix)

Alarm calls were often followed by mobbing behaviour: the bird that had spotted the threat would hover one to two metres above it, all the while producing the alarm call and staring intently. Lone wheatears would quickly be joined by their partners, and immature birds more than three weeks post-fledging initiated and participated. Wheatear mobbing normally attracted the attention of other bird species, particularly the Desert Lark and Sinai Rosefinch, who would themselves become involved. On one occasion, a Desert Sand Snake (*Psammophis*

schokar) attracted the attention of three larks and a pair of wheatears and mobbing continued for almost half an hour. Half-way through a nest inspection, I was once the mobbing target of returning adult birds.

Many birds are killed and eaten by Bedouin, particularly the Chukar Partridge (*Alectoris chukar*), pigeon species (Columbidae) and songbirds such as the Desert Lark. Despite the fact that hunting for food is important to the Bedouin way of life, due to its eminent position in folklore (see Appendix), wheatears are not consumed because killing them violates Bedouin law. This possibly contributes to the bird's confidence around humans. Despite this, one black-crowned female was maimed by a teenager using an air rifle losing the function of one leg, but she survived and was seen building a nest towards the end of the field season.

Despite spending 100 days in the field, overt courtship behaviour as illustrated extensively in Palfrey (1988) was not fully witnessed and therefore cannot be adequately described here. Only the brief pursuit stages were observed, during which the male chased his partner in close order through the air in a similar way to intruding wheatears. Pursuit time varied, lasting between 5 to 30 seconds. When the female came to land, the male copied immediately, landing nearby. On the few occasions this was observed, there were no vocalisations from either bird.

The earliest nest construction was observed on the 24th February, more than three weeks later than observed by Pio (2011). Nests were either built in natural rock holes and crevices, or in gaps in the brickwork of buildings (Figure 5). Most pairs constructed one nest, but two pairs built at least two nests in different locations simultaneously. Nest building was most intense during the first five to seven days, with up to four trips an hour made by each bird to collect nesting material. Plant matter in the form of twigs and fibres constituted around half of all material collected, with the remainder comprised of man-made substances, chiefly electrical wiring and plastic plucked with considerable effort from

camel feed sacks. Females contributed most of the work in building the nest cup, with only two observed instances of males carrying material. Despite this, males were frequently observed accompanying a working female into the nest, despite not contributing material themselves.



Figure 5: Wheatear nests were found located in three different substrates as shown in three photographs; clockwise from left: Nest in natural rock crevice; nest in a natural hole in a rock; Nest inside of house. For scale, stones in the rampart are on average 3 cm in length (Pio 2011).

The building of the rampart was witnessed in three locations, and was concurrent with the construction of the nest cup. During this period, the collection of stones was not as frequent as the collection of material for the nest cup. As for nest building, the carrying of stones was mostly done by the female (Fischman 1977), but on one occasion a black-crowned male was observed collecting a large stone from approximately 10 metres away and placing it in the nest entrance. This is the first recorded incidence of males participating in this behaviour (cf. Fischman 1977). Stones were transported from various distances within their territory and brought towards the nest entrance. Birds always landed a few metres short of the nest and dropped the stone

before picking it up again and flying into the nest entrance. The stone was again dropped and its position altered by flicks of the wheatears beak similar to movements used by birds foraging in sand.

Not only were new nests constructed, but old nests were reused. At least two pairs are known to have used the same nest site in 2012 as they used in 2011. Furthermore, birds have been seen using nests that were probably constructed before they were born; a pair of black-crowned birds known to have moved into the area between 2011 and 2012 used a nest that was constructed at least two years previously (Faraj Mahmoud, pers. comm.). Birds that reuse a nest also rebuild the nest cup and bring stones to extend and repair the rampart. This supports the predictions of Pio (2011) who suggested that the large increase in the average number of stones making up the rampart since Fischman (1977)'s study could be due to their continual addition to pre-existing nests.

The first eggs were discovered on the 18th March, more than a month later than the previous season. Incubation lasted approximately a fortnight and only females were observed incubating the eggs. Contrary to Palfrey (1988), males did enter the nest, but only when the female was already inside, and never for a sustained period of time. Incubation sessions lasted about half an hour and were followed by a period of about 10 minutes of foraging away from the nest. After the eggs hatched, both male and females contributed to feeding the young inside the nest for a further 14 days.

For about one week after fledging, young birds were difficult to locate. When seen, they were typically sheltering under rocks high up the slope of the wadi, occasionally making short flights. Only when adults carrying food arrived would chicks become conspicuous, climbing to the top of the rocks and uttering frequent, loud begging calls accompanied by a low hunched posture with wings spread, facing backwards (Figure 6). Birds were observed foraging just over a week after fledging. They were not only confident enough to forage in and around houses and gardens, but also within half a metre of researchers.



Figure 6: A fledgling of unknown age (right) begging for food of a white-crowned adult. Begging was frequently observed when the adult had no food to provide. Photograph taken by Andrew Power of Nottingham University, May 2012 in St. Katherine.

At this point, fledglings could be trapped and ringed using the same methods used for adults, but differed markedly from their parents and other adult birds (Figure 7): their beaks were dull and pale, with the yellow lining visible from the outside, rather than black and glossy, their tail and wing feathers were still developing, with the outer greater covert feathers dull and pale, comparable to those of yearlings rather than the dark glossy appearance of the white-crowned birds, and there



Figure 7: Photographs comparing the appearance of a two week old fledgling. (A): Head photograph showing absence of any white crown, pale beak and yellow tissue visible in comparison to the adult in (B). (C) and (D): Tail feathers and wing feathers housed partially in the cuticular sheath.

were bald patches on legs and breasts that were never found on adult birds.

Recent fledglings were typically seen together. After three weeks one or more would occasionally spend time foraging away from the others, often in association with one of the adults. At this age, two fledglings were seen acting very aggressively to Desert Larks, pursuing them closely for about 5 minutes, uttering a very distinctive and novel call. Unlike when adults chase off non-conspecifics, there appeared to be no trigger for this behaviour: the larks were not encroaching on a food source and were more than 20 m away when it began.

The aims of this study

The White-crowned Black Wheatear displays an age-related plumage dimorphism. This could be a badge of status, or merely delayed plumage maturation, but in either case it should be accompanied by a corresponding difference in quality. Black-crowned birds are known to be capable of holding a territory and breeding successfully (Fischman 1977; Palfery 1988; Pio 2011), but we do not know whether there is a difference in fighting ability, survival, home range size, mate preference

or levels of aggression between white-crowned and black-crowned birds. If the older white-crowned individuals are 'better' on measures associated with fitness, this would indicate that the white-crown is an age-dependent honest signal.

This thesis focusses on two main aspects: the potential signalling function of the crown and the differences in breeding success of white-crowned and black-crowned birds.

2. Comparison of levels of aggression, morphology, survival rate and home range size between crown-morphs

As discussed in the previous chapter, the age-related plumage dimorphism in this species of wheatear is potentially indicative of an age-related status signalling system. Such signalling systems are well described in temperate-living species, yet not discussed in sedentary birds in arid environments. This chapter attempts to test whether the difference in appearance between the older white-crowned and juvenile black-crowned wheatears corresponds to a difference in success, measured by body size, territorial aggression, territory characteristics and survival: Such differences are required for both the delayed plumage maturation and badges of status hypothesis.

Methods

Ringling and home range

Wheatears were located using Opticron Discovery WP PC binoculars and a Vanguard Signature Plus 680 spotting scope as well as local knowledge. All areas observed by Pio (2011) were revisited weekly for the initial two months to establish if birds were present. Attempts were made to ring all of the birds that were located in the study sites. The traps used were traditional, Bedouin built, box traps baited with the yolk of hard boiled eggs, cooked rice, crushed tomato or black olives. In exceptionally windy conditions, or in difficult terrain, traps were rigged to be manually triggered using a 5 m cable connected to the mechanism.

Birds were ringed with a unique combination of two colour bands on each leg. Both recaptured and newly trapped birds were measured for

morphometric data on wing, tail and tarsus length, beak length from tip to skull, beak depth at the nostril and maximum beak width. Body weight was taken using a Pesola 50 g balance.

Birds were categorised by crown morph as black-crowned or white-crowned. Some individuals were trapped in the middle of their crown-moult (as in Figure 2). As the white-feathered area was fragmented and less than a tenth of the size of that for the white-crowned group, these individuals were considered non-mature birds and placed in the black-crowned category. The size of the crown was measured for all white-crowned individuals. Measurements were obtained by producing a photograph of the top of the bird's head incorporating a scale bar and using the "set scale" and "measure" function in ImageJ v. 1.45 (National Institutes of Health) software package.

All birds in the study area were regularly observed and information regarding sex, home range, foraging, social behaviour and breeding behaviour was gathered. Following Pio (2011), home-range size as opposed to territory size is used because of the inherent difficulties and inaccuracies in measuring territory size when intrusion by conspecifics is rare. By using home-range size, a more accurate description of distribution and behaviour can be given (Burt 1943). Home range was measured by extensively observing movement for each pair of wheatears and collecting GPS co-ordinates of the extent of their ranging using a Garmin e-trek Legend H GPS unit.

Areas were calculated by constructing minimum polygons using these co-ordinates in the ArcGIS v 10.0 (ESRI) software package and exporting the scaled image to ImageJ, where the area was determined as before. The total observed area in St. Katherine was measured and can be seen in Figure 8. Wheatear density was calculated by dividing this area by the total number of wheatears. Each study site was classified as either *wadi* or *town*, with *town* defined as any area with two or more permanent human residences, and *wadi* as areas with one

or fewer residences. Any home range that overlapped with an area classified as *town* was classed as such in its entirety.

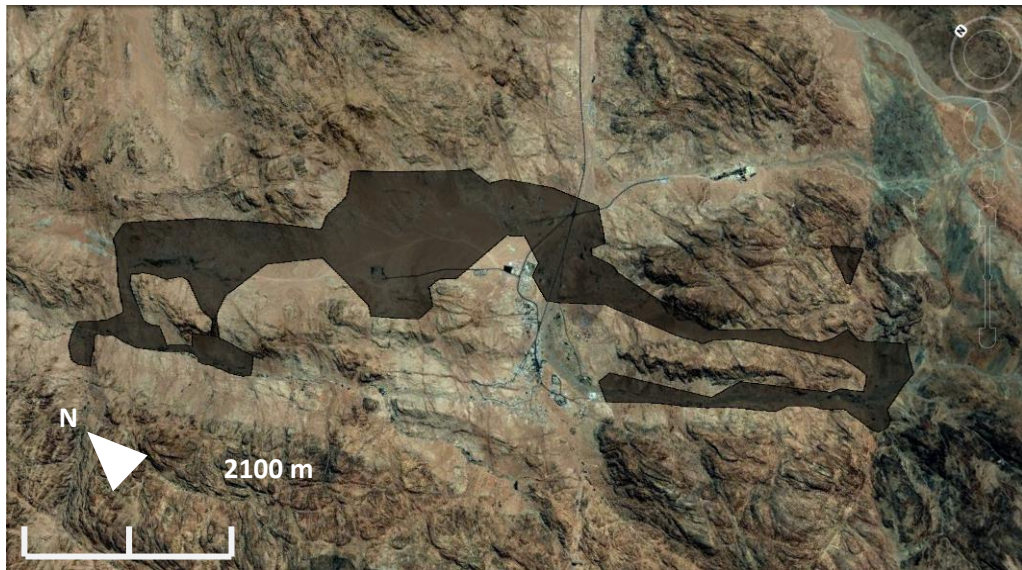


Figure 8: Total area observed. Scale bar signifies 2100 m

Song and aggression - playback experiment

The full territorial songs produced by four Wheatears, two white-crowned and two black-crowned, were recorded using a Benro MZW 70-1 microphone connected to a Marantz PMD 660 recorder. The four recordings were made between the hours of 0500 and 0700, the time in which the birds are most territorially active. Using Audacity v.1.3 software, the song fragment was looped to produce five minutes of continuous territorial song for all four birds. These tracks were exported onto a Samsung GT-S5560 mp3 player connected to an Altec Lansing Orbit MP3 model iM237 field speaker. Spectrograms of each recording and links to download the audio file can be found in the Appendix.

Experiments were performed from the 14/05/2012 to the 29/05/2012 between the hours of 0500-0700 and 1700-1830. Male birds were located and observed to confirm there were no intruders in the territory and the bird was not currently singing. The speaker was placed on the ground approximately 30 m from the male, inside its known home range. Following the adjusting of the device volume by ear to an equal volume equivalent to the bird's natural song, playback was initiated and

observation begun from a distance of 20 metres from the source. Birds were played one of the four recordings at random. Males were observed using binoculars for 15 minutes after playback initiation and their behaviour monitored. Variables measured for each bird during this time were: latency to respond to the playback with territorial song; total singing time; minimum distance from male to the speaker; performance and duration of territorial posturing displays and the number of song posts visited.

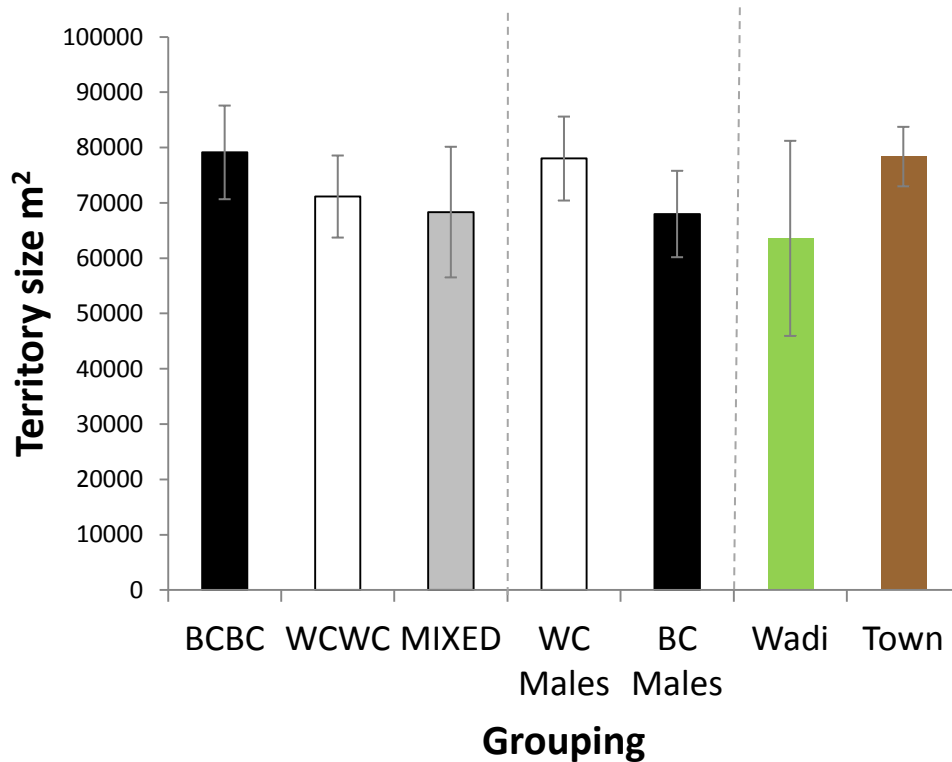
Statistical tests

The R software package version 2.13.2. (The R Foundation for Statistical Computing 2013) and SPSS version 16.0 (SPSS Inc.) were used to perform all statistical tests in this chapter. Residuals for each analysis were tested for normality (Shapiro-Wilk test). If they were normally distributed, ANOVA or equivalent was performed; if not a Kruskal-Wallis test was utilised.

Results

During the field season, a total of 67 wheatears were regularly observed. These birds occupied 32 home ranges in the St. Katherine region. For the majority of the time, each home range was occupied by a pair of birds, but losses later in the season lead to one empty and two with single occupants. The spatial arrangement of these home ranges (Figure 9) was scattered throughout the study area: the average size for a home range was found to be 75200 m² (*circa* 25 observations per range). The mean home-range size for three different ways of partitioning the data (Figure 10) show that black-crowned pairs had the largest home range and mixed pairs the smallest, but the three crown-morphs did not differ significantly (ANOVA, $F_{2,30} = 0.324$, $p = 0.73$). White-crowned males tended to have larger home-ranges than black-crowned males, but the difference was not significant (ANOVA, $F_{1,31} = 0.828$, $p = 0.37$). Differences between the home-range sizes for wadi-living and town-living birds were likewise not statistically different

(ANOVA, $F_{1,31} = 1.789$, $p = 0.191$). There was no significant difference in home-range size between my study of 2012 and Pio's (2011) average of 89660 m^2 (Shapiro-Wilk Statistic = 0.895, $p = 0.04$; Kruskal-Wallis test $Z = 0.561$ $p = 0.575$). The size of the overall study area was 5.59 km^2 , giving an overall density of $11.3 \text{ individuals/km}^2$. The density of wheatears in the town regions was greater than that for wadi regions



(16.2 vs. $7.8 \text{ individuals/km}^2$).

Figure 10: Comparison of mean home-range size, separated three different ways; by pair crown-morph combination, male crown-morph and home-range environment. Error bars shows standard error.

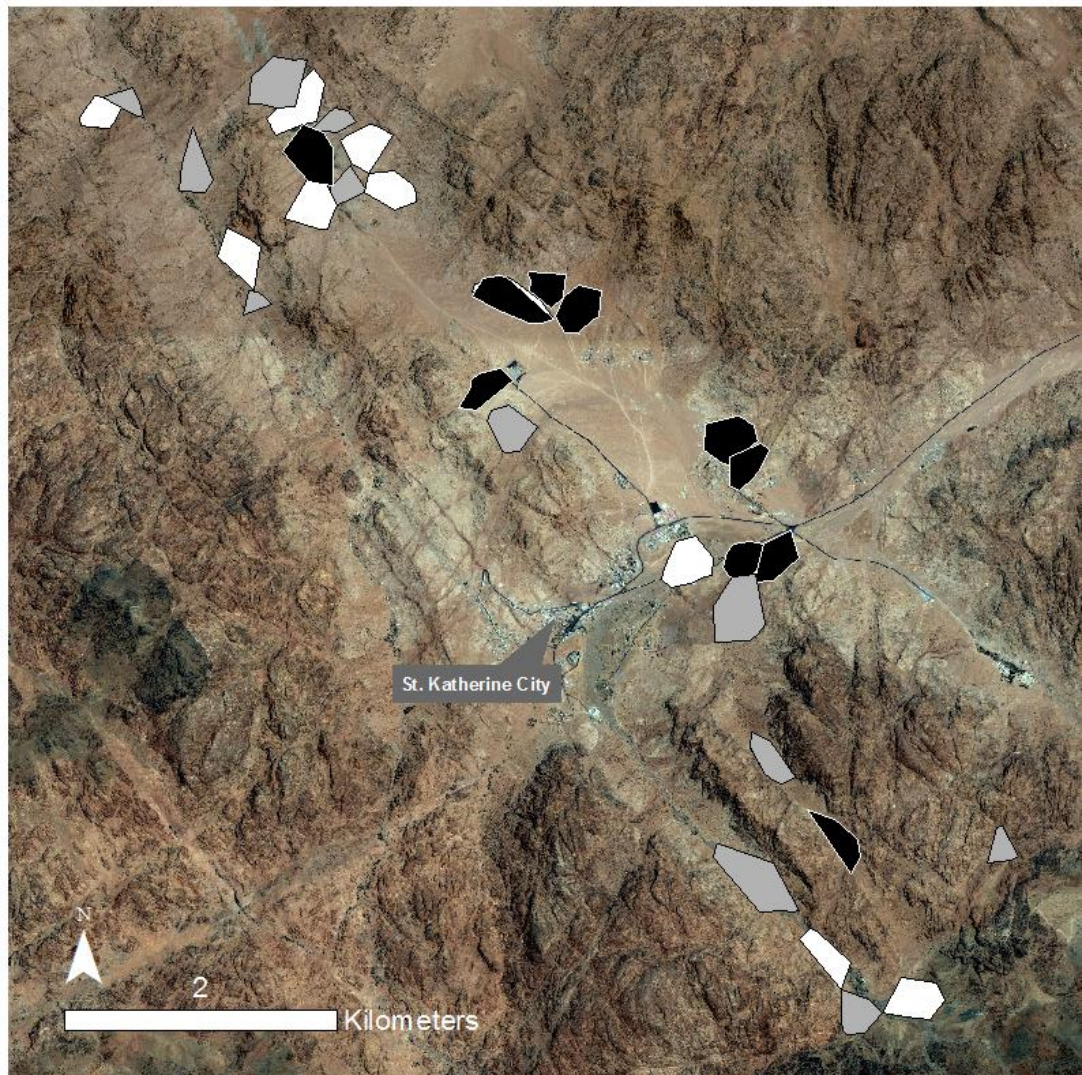


Figure 9: Map of the home ranges of White-crowned wheatears in the St Katherine area. The fill colour indicates the crown colours of birds in the pair: black = two black-crowned birds; white = two white-crowned birds; grey = one of each crown colour.

Of the 67 birds in the study area, (Table 1) 35 birds were white-crowned and 32 black-crowned (ratio 1.09:1). Among the 34 females and 33 males (ratio 1.04:1), the ratio of crown types was similar between sexes ($\chi^2 = 0.367$, $df = 1$, $p = 0.544$). There were approximately equal numbers of the different crown-type pairings (Table 1), but random pairings would generate a 1:2:1 ratio: however, the observed numbers are not significantly different from the expected ($\chi^2 = 4.62$, $df=2$, $p=0.10$). Lumping the data slightly differently, matching

crown-type pairs were more common than mixed pairs, but again this is not different from the 1:1 expected ratio ($\chi^2 = 2.45$, $df = 1$, $p = 0.12$). Most of the town pairs had matching crown types, but in contrast most of the wadi pairs were of mixed crown types (Table 1: $\chi^2 = 8.9$, $df = 2$, $p = 0.012$)

Table 1: Break down of all wheatears observed in the study area. The crown-morph of individual birds is further broken down by sex. The colour combination of pairs is subdivided by environment.

	Individuals			Pairs		
	All birds	Males	Females	Total	Wadi	Town
Black Crown	33	18	15	10	1	9
White Crown	34	15	19	11	3	8
Mixed				12	9	3
Total	67	33	34	33	13	20

Fourteen of the 28 wheatears ringed in Pio (2011) were re-sighted in the study area in 2012 (Table 2), giving a known year-to-year survival rate of 0.5. Differences in survival between black-crowned and white-crowned birds were not significant ($\chi^2 = 1.35$, $df = 1$, $p = 0.246$), nor were they between birds living in towns or in wadis ($\chi^2 = 0.583$, $df = 1$, $p = 0.445$), or between males and females ($\chi^2 = 0.583$, $df = 1$, $p = 0.445$).

Table 2: Number of birds in the study area that were ringed in 2011, numbers of those birds resighted in 2012 and number of new birds in 2012. Birds are divided by crown-morph, sex, and environment.

	All	WC	BC	Male	Female	Wadi	Town
New in 2011	28	17	11	16	12		
Resighted in 2012	14	10	4	7	7	7	7
New in 2012	53	24	29	26	27	19	34

Overall, 51 separate birds were captured and measured over the course of the field season (averages in morphometric traits are given in Table 3), consisting of 10 recaptured individuals and 41 new birds. Four

fledglings from the 2012 breeding season were also trapped; these were analysed separately to the other birds.

Table 3: Summary of morphometric data separated into gender and crown-morph.

	Mean \pm SE (cm)			
	Male		Female	
	WC	BC	WC	BC
Wing	110.6 (\pm 0.81)	110.3 (\pm 0.88)	105.1 (\pm 0.58)	104.2 (\pm 1.02)
Tail	72.4 (\pm 0.58)	71.4 (\pm 0.6)	70.3 (\pm 0.71)	66.9 (\pm 0.84)
Tarsus	26.82 (\pm 0.335)	27.2 (\pm 0.343)	25.53 (\pm 0.286)	26.18 (\pm 0.243)
Width	0.77 (\pm 0.0052)	0.76 (\pm 0.0126)	0.762 (\pm 0.0129)	0.732 (\pm 0.0105)
Depth	0.457 (\pm 0.0114)	0.473 (\pm 0.0098)	0.444 (\pm 0.0136)	0.455 (\pm 0.0062)
Length	22.99 (\pm 0.236)	22.77 (\pm 0.353)	22.09 (\pm 0.23)	21.99 (\pm 0.209)
Weight	31.32 (\pm 0.581)	30.63 (\pm 0.418)	29.77 (\pm 0.767)	29.15 (\pm 0.478)

In order to look for differences between crown types, the multivariate data were reduced to their main features using Principal Component Analysis (see Table 4). This suggested that two components explained 58.1% of the variation (40.6% and 17.5% respectively). From the correlations between the new factors and the measured variables (the Component Matrix, Table 4b), the first of these components can be considered “*body size*” because all the correlations are positive and fairly large (except beak depth and width); the second is interpreted as “*beak shape*” because only the beak variables have correlation coefficients large enough to be interpretable, particularly beak depth and width. Using the factor scores generated from the PCA, in a two way-ANOVA (sex x crown type), males have a significantly greater *body size* than females (ANOVA $F_{1,45} = 48.3$, $p < 0.001$). This difference is not present for the second component, *relative beak size* (ANOVA $F_{1,45} = 0.019$, $p = 0.890$).

Black-crowned and white-crowned birds are similar for both *body size* (ANOVA $F_{1,45} = 1.045$, $p = 0.312$) and *relative beak shape* (ANOVA $F_{1,45} = 0.002$, $p = 0.963$). There is no interaction between crown-morph and sex ($F_{1,45} = 1.724$, $p = 0.196$).

There were ten birds marked and measured by Pio (2011) that were recaptured and remeasured in 2012. There were no significant differences between years except in tarsus length, probably caused by different methods of measurement (see Appendix for a table of comparisons between years). All birds recaptured in 2012 that were black-crowned in 2011 had moulted into the white-crowned form ($n = 4$).

Table 4: Results from a PCA of morphometric data. (a) eigenanalysis showing that 58% of the total variance is explained by the first two components; (b) the component matrix - it can be seen that component 1 relates to body size and component 2 to relative beak dimensions.

(A) Total Variance explained

Component	Initial Eigenvalues			Extraction Sums of Squared Loadings		
	Total	Variance%	Cumulative%	Total	% of Variance	Cumulative %
1	2.842	40.594	40.594	2.842	40.594	40.594
2	1.224	17.491	58.085	1.224	17.491	58.085
3	0.882	12.596	70.681			
4	0.679	9.699	80.379			
5	0.620	8.860	89.239			
6	0.510	7.283	96.522			
7	0.243	3.478	100.000			

(B) Component Matrix

	Component	
	1	2
Wing	0.886	-0.145
Tail	0.757	-0.168
Tarsus	0.679	-0.350
Beak Width	0.417	0.581
Beak Depth	0.274	0.696
Beak Length	0.590	0.399
Weight	0.652	-0.269

In order to develop a method of aging the White-crowned Wheatear, photographs of 13 individuals were collected of the wings, specifically of the outer greater covert feathers. Of these, two were black-crowned fledglings, four were black-crowned birds in breeding pairs, three were



Figure 11: Field photographs of the wing-moult stage in four birds. From top to bottom: a mature white-crowned bird with bright/dark outer greater coverts; a black-crowned bird in mid-crown moult with bright/dark outer greater coverts; a black-crowned bird in mid-moult with dull/pale outer greater coverts; and a black-crowned bird with dull/pale outer greater coverts. Main areas of comparison are ringed in red.

white-crowned birds and four were birds in mid-crown moult (average 28 mm² of white feathers) (examples in Figure 11). The wing-moult stage was compared to the crown-moult stage. White-crowned birds had completed a full moult of both wing and crown feathers, with the tips of the outer greater coverts dark and matching the remainder of the

bright wing feathers. The outer greater coverts of fledglings were dull, with pale tips, as were those of black-crowned birds in breeding pairs. Birds in mid-crown moult were found with outer greater coverts either dull and pale, or bright and dark.

Playback Experiment

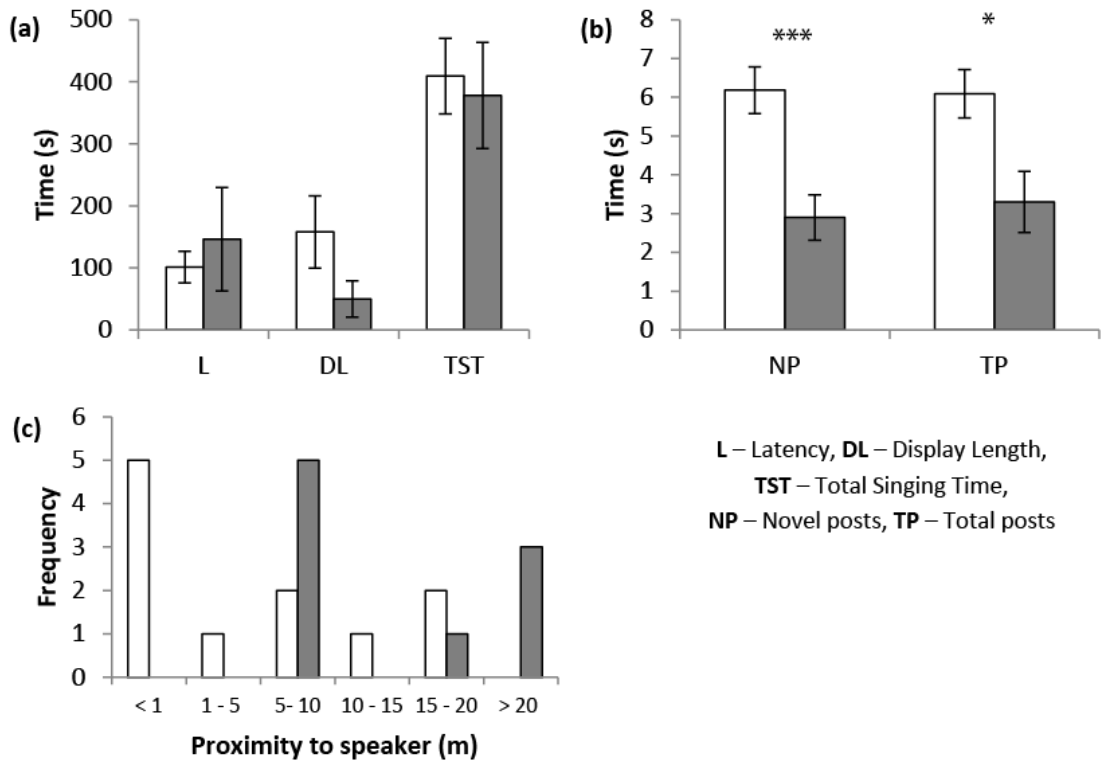


Figure 12: Response of experimental birds to the playback experiment. Showing differences in (a) latency to respond, display length and total singing time (b) Novel and total singing posts used and (c) approach to the speaker between black crowned and white crowned birds. White bars = white crowned responders, black bars = black crown responders. $p < 0.05 = *$, $p < 0.001 = *$.**

Twenty-one males were included in the playback experiment, 10 black-crowned and 11 white-crowned males. All but one responded to the recordings by singing. Strong responses had a low latency, high number of song posts, long display length, long total time and close proximity to the source. The individual response variables (Figure 12) are clearly inter-correlated, and so I reduced these data to the main independent axes of variation via Principal Components Analysis.

Only the first axis had an eigenvalue greater than 1.0 (Table 5a), and it explained 61.9% of the total variance in the data. The correlations of the scores along this axis with the original variables (Table 5b) suggest that the axis can be interpreted as one of ‘strength of response’: birds that responded strongly for one variable did so across all others. For the analysis below, I use the term ‘response’ to refer to the factor scores along this axis.

Table 5: Results of a PCA showing (a) that the first component explains 61.897% of the variation in responses between white-crowned and black-crowned males in the playback experiment. The component matrix (b) shows the relationship between the 6 variables.

(A) Total Variance Explained

Component	Initial Eigenvalues			Extraction Sums of Squared Loadings		
	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	3.714	61.897	61.897	3.714	61.897	61.897
2	0.810	13.493	75.390			
3	0.783	13.053	88.443			
4	0.439	7.321	95.764			
5	0.227	3.785	99.549			
6	0.027	0.451	100.000			

(B) Component Matrix

	Component
	1
Latency	-.629
Novel	.941
Total	.949
Puffback	.736
Distance	.625
TST	.775

A 2-way ANOVA tested the response (scores along PCA1) to singers with different crown colours (i.e. the playback) of responders with different crown colours (Table 6). The analysis showed that white-crowned birds displayed a significantly stronger response to song

playback than black-crowned birds, but the crown colour of the singers made no difference, and there was no interaction.

Table 6: Results of the 2-way ANOVA into the effect of responder crown colour and recording crown colour on the overall response (measured through factor scores extracted from the PCA.)

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Crown colour of responder	4.560	1	4.560	5.511	0.031
Crown colour in recording	.551	1	0.551	0.666	0.426
Crown colour of responder *Crown colour in recording	.302	1	0.302	0.365	0.554
Error	14.065	17	0.827		
Corrected Total	20.000	20			

a. R Squared = .297 (Adjusted R Squared = .173)

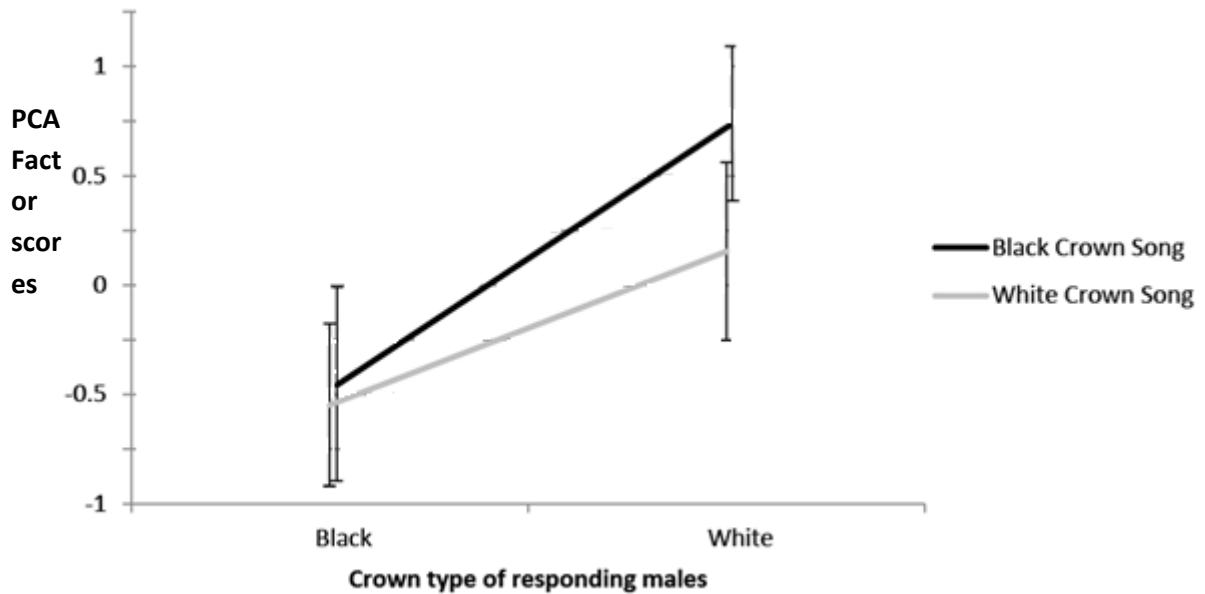


Figure 13: The effect of crown-colour of the recorded bird on the response (measured through PCA factor scores) of white-crowned and black-crowned males. Error bars show standard error.

It is perhaps worth noting that for one of the component variables of the PCA axis, the total singing time, approached a significant difference

between the crown colours of the recorded singers: males responding to the songs of black-crowned birds sang longer than in response to the songs of white-crowned birds (two-tailed t-test, $t = 2.12$ $df = 13.1$, $p = 0.054$).

In some territories, females joined their partners in singing in response to the recording. Of the pairs tested, 4 out of the 14 possible white-crowned females participated in territorial singing in response to the recording, although. None of the 7 possible black-crowned females contributed, yet this was not a significant difference ($\chi^2 = 2.47$, $df = 1$, $p = 0.11$).

Discussion

This study has given us the first opportunity to investigate a possible function of the white crown, and of its delayed maturation. Despite presenting evidence to suggest white-crowned birds are more aggressive than black-crowned and that an age-related assortative mating system could exist, this is not conclusive evidence that a status signalling system is found in the wheatear. Should future studies show that there are further differences in quality between white-crowned birds and black-crowned birds (such as in breeding success) and that the crown-colour is used to modify levels of aggression in territorial encounters, then there would be sufficient evidence to conclude that crown-colour in this species of wheatear is a signal of age and status. Furthermore, this would be the first case of such a signalling system in the wheatears, and the first case in any arid-living, sedentary bird.

White-crowned birds responded more strongly in the playback experiment than black-crowned birds. This is most evident in the higher total number of song posts used and the closer approach to the speaker by the white-crowned males. Approaching an intruder is seen as a sign of aggression in other bird species and is the precursor to escalated agonistic behaviour (Peake *et al* 2001). Number of song posts has not been directly linked to levels of aggression; however, in blue tits (*Parus caeruleus*) number of flights per minute has been so

linked (Poesel and Dabelsteen 2005). Flights per minute can be considered analogous with song posts per minute since birds must fly from one post to another. Therefore the total number of song posts in a defined period of time can be used in a test for aggression. As a result, it can be seen, that white-crowned birds are more aggressive than their black-crowned conspecifics.

The focal male's reaction was independent of the crown colour of the male used to produce the recorded song. This suggests that either; males are not able to infer the crown colour of an intruder through song alone, or that males are able to recognise whether the song is produced by a white-crowned or a black-crowned bird but react to both with equal levels of aggression. There are insufficient data to conclude which of the above assumptions is likely to be correct; this species of wheatear has a large repertoire of songs and there appears to be great variation between any two birds' territorial song (Svensson *et al.* 2010; Hareeb Mansoor, pers. comm.). With a sample size of just four, no obvious difference in the characteristics of white-crowned and black-crowned song can be determined by spectral analysis.

In birds, larger body size is generally linked with greater aggression (Breitburg 1987). White-crowned birds were not significantly larger than black crowned birds. Consequently, larger body size does not appear to be the cause of the higher levels of aggression in white-crowned males: another factor could be responsible. The variables for which white-crowned birds reacted most aggressively were in song posts visited and how close they approached to the source of the sound. Both of these variables could be attempts by the males to locate the intruder within their territory. In visualising their competitor, birds with honest signals of status are able to exchange information regarding the threat they face and the threat that they themselves pose (Greene *et al* 2000). For black-crowned wheatears, lower levels of aggression combined with the lack of adult crown colour could be a strategy to avoid the aggression of mature white-crowned birds through a status signalling system similar to that described in Lyon and Montgomerie (1986).

Across the entire study, there is no effect of crown morph on partner preference: same-colour pairs are no more prevalent than mixed pairs. However, in towns, mixed pairs are significantly rarer than matching pairs. This result suggests that age-related assortative mating is present to some degree in town environments. It could be an artefact of pairs remaining together for many years, and therefore their original mate choice would be independent of current crown colour – birds that paired when one individual was black-crowned and the other was white-crowned would both appear white-crowned two years later. This possibility is supported by the similar survival rate between crown-types which could suggest that younger birds are equally capable of finding food and avoiding predation as older animals. It might be that the most favoured territories occur in towns and hence older, more aggressive and more experienced pairs obtain and hold them. Continued monitoring and specifically following divorced birds and recording newly formed pair, could help to explain why there appears to be age-related assortative mating in town but not in wadi pairs.

Home range size was independent of crown morph, as it was in town versus wadi habitats. Therefore, despite differences in aggression, both crown colours had access to a similar amount of resources. Year-to-year survival was also similar between crown colours. The recorded year-to-year survival rate of 0.5 is a minimum estimate because emigration can mean ringed birds leave the area and are not recorded. No previous studies have looked at survival rate in this, or any other, species of non-migratory wheatear, but it has been investigated in the migrant Northern Wheatear and in the fellow Muscicapid and partially migratory European Robin (*Erithacus rubecula*). Year-to-year survival rates in these species are 0.46 (Low *et al.* 2010) and 0.42 (Siriwardena *et al.* 1998) respectively. However our figure is based on just 28 individuals, too small for testing for differences between the wheatear's survival rate and the values for the two other species. Consequently, monitoring survival in future years will be necessary to provide an estimate with a greater level of confidence. The prediction to be tested

is that survival rates of passerines in arid environments are greater than conspecifics and closely related birds in wetter climates (McCleery *et al.* 1998; Newton 1998). The similar survival rates between wadi and town birds means that birds in both habitats are equally effective at finding food and avoiding predation. In temperate climates, survival in urban environments is expected to be greater than in rural environments (Hörak and Lebreton 2008). Human settlement comes with a steady food supply, but also a greater threat of predation and an increased level of disturbance. It appears that the combined effect of these factors may neutralise any survival benefit, giving town birds similar survival rates to wadi inhabitants. However, the study area was relatively small, and wadi habitats were still frequently visited by humans. Increasing the size of the study area to include wadis much further away from towns would give a better idea of survival in wadi-living birds.

Wheatear density has increased in the study area since 2011 to a value more comparable with the 11.1 birds per km² found by White *et al.*'s (2007) study in the St. Katherine region. This indicates that there is high temporal variability in wheatear numbers in the area. It is unlikely that the increase in density can be explained by local breeding because nesting success was estimated to be low in 2011 (Pio 2011). Therefore, it is more likely that there has been migration of individuals into the area. Pio (2011) observed significantly more females than males in the St. Katherine region as well as significantly more white-crowns amongst male wheatears, neither of which were observed this year. This could therefore suggest that there has been a large number of young males moving into the study site between seasons. The higher density values indicate that town environments are able to support a larger population of wheatears than wadi environments. However, this was without a corresponding decrease in overall home range size. Most of the town pairs had home ranges that only partially overlapped the settlements, with the predominant proportion being bare ground or the side of surrounding mountains. It is in these surrounding mountains

that most roosts and nest were observed and therefore it is likely that in both towns and wadis, a similar home range size is necessary to provide an adequate range of habitat types to support all behaviours.

Morphometric data from recaptured birds does not suggest significant growth in adults over a twelve-month period; however, the sample size was small. All surviving birds that were black-crowned in 2011 had developed full white crowns in 2012, implying a low moult age: the greater the moult age, the lower the probability that any given bird will pass through it in a 12 month period. Therefore in order for all four birds to change within one year, a low moult age is more probable than a high one. Again, the low sample size and the inability to age birds accurately during this field season meant that this cannot be supported statistically.

Comparing the moult stage of the outer greater coverts to that of the crown revealed that the crown moult can coincide with wing moult. Birds of this subfamily begin to go through wing moult nine months after fledging (Andy Lowe, pers. comm.); and hence the crown moult may begin as early as nine months into a bird's life. Subsequent researchers can now more accurately age wheatears in the hand; birds with dull blackish-brown outer greater coverts and a fully black crown should be considered to be less than one year old; black-crowned birds with glossy black outer greater coverts are likely to be between one and two years old, with their white crown developing in this time.

This study confirms that age-related variation in aggression is present in birds living in arid habitats, whilst previous studies have only shown its existence in temperate-living species. Our understanding of arid-living birds is currently poor compared to what we know of birds in temperate regions.

3. Nest success in relation to location, crown morph and rampart function

In the previous chapter, differences in body size, aggression and home-range area between crown morphs was measured. White-crowned birds were found to be more territorially aggressive than black-crowned. This suggests that the colour of the crown could be used as a signal of status, as in many well documented cases in other species where honest signalling of aggression through plumage variation/dimorphism is understood.

The majority of discussion so far has been concerned with the male of the species, particularly in regards to territorial aggression as this offers us the ability to assess male quality. However in an apparently sexually monogamous species with a sex ratio of around 0.5, it is important we consider both male and female. This chapter shifts focus onto the female wheatear, where quality can be measured primarily through breeding success.

A bird's breeding success is also an important measure of quality which can (and often is) signalled through plumage variation. The presence of differences in breeding success between white-crowned and black-crowned birds could also indicate that the white crown could be a signal. Prior to Pio (2011), no studies have been carried out looking at the wheatear's breeding success, perhaps because data must be gathered over many seasons and, due to the environmental conditions, long-term field studies are more difficult to perform in arid environments than in temperate conditions. The records that are available suggest that clutch size and breeding success is lower in arid-living birds than in temperate-living species (Nice 1957; Ashmole 1963; Ricklefs 1980; Suarez and Manrique 1992; Engelbrecht 2008), whereas year-to-year

survival is generally, but not always, higher (Newton 1998; McCleery *et al.* 1998; Schaefer *et al.* 2006; see chapter 1).

As well as being inadequately studied in terms of breeding success, the wheatear displays some rare and poorly understood nest-building behaviour by building an extensive rampart of flat coin-like stones leading from under the nest cup out through the entrance hole of the nest (Fischman 1977, Palfrey 1988, Pio 2011). Fischman (1977) observed only females performing this behaviour in the weeks before laying.

The White-crowned Black Wheatear is one of only 29 known passerine species that use stones to build a rampart from the nest; the function of the structure is unknown. It had been suggested in other species that it may serve to regulate nest temperature, provide support to the nest cup and to offer protection from the weather (Afik *et al.* 1991; Richardson 1965; Moreno *et al.* 1994), yet evidence does not support these hypotheses (Leader and Yom-Tov 1998; Moreno *et al.* 1994). In the Black Wheatear, the building of the rampart (conducted mostly by the male) appears to be a form of sexual display (Moreno *et al.* 1994) allowing the female to judge the male's quality, which in turn alters their own breeding efforts. In the White-crowned Black Wheatear, only females have been observed carrying stones (Fischman 1977) and therefore rampart building is unlikely to be a sexual display (Moreno *et al.* 1994). Leader and Yom-Tov (1998) found that the rampart built by the Blackstart (*Cercomela melanura*) was not constructed as a sexual display, and in turn suggested it provides the nest with protection from predators by providing audible and visual warnings of an approaching predator, allowing the birds to flee the nest; a hypothesis that is so far untested in the wheatear (although see Pio (2011)).

This chapter presents data collected during the 2012 breeding season. The primary aim of this chapter is to compare breeding successes between the crown morphs, both in terms of the individual females and their breeding pair combinations. Differences in breeding success

between crown colours in favour of white-crowned birds would complement their higher levels of aggression and potentially implicate the crown colour's role as a potential signal of status. This chapter also analyses breeding success based on nest structure and location, providing information currently lacking for arid-living bird species. Finally, the defensive hypothesis for the function of the rampart is tested to try to understand the role of such an energetically costly behaviour.

Methods

Observations

The results in this chapter were gathered from the same population of wheatears described in Chapter 1. Nests of breeding pairs were located by following behavioural cues, such as birds carrying nesting material. The apparent absence of the normally conspicuous females indicated birds were nesting. Nest locations were recorded using a Garmin e-trek Legend H GPS unit and Google Earth version 6.2 (Google Inc.). Nests were categorised based upon the crown colours of the breeding birds and the nest substrate (i.e. in natural rock holes/crevices or in man-made buildings), A USB endoscope (Vonics Snake Vision) was inserted into the nest cavity to observe the stage and status of the nest. This was repeated approximately every 4 to 5 days per territory. The success of each nest was calculated using Mayfield's-40% analysis (Johnson 1979).

Playback experiment on rampart function

Recordings for the playback experiment were produced as in Pio (2011), but instead of producing a single two-minute sound file containing both the ambient noise control and the experimental sound, sound tracks one-minute long of each were recorded. The recording apparatus was constructed as in Pio (2011) on a granite slope of

approximately 10°. Stones were retrieved from a permanently abandoned wheatear nest and placed across the centre of the frame to resemble a natural rampart. A Benro MZW 70-1 microphone connected to a Marantz PMD 660 recording device was placed 30 cm from the rampart. A Samsung ST90 camera was also used to observe the movement inside the apparatus (see appendix). The 1 minute *ambient* track was recorded before the snake was introduced. The snake used for the recording was a desert sand snake (*Psammophis schokari*) 98 cm long trapped by a local Bedouin. Immediately after the snake's introduction a further minute was recorded to make up the *snake* sound file. Furthermore, the sound file made in 2011 was split using Audacity v.1.3 software to separate the ambient minute from the experimental minute and therefore provide a second pair of recordings. Links for downloading all four sound files (two *ambient*, two *snake*) can be found in the Appendix and a spectrogram can be seen in Figure 19.

Experiments were carried out between the hours of 1100 and 1400 on dry days with low winds. Nests were only investigated during the incubation stage, as after this time, females did not remain inside the nest for extended periods. Nests were observed until any incubating female exited. An Altec Lansing Orbit MP3 model iM237 field speaker was placed 30 cm to the side of the nest entrance and connected via a 5 m long stereo cable to a Samsung GT-S5560 mp3 player. Ten minutes after the female returned to the nest, the playback began. Birds were provided with one of the four recordings chosen at random and observed from a 5 m distance, out of sight of the bird within the nest. Should the bird flee the nest, the time that this occurred was recorded. If possible, birds were tested again after a minimum of three days using the corresponding recording (ambient or experimental); this was not possible if nests had hatched or failed.

Ambient noise levels at the nest entrance were measured using a Maplin Mini Sound Level Meter, by recording the greatest dB value during 3 minutes. Recordings were made during the same time of day as the playback experiment, however, due to a delay in getting this

piece of equipment to the study site, sound level measurements were performed on different days to the playback experiment.

Statistical tests

The R software package version 2.13.2. (The R Foundation for Statistical Computing) and SPSS version 16.0 (SPSS Inc.) were used to perform all statistical tests. Residuals for each analysis were tested for normality (Shapiro-Wilk test). If the data was normally distributed, ANOVA or equivalent was performed; in the case that the data was non-parametric, a Kruskal-Wallis test was utilised.

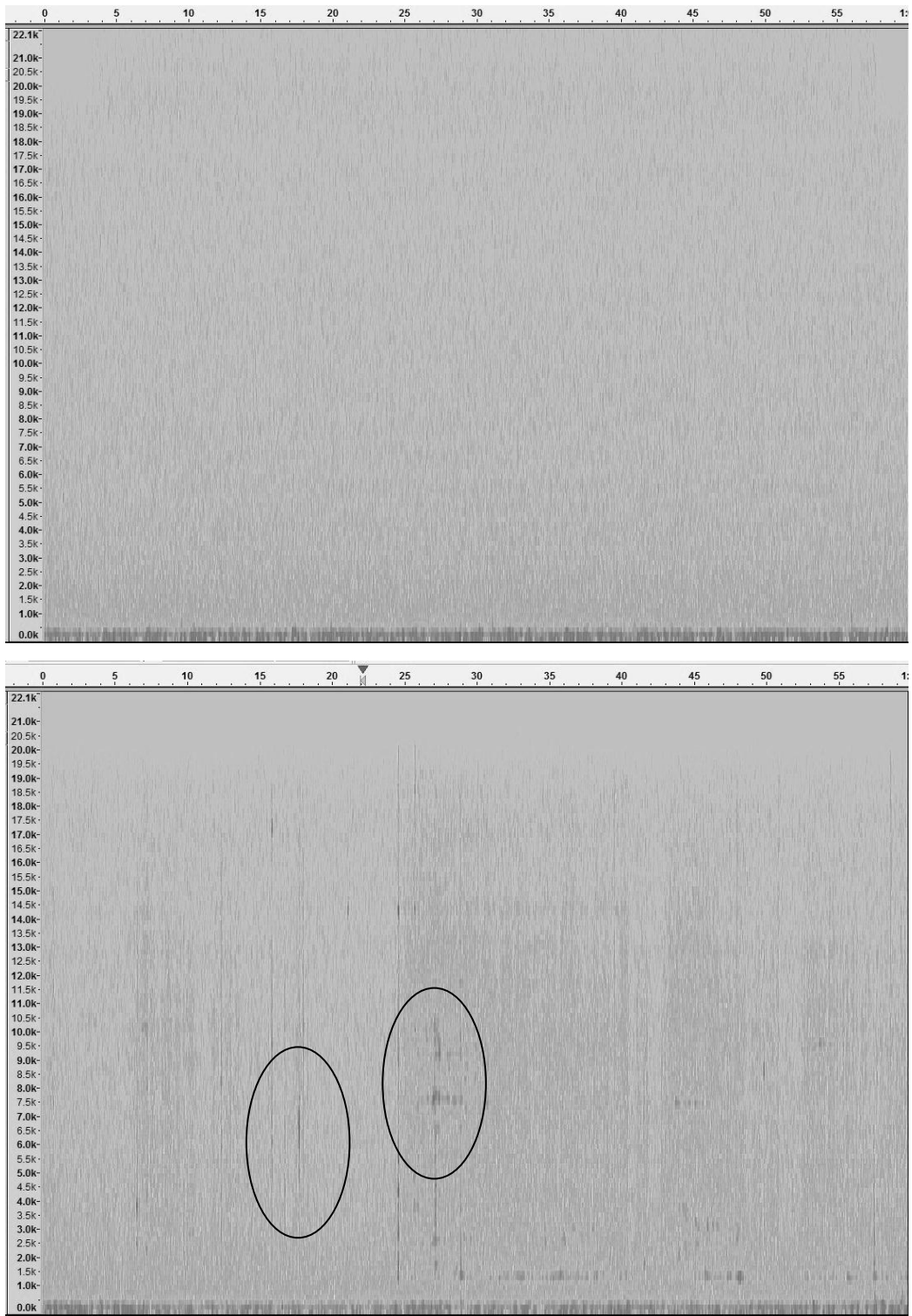


Figure 14: Spectrograms of recordings from the rampart. Top: *Ambient*. Bottom: *Snake*. Axis show frequencies in kHz (x-axis) and Time in seconds (y-axis). Circles indicate noise caused by disturbance of the rampart.

Results

Nesting Success

Between the 18th March and the 27th May, 14 nests were observed across 12 breeding pairs. It is likely that more pairs in the study site nested, but these attempts were not seen because nests were inaccessible either due to terrain or lack of local permission. Of the 12 breeding pairs, there were four black-crown/black-crown, five white-crown/white-crown and three mixed pairs; the female was white-crowned in seven pairs and black-crowned in six (additional female due to remating). These numbers are similar to the crown colour ratios found in the St. Katherine population as a whole (numbers of each pair type in the total population compared to the nesting population: $\chi^2 = 0.566$, $df = 2$, $p = 0.75$; number of white crowned females in total population compared with the nesting population: $\chi^2 = 0.357$, $df = 1$, $p = 0.55$).

The summary of the nesting data (Tables 7 and 8 - also see Appendix for proportional survivals and binomial confidence intervals) shows the total counts used for the Mayfield's, clutch sizes and fledgling numbers as well as the calculated measures of breeding success. Also presented are comparable numbers from the previous year, from Pio (2011). The results for the Mayfield's analysis are separated into four measures of success – nest success, the probability of a nest producing at least one fledgling; incubation success, the probability of any given egg surviving to hatch; hatchling success, the probability of any given chick surviving to fledge; and Egg success, the probability of any given egg to survive to fledge. For successful birds, the average clutch size was 2.5 ± 1.04 ($n = 6$) and number of fledglings was 1.8 ± 0.983 ($n = 6$). Incubation success and hatchling success were not significantly different ($\chi^2 = 1.02$, $df = 1$, $p = 0.31$), meaning that there was no evidence of any difference between survival rates of eggs and hatchlings.

Table 7: Values of the variables using in the Mayfield's Estimation. "Nest days" is the total number of days with nest contents present; "Egg days" is the number of days with eggs present. "Hatch days" is the number of days with hatchlings present. "Eggs lost", "Hatch lost" and "Nest lost" is the count of eggs, hatchlings and entire nest contents lost respectively. The total for all birds is then broken down based of female crown-morph and pair crown-morph combinations.

Mayfield's Variables						
	NEST DAYS	EGG DAYS	HATCH DAYS	EGGS LOST	HATCH LOST	NEST LOST
ALL	133	122	191	3	9	4
WC Female	105	90	112	1	4	1
BC Female	28	32	82	2	5	3
WC Pairs	65	42	80	1	3	1
Mixed Pairs	42	48	63	0	3	1
BC Pairs	26	32	48	2	3	2

Table 8: Summary of the wheatear breeding season in 2012. Descriptives of clutch size and fledgling numbers, and the results from the Mayfield's estimations are given broken down by female crown-morph, pair crown-morph combinations and nest location. Mayfield's estimations give probabilities – for instance the Incubation success is the probability that any egg will survive the incubation period to hatch; they are not direct proportions of eggs or hatchlings which survive to the next stage. ^a Pio (2011) did not produce Mayfield's estimations. These values are proportional survival numbers and are included for comparison.

	Descriptives:			Mayfield's estimations of:			
	# Nests	Mean Clutch Size ± SE	Mean Fledglings ± SE	Nesting Success	Incubation Success	Hatchling Success	Nest Success
2012	14	2.62 ± 0.24 n = 13	1.00 ± 0.36 n = 11	0.43	0.71	0.51	0.35
2011 (Pio)	11	3.00 ± 0.38 n = 8	1.13 ± 0.48 n = 8	0.375 ^a	0.75 ^a	0.5 ^a	0.3 ^a
WC F	7	2.38 ± 0.29 n = 6	1.50 ± 0.56 n = 6	0.76	0.86	0.60	0.76
BC F	6	2.50 ± 0.43 n = 6	0.40 ± 0.25 n = 5	0.04	0.41	0.41	0.04
WCWC	5	2.60 ± 0.24 n = 5	1.67 ± 0.88 n = 4	0.65	0.71	0.59	0.42
BCBC	5	2.25 ± 0.48 n = 4	0.50 ± 0.29 n = 4	0.11	0.41	0.41	0.16
Mixed	3	2.66 ± 0.58 n = 3	1.33 ± 0.89 n = 3	0.51	1.00	0.51	0.51
House	6	3.00 ± 0.36 n = 6	1.00 ± 7.1 n = 4	0.46	1.00	0.46	0.32
Natural	6	2.50 ± 0.22 n = 6	1.00 ± 0.52 n = 6	0.18	0.37	0.48	0.28

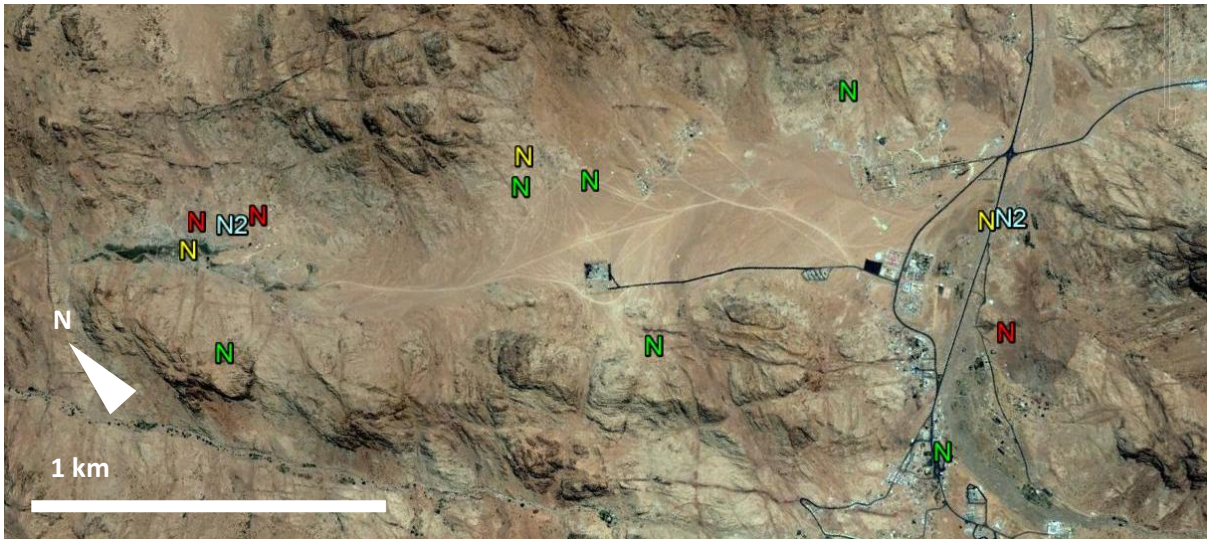


Figure 15: Map of the locations of nests in the St. Katherine study area. First nesting attempts have the symbol “N” and second broods are “N2”. Nests that succeeded in raising one or more fledglings are shown in **green**; failed nests are shown in **yellow** if they failed during incubation and **red** if failure occurred with hatchlings. Nests still in use after the 29/05/2012 appear in **blue**, the outcome of these nests is unknown.

The locations and survival status of nests are plotted in Figure 15. Of the 14 nests observed, six failed between initiation and fledging; of these the cause of failure is known in five cases; foxes dug up and destroyed two at the incubation stage (Gecchele, pers. comm.) and children removed the hatchlings from the other three. In the remaining case, there were no obvious signs of disturbance around the nest, yet eggs could no longer be found inside. The lack of nest contents indicates predation, possibly by snakes or rodents which, in comparison to larger predators such as foxes, would be more likely to be able to enter the nest without disturbing the rampart.

Nests in the walls of buildings were more likely to survive the incubation stage than nests in natural holes and crevices ($\chi^2 = 4.2$, $df = 1$, $p = 0.04$), whereas, overall nest success and Nestling success were similar for both. The decision to use nests in natural holes or holes in walls was independent of the breeding female’s crown colour ($\chi^2 = 0.75$, $df = 1$, $p = 0.39$).

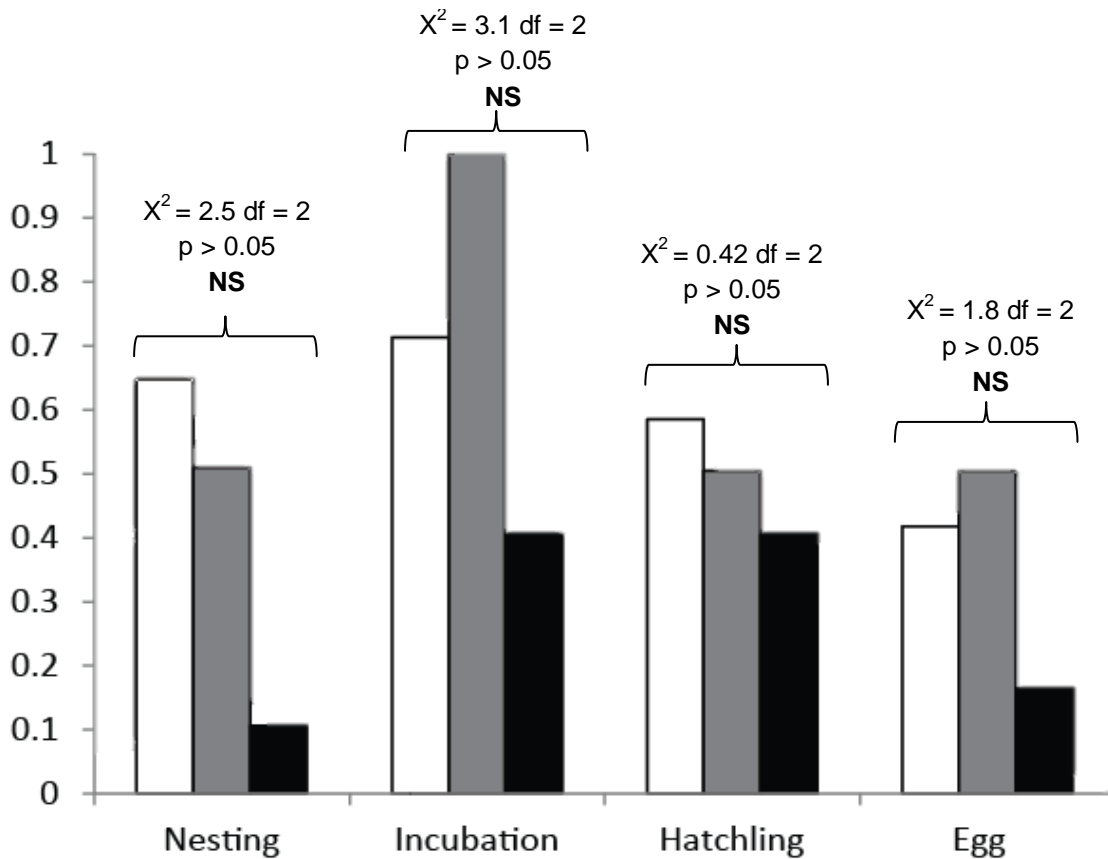
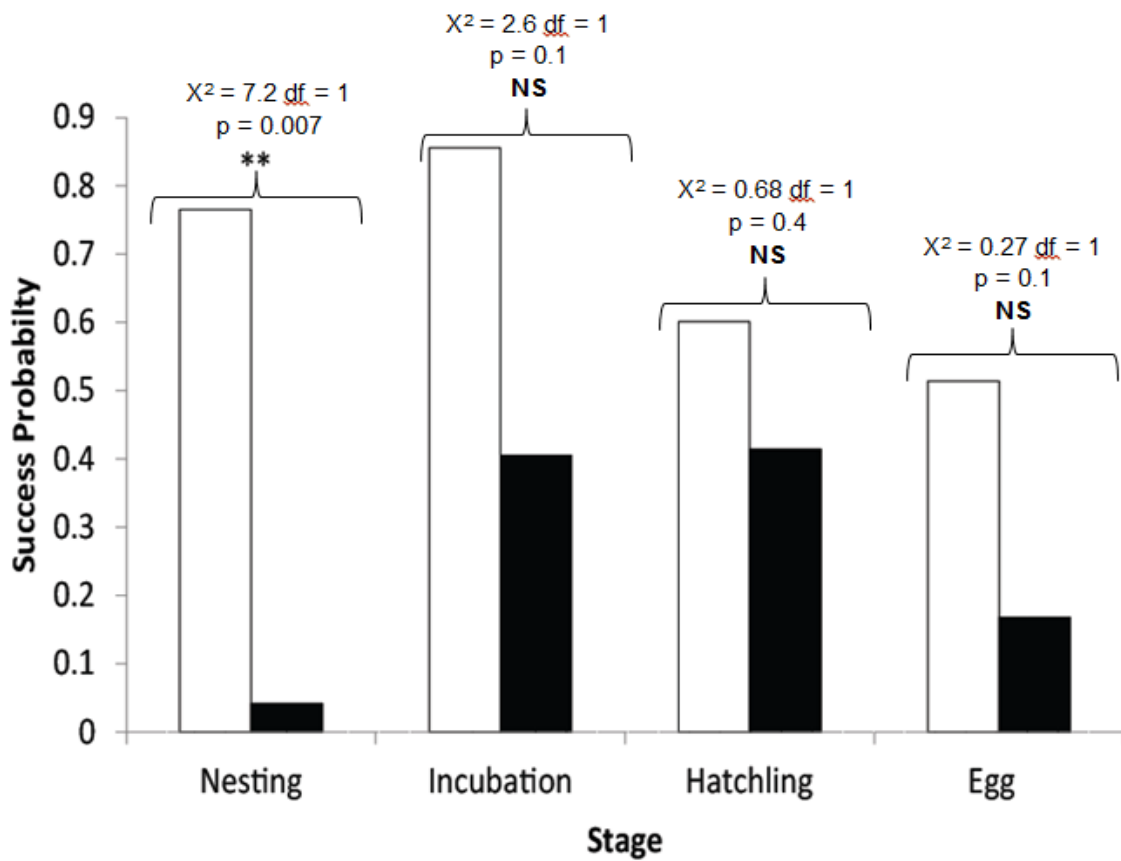


Figure 16: Nesting success estimates following Mayfield's analysis. TOP: Success over the four different measures by female crown-morph (white-crowned and black-crowned respectively). BOTTOM: Success over the same four measures by pair crown-morph combination, white-crowned pairs (white bars), mixed crowned pairs (grey bars) and black-crowned pairs (black bars). Values and probabilities obtained from Chi squared tests. NS = not significant, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

There was no evidence that average clutch sizes differed depending on the females crown colours ($t = 0.4472$, $df = 1.531$, $p\text{-value} = 0.71$). Pairs with white-crowned females were significantly less likely to have nests fail, and therefore significantly more likely to rear at least one fledgling than black-crowned females ($\chi^2 = 7.22$, $df = 1$, $p = 0.007$.) There was no evidence that incubation, hatchling and nesting success differed between female crown-morphs (Figure 16). There was also no evidence that white-crowned pairs, black-crowned pairs and mixed pairs differed across any indicator of breeding success (Figure 16).

Two pairs whose first nests had failed were the only birds witnessed initiating a second brood. New eggs were laid between one and two weeks after the first nest failed. Both pairs lost their first nests due to human interference (children removing hatchlings from nests), but this did not prevent both pairs raising their second brood in the walls of houses. In both cases, the wheatears used old nests that had existed in their territory for at least two seasons; they were never seen carrying new nesting material to these nests, but it is possible this occurred whilst not being observed.

Playback experiment on rampart function

The spectrograms of the *snake* recordings were analysed in conjunction with the video recording to determine when the snake was disturbing the rampart. This was found to be after 3 seconds in the 2011 recordings, and 30 seconds in 2012. Before these times, the *snake* sound files were equivalent to the *ambient* sound files and any response by the experimental birds in this period could not be due to the presence of the snake.

Seven accessible nests were discovered during the incubation stage. Six nests were tested with just one of the recordings (*snake* or *ambient*) and one nest was provided with both. Because the second test nest was not independent, it was excluded from analysis. Three nests received the *ambient* noise recording; four received the *snake* sound

file. All three birds that fled the nest were presented with the *snake* sound file, but one of them fled during the ambient section of the track and therefore its behaviour was not caused by the sound of the snake on the rampart. All birds that received the *ambient* recording remained in the nest. When only the type of sound file was considered, birds were significantly more likely to flee the nest when presented with the *snake* recording (Fisher's exact test, 0/3 v 4/0, $p = 0.029$). But more accurately, when you consider the bird that fled during the ambient section of the *snake* recording as a bird fleeing to ambient noise, not to the sound of the snake, there is no significance (Fisher's exact test, 0/3 v 3/1, $p = 0.14$).

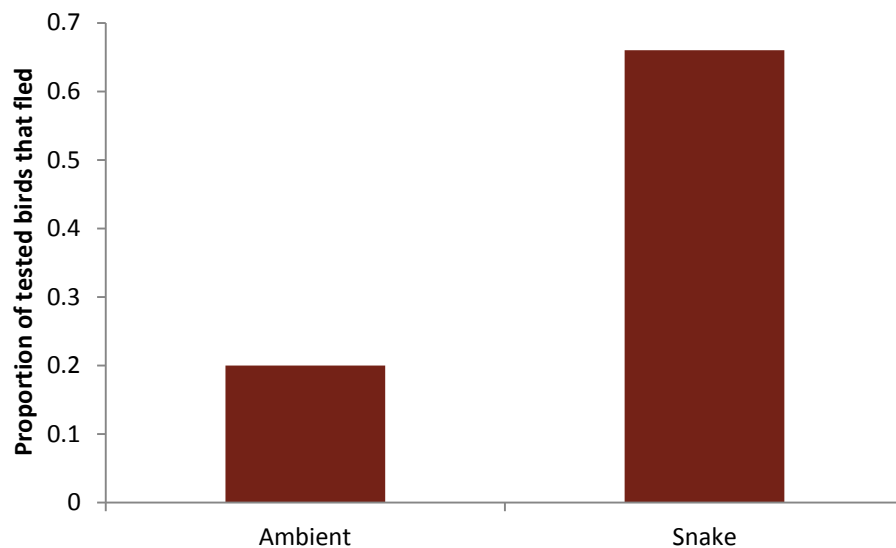


Figure 17: Proportional responses of incubating females to being played the *ambient* and the *snake* recordings.

The bird that was tested with both the *snake* and the *ambient* recordings remained in the nest for the ambient noise and fled when the sound of the snake was present.

Discussion

The breeding data presented here is the first detailed examination of differences in breeding success between wheatear crown morphs. White-crowned birds had significantly fewer nest failures than black-

crowned birds and were therefore more likely to succeed in raising at least one fledgling. Therefore, there is a difference in quality measured by breeding success between the two crown-morphs. Advertising breeding success through plumage variations/dimorphisms is commonly seen in other bird species, yet this data is unable to confirm the presence of such a signalling system in the White-crowned Black Wheatear.

Despite fewer complete nest failures, the overall survival probability of a single egg or nestling is similar for black-crowned and white-crowned birds. This indicated that white-crowned birds avoided total nest failure more frequently than black-crowned, but were equally unable to prevent the loss of individuals eggs or hatchlings. The main causes of complete nest failure were predation and human interference; the results therefore suggest that white-crowned birds are more adept at avoiding nest destruction than black-crowned birds.

Local habitat can be a significant contributor to nest success and predation rates in Muscicapidae birds (Burhans and Thompson 1999; Pärt 2001; Schneider *et al.* 2012). In the Northern Wheatear, nest success is dependent on habitat type (Pärt 2001; Schneider *et al.* 2012). There are two major habitat types in the St. Katherine study site; *town and wadi* (as defined in Chapter 1). No nests were observed in wadi areas, so therefore a direct comparison between the two cannot be performed. However, due to the similar ratios of crown colours distributed between the two habitat types (see Chapter 1), broad-scale choice of habitat for nesting is unlikely to explain the greater breeding success in white-crowned birds.

In both the towns and the wadis, nests could either be built in natural rock crevices or in the walls of buildings. Pairs with nests in buildings were less likely to lose eggs than those using natural nesting sites. There are many potential explanations for this: firstly, predators which usually take wheatear eggs in the region (snakes, rodents and foxes) may be unable to climb the vertical surfaces to nests in the sides of

houses. Secondly, the significant amount of anthropogenic waste in the area means much more food is available in this habitat than elsewhere; consequently predators may not need to raid bird nests for sustenance. Furthermore, local people actively kill all snakes in the area surrounding their houses because they are considered a threat to themselves and their livestock, thus eliminating a major threat to eggs.

Unlike the incubation stage, failure rates during the nestling stage in wall-nests were similar to those observed in natural holes during the nestling stage. The reason for this is slightly less clear given that the supposed advantages afforded to wall-nesters against predators should persist between nest stages. Wheatear nests are far more conspicuous during the nestling stage than the incubation stage due to the constant trips to and from the nest by adults feeding the young. Human destruction was equal to predation in causing nest failures in St. Katherine and it is possible that this increase in visibility led to more nests being discovered and destroyed. The differences in breeding success between nest types cannot be used to explain the differences in breeding success between crown colours as there was no evidence to suggest white-crowned birds preferred nesting in buildings rather than holes.

From the results on this year and the previous field season, it appears that successful breeders reuse nest sites. Also, birds whose nests have failed will either build at a new location or use a different old nest for the following breeding attempt. As white-crowned birds are older than black-crowned birds, they have survived more breeding seasons, and probably through trial and error have located a safe nest site. Conversely, black-crowned birds have only been territory holders for a maximum of two years, and have therefore had fewer chances to find a good nesting location. Similar age-related differences in breeding success are found in other species (Pärt 2001; Bradley *et al.* 1995; Sæther 1990). In the Northern Wheatear, Pärt (2001) found that the greater success of older birds was due to selecting nesting sites and

breeding territories associated with lower rates of predation than those selected by younger birds.

Nest defence can be both structural (in the form of site selection and construction) and behavioural. Nest defence behaviour was observed in the form of mobbing at many nests. Both white-crowned and black-crowned birds performed this behaviour and there was no evidence to suggest white-crowned birds mobbed more frequently or more effectively than their black-crowned conspecifics. White-crowned birds have been shown to be more aggressive in territorial defence than black-crowned birds (see Chapter 1). Male aggression has been shown to influence nesting success in tree sparrows (*Tachycineta bicolor*) in that more aggressive males have a higher nest success than less aggressive males (Betini and Norris 2012), however, this study measured aggression towards human intruders by males near the nest, unlike the method used in Chapter 2.

Rampart function

Our hypothesis of the function of the stone rampart is that it provides the wheatear nest with a defence against incoming predators by making a predator's approach audible to the bird inside, who could then react accordingly. As the sample size was low, results from the playback experiment are currently unable to test the prediction that females flee the nest upon hearing the sound of a snake on the rampart. The small sample sizes occurred because nests needed not only to be in an area with local permissions but also accessible to the researcher on foot, not always possible in mountainous terrain. Furthermore, nests frequently failed before they could be tested a second time. As a result of these difficulties, this study was unable to test the impact the rampart has on nest success. Should future study establish its function, it will be important to consider what effect, if any, differences in its structure and composition will have on nesting success. Furthermore, if there are differences between ramparts built

and used by white-crowned birds to those built and used by black-crowned birds, this could play a role in their differing nest failure rates.

General features of the wheatear breeding season.

The breeding season studied here and the previous season studied by Pio (2011) have obvious differences, primarily in their timing. All stages of nesting were delayed by around a month in 2012 compared to 2011. The summer of 2011 and the winter of 2011/12 were characteristically dry for the St. Katherine region, whereas there had been an unusually large amount of precipitation in the previous two years (Pio 2011). This wetter weather likely led to high invertebrate numbers earlier in the season, which in turn appears to drive wheatears to initiate breeding behaviour (Dingle and Khamala 1972; Sinclair 1978; Delinger 1980; Fischmann 1977). The month-long delay in nesting was also observed in concurrent studies on arthropods in St. Katherine (Katy Thompson, pers. comm; Olivia Norfolk, pers. comm).

Clutch size was smaller than any previous study (Pio 2011; Heim de Balsac and Mayaud 1962). Fischmann (1977) and Palfrey (1988) found a typical clutch size ranged between two and five eggs, with some birds producing up to seven. Such diversity in clutch size was not seen this field season; all nests had two or three eggs with the exception of one nest which had four. The average number of fledglings per breeding attempt (1.0) was also lower than in Pio (2011) (1.5). Previous studies (Fischmann 1977; Palfrey 1988) did not record fledglings per breeding attempt, so could not be compared.

Despite the smaller clutch size and fledgling number, nest survival at each stage was similar between Pio 2011 and 2012. However, as Pio (2011) estimated nesting success simply as a proportion of successes to failures rather than performing a Mayfield estimate, the effect of the failures is likely to be exaggerated, artificially lowering nesting success (Mayfield 1975). This means nesting was probably less successful in 2012 than in 2011.

Nesting success in wheatears has not been well studied in arid environments. One study showed that nesting success in the Black-eared Wheatear (*Oenanthe hispanica*) was 0.264 in semi-arid Iberia (Suarez and Manrique 1992). The probability of nest success in another desert Muscicapid, the Kalahari Scrub-Robin (*Cercotrichas paena*), was 0.271 (Engelbrecht and Derek 2008). In non-Muscicapid desert passerines with a similar range to the wheatear, the Thekla Lark (*Galerida theklae*) and the Lesser Short-toed Lark (*Calandrella rufescens*), success estimates were lower still at 0.149 and 0.157 respectively (Suarez and Manrique 1992). At 0.35, wheatear breeding success appears greater than in all these desert species (although only estimated for one breeding season). It is lower than for Muscicapids in temperate regions such as the European Robin (*Erithacus rubecula*) and Pied Flycatcher (*Ficedula hypoleuca*) where nest success can be as high as 0.55 and 0.735 respectively (Nice 1957). The high nest success compared to other desert birds could be an artefact of all nests being found within a small area; all nests were found in a 3.6-km² segment of the study area and all were within towns. As nesting success is so dependent on nest location and habitat type (Burhans and Thompson 1999; Pärt 2001; Schneider *et al.* 2012), a larger variety of nest locations needs to be studied to get a more clear understanding of the factors influencing nesting success in wheatears.

4. Overall discussion

The White-crowned Black Wheatear displays an age-related plumage dimorphism. In species of passerine living in temperate environments, similar dimorphisms have been shown to be signals of quality, typically as 'badges of status' or, more simply, as delayed plumage maturation.

The aims of this study were to investigate whether there was a corresponding difference in quality between white-crowned and black-crowned individuals measured through territorial aggression and breeding success. If the older white-crowned individuals are 'better' on measures associated with fitness, this would indicate that the white-crown is an age-dependent honest signal (Butcher and Rohwer 1989; Møller 1990; Reyer et al. 1998).

We found that, whilst body size and territory characteristics were independent of crown-morph, white-crowned birds were significantly more territorially aggressive. There was also some evidence of age-related assortative mating in town habitats, as pairs with matching crown types were significantly more prevalent than mixed.

We describe how white-crowned birds are also more successful breeders as measured by their fewer complete nest failures. Despite white-crowned birds being as likely to lose individual young throughout the breeding season, they were significantly more effective at avoiding complete brood destruction and therefore at raising at least one fledgling.

Consequently, both of these chapters have provided evidence that white crowned birds are 'better' on multiple measures associated with fitness. Thus, there is evidence to suggest that the white-crown could

be used as an age-dependent honest signal of a bird's quality (Møller 1990; Reyer et al. 1998; Pärt and Qvarnström 1997).

The data presented here do not confirm the use of the crown as a signal; they only suggest that crown morph and measures of quality are correlated. In order for the white-crown (or lack of) to be a signal, the appearance of the crown needs to influence the behaviour of others. In other words; 1) individuals should be more aggressive towards matching-crowned birds; and 2) crown morph should influence mate choice because higher-quality birds will be better able to identify equal quality mates. Whilst there appears to be evidence of the second statement within town birds, no direct test of the first statement was performed in this field season. Birds responded with similar intensity to songs produced by males of either crown-morph, and therefore it does not seem that crown morph is detectable from song alone.

To test for differences in aggression, the reactions of individuals when presented with intruders of different crown morph should be measured. This could be done by presenting artificial models of white-crowned and black-crowned wheatears to birds in the field and measuring the agonistic response. Should birds respond differently according to crown morph, then this will provide convincing evidence of the signalling function of the white crown.

A further function for crown morph to be a useful means of signalling quality would be the effective prevention of cheating (Zahavi 1975; Rohwer 1982; Grafen 1990; Qvarnström 1997). Whilst the mechanisms for preventing cheating may be complicated, the test for the presence of these mechanisms relies simply on observing a cheat's quality drop below its expected value due to being unable to respond to the increased aggression it receives from honest, higher quality birds (Rohwer 1982). This can be measured by, for example, the ability to establish territories or a change in territory quality (Pärt and Qvarnström 1997; Galvan and Sanz 2009). Experimental manipulation of wild birds has been used in the past to study the effect of cheating in

signalling systems (Qvarnström 1997; Galvan and Sanz 2009), but ethical issues could prevent this being used in future studies on the wheatear – particularly in regards to the bird's status in Bedouin folklore (see Appendix).

Future work by researchers in the St. Katherine Protectorate and other desert environments may be able to shed further light on the role of the crown in this species. It is also important to continue to gather more basic biological information about this and other desert species to close the sizeable gap between our understanding of birds living in temperate environments and those living in deserts. Although only in its second year, this long-term project focussing on the White-crowned Black wheatear has already produced interesting results on survival rates, size, distribution, breeding successes and nest structure. Together with Fischmann (1977), the project has also uncovered a number of interesting phenomenon and behaviours – including a potential age-related signalling system and the building of a stone nest rampart.

The wheatear's large population, its conspicuousness, and its confidence around humans mean working with this species overcomes many of the traditional problems with working with desert passerines. The fact that the bird displays such a range of often complicated behaviours and its cultural significance suggests that the species is worthy of many more years of study in order to further our understanding of desert birds and, furthermore, the field of ornithology as a whole.

Appendix:



Tales of Bedouin people and the White-crowned Black Wheatear in St. Katherine, Sinai.

How valuable wild animals are to humans is often considered by ecologists and conservationists when examining an environment. Often this consideration is based upon their worth as a commodity providing food and materials that can be used by the local population, with their role as a pest or a disease vectors also frequently examined. How humans utilise certain wild species affects the whole ecosystem. Hunting not only reduces the population of the hunted species, but also the population sizes of the animal's natural predators through decreased food supply or direct killing by humans to reduce competition. A human's desire for honey leads to the destruction of beehives but has also driven the formation of a mutualistic relationship

between humans and the Greater Honeyguide (*Indicator indicator*) (Isack and Reyer 1989; Dean *et al.* 1990). Both of these examples have humans directly profiting from their use of wild animals.

Many examples exist where humans persecute or favour a particular species, not based on the animal's material worth, but based on an innate fondness or aversion. This concept has been an important consideration in conservation efforts both locally and globally, with flagship species, selected based upon their charm and charisma, being used to inspire and educate (Western 1987; Verissimo *et al.* 2011). Species and environments that are esteemed by humans in such ways often never require conservation efforts due to the advantages they obtain by being so (Tiwari 1998). The reasons why humans are fond of some species but not of others are not always clear, but an animal's position in religion and folklore can influence how they are regarded by humans. The light in which some species are regularly portrayed in folklore affects how they are treated in reality, with some being feared (such as Crows and Ravens (*Corvus* sp.) which are represented as birds of ill omen, associated with death and doom) whilst others are celebrated as symbols of good luck, such as the White Stork (*Ciconia ciconia*) and the White-crowned Black Wheatear.

Unlike many resident, sedentary birds in the region, the White-crowned Black Wheatear can be very conspicuous, especially when demonstrating its varied range of songs and displays. The close association this species shares with humans has been noted by Fischman (1977) who termed them "The Bedouin's little friends."

Bedouin culture is rich in folklore and tradition. Despite many dramatic changes within the last 200 years, including the transition from a desert-living, nomadic lifestyle towards a semi-nomadic and sedentary way of life, these traditional stories are still very popular amongst many Bedouin men and women. The Wheatear (or Baga'a, Arabic بقعة) features frequently in these stories, where traditionally it is seen as a highly intelligent bird and a symbol of good luck.

What follows is a brief summary of the traditional stories associated with the Wheatear as told by Bedouin communities in St. Katherine, Sinai. All tales were collected in the 2012 field season alongside research into the Wheatear's biology.

Multiple stories mention the Wheatear helping lone individuals survive in the desert. The most common tale involved a young man out in the desert on his own. Becoming tired, the man attempts to sleep through the heat of the day. He lay down and rested his head upon a stone. Briefly afterwards, the man was woken by a Wheatear hovering over him, singing. The bird had spotted a venomous snake behind the man's improvised pillow and was attempting to warn the nomad of its presence (Faraj "Fox" Mahmood, pers. comm.; Mohammed Khedr, pers. comm.). Variants of this story mention the bird following the man to a new location and continuing to stand guard (Hareeb Mansoor, pers. comm.). Wheatears warning of snakes have been observed by multiple researchers (Fischman 1977; Palfrey 1988; see Introduction) in the form of mobbing. As described in the story, birds hover above the threat, issuing an alarm call. The Bedouin still use Wheatear mobbing to locate snakes around their houses.

Another popular story features the Wheatear as the saviour of a lone Bedouin stranded in the desert. A man releases his camel to graze whilst he rests. Before long, it had strayed beyond sight, leaving the man stranded. Whilst the man is searching, a Wheatear begins singing in front of him, before flying a short distance. The man follows and eventually is led to his camel (Faraj "Fox" Mahmood, pers. comm.; Hareeb Mansoor, pers. comm.; Ahmed Mansoor, pers. comm.).

A similar tale involves another man and his lost camel, this time in a Bedouin camp. The community's camels were all tied up outside the tallest tent in the camp. Because of its height, this tent became a popular singing post for a local male Wheatear, who was seen there every day. One day, a man woke to find his camel had got free in the night and wandered off; furthermore, the Wheatear no longer

performed his daily song and had disappeared. After a week, the man had still not found his camel, but the Wheatear had returned. The bird still snubbed the tall tent and instead began singing and hopping near to the man. The man began to follow the Wheatear and if he made a wrong turn, the Wheatear would fly to his other side. Eventually, the Wheatear led the man to a canyon where, unfortunately, the camel had fallen to its death. The Wheatear then returned to sing at the top of the tent (Hameeda Faraj, pers. comm.).

These stories bear many similarities to stories told about other birds, including the honeyguides of Africa. Whether, like the honeyguides, these stories have a basis in biology is uncertain, yet it is stories such as these that have led to the bird being considered intelligent, helpful and therefore a species to encourage to settle nearby.

Wheatear aggression and territoriality are seen as the bird showing loyalty to the land owners themselves (Fischmann 1977; Pio 2011). This belief is supported by numerous stories from the days where the Bedouin were solely nomadic. When the camp was moved a short distance away, there are reports of the birds from the original camp moving with the families to their new location (Faraj “Fox” Mahmood, pers. comm.). Thus a camp could exist alongside the same pair of Wheatears for a long period of time. In acknowledgement of this supposed loyalty, Bedouin families permit the bird to nest in the walls of their houses – a luxury not afforded to any other songbirds in the area. Families occasionally name their birds; during the 2012 field season a pair of birds, both called Zainab (Arabic زينب) were frequently observed. The owner of the garden called them both the same name because he was unable to tell the two adult birds apart. Another bird was jokingly named after me.

Killing the Wheatear contravenes the Bedouin system of law – again, a privilege not extended to other passerines in the area, which are frequently killed and cooked. Instead, Wheatears are often supplied with food and water. This favouritism may explain the Wheatear having

a relatively high population among passerines in Sinai (White *et al.* 2007) and has probably contributed to the bird's confidence around humans. However, whilst many Bedouin tribes consider all Wheatears to be good luck, the Awlad Saiid tribe believe that, whilst older Wheatears with white crowns are good luck, the opposite is true of the younger black-crowned birds. No explanations for this distinction could be obtained during my fieldwork.

The ecological impact of human favouritism for the Wheatear is unknown. Having access to a reliable food and water supply in such an arid environment is likely to give the Wheatear an advantage over other species that share a similar niche in the area, such as the Desert Lark (*Ammomanes deserti*) and Sinai Rosefinch (*Carpodacus synoicus*). Conversely the benefits the Wheatear obtains may trickle down to other species in the area – perhaps due to other species being able to take the food and water provided, or due to decreased competition for natural food. This will be an important avenue of study for future field seasons. It will also be interesting to investigate the biological basis of these stories; whilst it is known that Wheatears mob snakes and are attracted to camels for foraging opportunities (see chapter 2), the more complex behaviours described in the stories remain conjecture.

Examples of wheatear calls.

The recording of a black crowned female **alarm calling** can be found at the link below.

<https://www.dropbox.com/s/zoqpbafvso1ufle/Alarm%20call%20FCW%20female%20at%20nest.wav>

Spectrograms of four different copies of the **territorial song** of the white crowned black wheatear can be found in Figure 19 below.

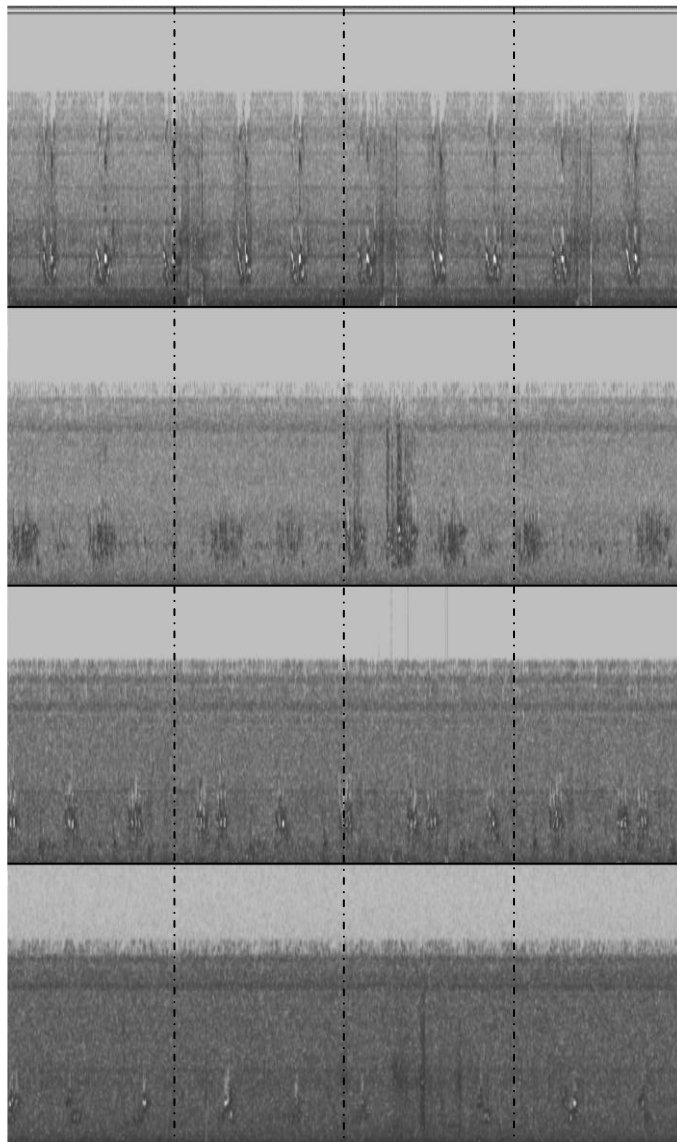


Figure 19: Spectrograms of the four sounds used in the playback experiment. The figure shows the one minute repeat which was replicated five times to produce the playback song.

The audio files used to produce these spectrograms can be found in the following link. The files were used in the song playback experiment and are labelled by crown-morph and location. These are the files used in the playback experiment so the full song has been looped to create songs of equal length.

<https://www.dropbox.com/sh/hp8b0jxzqktfmus/nUB2WyMOAD>

Ringling data – comparison between years.

Table 9: Comparison of morphometric data across 4 variables showing changes between Pio (2011) and 2012. N = 10 for all values. T-value obtained from a paired sample t-test, with significance indicated by asterisk. $p < 0.001 = *$. The change in tarsus size between years is a result of changing the system of measurement.**

Measurement	Value (cm) (\pm SE)		t-value
	2011 (n = 27)	2012 (n = 47)	
Wing	107.2 (0.81)	106.45 (1.21)	0.86
Tail	71.3 (0.75)	69.3 (1.38)	2.02
Tarsus	25.88 (0.36)	27.1 (0.36)	-5.91***
Weight	30.85 (0.88)	28.79 (0.67)	2.18

Snake recording

All four recordings used in testing the defensive function of the rampart can be downloaded from the link below. There are two control *ambient* sounds and two experimental *snake* recordings. One set of recordings was edited from Pio (2011) and is labelled as such, the other was produced entirely in 2012.

<https://www.dropbox.com/sh/kgn7czu9qfp8v95/sDqmEny6hF>

2012 recordings were produced near the field accommodation in Wadi Sreig ($28^{\circ}33'50.44''$ N, $33^{\circ}57'33.47''$ E) using an animal trapped and released in Wadi Arbaeen ($28^{\circ}32'13.92''$ N, $33^{\circ}57'52.06''$ E). The recording setup can be seen in Figure 20.



Figure 20: Apparatus used for recording rampart sounds shown from the top (left) and the side. Circle indicates the position of the microphone during recording.

Nesting success as a proportion of survivors to losses.

Table 10: Estimates of nest success based on proportional survival of eggs or hatchlings through the nesting stages as opposed to the Mayfield's estimations used in Chapter 2 which provides the probability of surviving each stage based upon the number of loses each day. In this table, proportions are provided with their asymmetrical upper and lower confidence intervals for each nesting stage. Proportions are also given based on female crown-morph and pair crown-morph combinations.

	Eggs laid that Hatched			Hatchlings that Fledged			Eggs laid that Fledged		
	Proportion	Lower CI	Upper CI	Proportion	Lower CI	Upper CI	Proportion	Lower CI	Upper CI
All	0.76	0.51	0.92	0.62	0.34	0.83	0.47	0.25	0.71
WC Female	0.83	0.54	0.97	0.80	0.45	0.96	0.67	0.37	0.88
BC Female	0.60	0.19	0.92	0.00	0.00	0.63	0.00	0.00	0.50
BCBC	0.60	0.19	0.92	0.00	0.00	0.63	0.00	0.00	0.50
Mixed	0.75	0.25	0.99	1.00	0.37	1.00	0.75	0.25	0.99
WCWC	0.88	0.50	0.99	0.71	0.34	0.95	0.63	0.29	0.89

References

- Afik, D., Ward, D. & Shkedy, Y. (1991) A test of the self-incubation hypothesis for desert birds that build a rampart of stones in front of their nests. **Journal of Thermal Biology** 16(5): pp.255–260.
- Anava, A., Kam, M., Shkolnik, A. & Degen, A.A. (2001) Heat production and body temperature of Arabian Babblers (*Turdoides squamiceps*): a bird from hot desert habitats. **Journal of Arid Environments** 48(1): pp.59–67.
- Ashmole, N.P. (1963) The regulation of numbers of tropical oceanic birds. **Ibis** 103(3): pp.458–473.
- Baha El Din, SM (1999) Directory of Important Bird Areas in Egypt. **BirdLife International**.
- Betini, G.S. & Norris, D.R. (2012) The relationship between personality and plasticity in tree swallow aggression and the consequences for reproductive success. **Animal Behaviour** 83(1): pp.137–143.
- Bolger, D.T., Patten, M.A. & Bostock, D.C. (2005) Avian reproductive failure in response to an extreme climatic event. **Oecologia** 142(3): pp.398–406.
- Bradley, J. S., Woller, R. D. & Skira, I. J. (1995) The relationship of pair-bond formation and duration to reproductive success in short-tailed shearwaters *Puffinus tenuirostris*. **Journal of Animal Ecology** 64(1): pp.31–38.
- Breitburg, D.L. (1987) Interspecific Competition and the Abundance of Nest Sites: Factors Affecting Sexual Selection. **Ecology** 68(6): pp.1844-1855.
- Burhans, D.E. & Thompson III, F.R. (1999) Habitat Patch Size and Nesting Success of Yellow-Breasted Chats. **The Wilson Bulletin** 111(2): pp.210-215.
- Burt, W.H. (1943) Territoriality and home range concepts as applied to mammals. **Journal Of Mammalogy** 24(3): pp.346–352.
- Butcher, G.S. & Rohwer, S. (1989) The Evolution of Conspicuous and Distinctive Coloration for Communication in Birds. **Current Ornithology** 6: pp.51-108.
- Dean, W.R.J., Siegfried, R. & MacDonald, I.A.W. (1990) The Fallacy, Fact, and Fate of Guiding Behavior in the Greater Honeyguide **Conservation Biology** 4(1): pp.99-101.
- Denlinger, D.L. (1980) Seasonal and Annual Variation of Insect Abundance in the Nairobi National Park, Kenya. **Biotropica** 12(2): pp.100-106.
- Delhey, K. & Kempenaers, B. (2006) Age differences in blue tit *Parus caeruleus* plumage colour: within-individual changes or colour-biased survival? **Journal of Avian Biology** 37(4): pp.339-348.
- Desrochers, A. (1992) Age and foraging success in European blackbirds: variation between and with individuals. **Animal Behaviour** 43(6): pp.885-894.

- Dingle, H. & Khamala, C. (1972) Seasonal changes in insect abundance and biomass in an East African grassland with reference to breeding and migration in birds. **Ardea** 59(1): pp.216-221.
- Engelbrecht, G.D. (2008) Breeding biology of the Kalahari Scrub-Robin (*Cercotrichas paena*) (Muscicapidae). **Emu** 108(4): pp.293–300.
- Fischman, L. (1977) The White-crowned Black Wheatears at Saint Catharine. **Israel – Land & Nature** 2(1): pp.101-106.
- Flood, N. J. (1984) Adaptive significance of delayed plumage maturation in male northern orioles. **Evolution** 38(2): pp.267-279.
- Folstad, I., & Karter, A. J. (1992). Parasites, bright males, and the immunocompetence handicap. **The American Naturalist** 139(3): pp.603-622.
- Forslund, P. & Pärt, T. (1995) Age and reproduction in birds — hypotheses and tests. **Trends in Ecology & Evolution** 10(9): pp.374-378.
- Galvan, I & Sanz, J.J. (2009) Cheek plumage uniformity as a social status signal in great tits. **Annales Zoologici Fennici**. 46(4): pp.271-282.
- Ghalambor, C. K. & Martin, T. E. (2001) Fecundity-survival trade-offs and parental risk-taking in birds. **Science** 292(5516): pp.494-497.
- Grafen, A. (1990) Biological Signals as Handicaps. **Journal of Theoretical Biology**. 144: pp.517-546.
- Grainger, J, & Gilbert, F. (2008) Around the sacred mountain: the St Katherine Protectorate in South Sinai, Egypt. in Mallarach J.M. (ed) **Protected Landscapes and Cultural and Spiritual Values. Vol 2 of 'Values of Protected Landscapes and Seascapes'**. IUCN, Kasperek Verlag, Heidelberg. pp. 21-37.
- Greene, E., Lyon, B.E., Muehter, V.R., Ratcliffe, L., Oliver, S.J. & Boag, P.T. (2000) Disruptive sexual selection for plumage coloration in a passerine bird. **Nature** 407(26): pp.1000-1003.
- Gustafsson, L., Qvarnström, A. & Sheldon, B. C. (1995) Trade-offs between life history traits and a secondary sexual character in male collared flycatchers. **Nature** 375(1): pp.311-313.
- Heim de Balsac, H. & Mayaud, N. (1962) **Les Oiseaux du Nord-Ouest de l'Afrique**. Paris.
- Hill, G.E. (1996) Subadult Plumage in the House Finch and Tests of Models for the Evolution of Delayed Plumage Maturation. **The Auk** 113(4): pp.858-874.
- Hörak P. & Lebreton J. D. (1998) Survival of adult great tits in relation to sex and habitat: a comparison of urban and rural populations. **Ibis** 140(2): pp.205-209.
- Isack, H. A. & Reyer, H.U. (1989) Honeyguides and Honey Gatherers: Interspecific Communication in a Symbiotic Relationship. **Science** 243(4896): pp.1343-1346.
- Johnson, D. H. (1979) Estimating nest success: the Mayfield method and an alternative. **Auk** 96(4): pp.651 – 661.

- Leader, N. & Yom-Tov, Y. (1998) The possible function of stone ramparts at the nest entrance of the Blackstart. **Animal Behaviour** 56(1): pp.207–217.
- Low, M., Arlt, D., Eggers, S. & Pärt, T. (2010) Habitat-specific differences in adult survival rates and its links to parental workload and on-nest predation. **Journal of Animal Ecology** 79(1); pp.214-224.
- Lyon, B.E. & Montgomerie, R.D. (1986) Delayed plumage maturation in Passerine birds: Reliable signalling by subordinate males? **Evolution** 40(3): pp.605-615.
- Mayfield H.F. (1975) Suggestions for calculating nest success. **The Wilson Bulletin** 87(4): pp.456-466.
- McCleery, R., Yom-Tov, Y. & Purchase, D. (1998) The effects of Rainfall on the survival rates of some Australian Passerines. **Journal of Field Ornithology** 69(2): pp.169-179.
- Møller, A.P. (1988) Badge Size in the House Sparrow *Passer domesticus*: Effects of Intra- and Intersexual Selection. **Behavioral Ecology and Sociobiology** 22(5): pp.373-378.
- Møller, A.P. (1990) Sexual behaviour is related to badge size in the house sparrow *Passer domesticus*. **Behavioral Ecology and Sociobiology** 27(1): pp.23-29.
- Moreno, J., Soler, M., Møller, A. P. & Linden, M. (1994) The function of stone carrying in the black wheatear, *Oenanthe leucura*. **Animal Behaviour** 47(6): pp.1297–1309.
- Newton, I. (1998) **Population Limitation in Birds**. San Diego: Academic Press.
- Nice, M.M. (1957) Nesting success in altricial birds. **The Auk** 74(3): pp.305-321.
- Palfery, J. (1988) Observations on the behaviour of the White-crowned Black Wheatear in Eastern Arabia. **Sandgrouse** 10(1): pp.1-25.
- Panov, E. N. (2005) **Wheatears of the Palaearctic: Ecology, Behaviour and Evolution of the Genus Oenanthe**. Moscow: Pensoft.
- Pärt, T. (2001) The effects of territory quality on age-dependent reproductive performance in the northern wheatear, *Oenanthe oenanthe*. **Animal Behaviour** 62(2): pp.379–388.
- Pärt, T. & Qvarnström, A. (1997) Badge size in collared flycatchers predicts outcome of male competition over territories. **Animal Behaviour** 54(4): pp.893-899.
- Patten, M.A. & Rotenberry, J.T. (1999) The Proximate Effects of Rainfall on Clutch Size of the California Gnatcatcher. **The Condor** 101(4): pp. 876-880.
- Peake, T. M., Terry, A. M. R., McGregor, P. K. & Dabelsteen, T. (2001) Male great tits eavesdrop on simulated male-to-male vocal interactions. **Proceedings of the Royal Society B** 268(1472): pp.1183–1187.
- Pio, J.P. (2011) **The White-crowned Black Wheatear: Testing the defensive hypothesis of the stone rampart**. MRes Thesis. University of Nottingham.
- Poesel, A. & Dabelsteen T. (2005) Territorial responses of male blue tits to simulated dynamic intrusions: effects of song overlap and intruder location. **Animal Behaviour** 70(6): pp.1419–1427.

- Procter-Gray, E. & Holmes, R. T. (1981) Adaptive significance of delayed attainment of plumage in male American redstarts: Tests of two hypotheses. **Evolution** 35(4): pp.742-751.
- Pryke, S.R. & Andersson, S. (2002) A generalized female bias for long tails in a short-tailed widowbird. **Proceedings of the Royal Society B** 269(1505): pp.2141-2146.
- Qvarnström, A. (1997) Experimentally increased badge size increases male competition and reduces male parental care in the collared flycatcher. **Proceedings of the Royal Society B** 264(1385): pp.1225-1231.
- Reyer, H.U., Fischer, W., Steck, P., Nabulon, T. & Kessler P (1998) Sex specific nest defense in house sparrows sparrow *Passer domesticus* varies with badge size of males. **Behavioral Ecology and Sociobiology** 42: pp.93–99.
- Richardson, F. (1965) Breeding and feeding habits of the black wheatear (*Oenanthe leucura*) in southern Spain. **Ibis** 107(1): pp.1–17.
- Ricklefs, R.E. (1980) Geographical variation in clutch size among passerine birds: Ashmole's hypothesis. **The Auk** 97(1): pp.38-49.
- Rohwer, S. (1978) Passerine subadult plumages and the deceptive acquisition of resources: Test of a critical assumption. **Condor** 80(2): pp.173-179.
- Rohwer, S. (1982) The evolution of reliable and unreliable badges of fighting ability. **American Zoologist**. 22(3): pp. 531-546.
- Rohwer, S., Klein, Jr, W. P. & Heard, S. (1983) Delayed plumage maturation and the presumed prealternate molt in American redstarts. **The Wilson Bulletin** 95(2): pp.199-208.
- Rohwer, S. & Niles, D. M. (1979), The Subadult Plumage of Male Purple Martins: Variability, Female Mimicry and Recent Evolution. **Zeitschrift für Tierpsychologie**, 51(3): pp.282–300.
- Rotenberry, J.T. & Wiens, J.A. (1991) Weather and Reproductive Variation in Shrubsteppe Sparrows: A Hierarchical Analysis. **Ecology** 72(4): pp.1325-1335.
- Sæther, B. E. (1990) Age-specific variation in reproductive performance of birds. **Current Ornithology** 7: pp.251–283.
- Schaefer, H.C., Eshiamwata, G.W., Munyekenye, F.B., Griebeler, E.M. & Katrin Böhning-Gaese (2006) Monthly survival of African Sylvia warblers in a seasonally arid tropical environment. **Ibis** 148(3): pp.411–424.
- Schneider, N.A., Low, M., Arlt, D. & Pärt, T. (2012) Contrast in Edge Vegetation Structure Modifies the Predation Risk of Natural Ground Nests in an Agricultural Landscape. **PLoS One** 7(2): e31517.
- Sheldon, B. C, Merilä, J., Qvarnström, A., Gustafsson, L. & Ellegren, H. (1997) Paternal genetic contribution to spring condition predicted by size of male secondary sexual character. **Proceedings of the Royal Society B** 264(1): pp.297-302.
- Sinclair, A.R.E. (1978) Factors effecting the food supply and breeding season of resident birds and movements of Palaeoartic migrants in tropical African savannah. **Ibis** 120(1978): pp.480–497.

- Siriwardena, G.M., Baillie, S.R. & Wilson, J.D. (1998) Variation in the survival rates of some British passerines with respect to their population trends on farmland. **Bird Study** 45(3): pp.276-292.
- Suárez, F. & Manrique, J. (1992) Low breeding success in Mediterranean shrubsteppe passerines: Thekla lark *Galerida theklae*, lesser short-toed lark *Calandrella rufescens*, and black-eared wheatear *Oenanthe hispanica*. **Ornis Scandinavica** 23(1): pp.24-28.
- Svensson, L., Mullarney, K. & Zetterstrom, D. (2010) **Collins Bird Guide the most complete guide to the birds of Britain and Europe**. 2nd ed. London: HarperCollins.
- Tiwari, B.K., Barik S.K. & Tripath R.S. (1998) Biodiversity Value, Status, and Strategies for Conservation of Sacred Groves of Meghalaya, India. **Ecosystem Health** 4(1): pp.20–32.
- Verissimo, D., MacMillan, D.C. & Smith, R.J. (2011) Toward a systematic approach for identifying conservation flagships **Conservation Letters** 4: pp.1–8.
- Western, D. (1987) Africa's elephants and rhinos: Flagships in crisis, **Trends in Ecology & Evolution** 2(11) pp.343-346.
- White, M. L. J., Gilbert, F. & Zalat, S. (2007) Bird surveys and distance sampling in St Katherine Protectorate, South Sinai, Egypt in 2007. **Egyptian Journal of Biology** 9(1): pp.60-68.
- Wooller, R.D., Bradley, J.S., Skira, I.J. & Serventy, D.L. (1990) Reproductive Success of Short-Tailed Shearwaters *Puffinus tenuirostris* in Relation to Their Age and Breeding Experience. **Journal of Animal Ecology** 58(1): pp.161-170.
- Zahavi, A. (1975) Mate selection - a selection for a handicap. **Journal of Theoretical Biology** 53(1): pp.205-214.
- Zalat, S., Semida, F., Gilbert, F., El Banna, S., Sayed, E., El-Alqamy, H. & Behnke, J. (2001) Spatial variation in the biodiversity of Bedouin gardens in the St Katherine Protectorate, South Sinai, Egypt. **Egyptian Journal of Biology** 3(1): pp.147-155.