Birds along a transect across KwaZulu-Natal: altitudinal preference and altitudinal migration

Tanya Scott
SCTTAN003

Dissertation presented for the Degree of Master of Science in Zoology,
Department of Biological Sciences, University of Cape Town,
South Africa

October 2017

Supervisor: Professor Les Underhill

Plagiarism declaration

I know the meaning of plagiarism and declare that all of the work in this dissertation, save for that which is properly acknowledged, is my own.

Signature: Signed by candidate

Date: 29 October 2017

Abstract

The special ornithological advantage of KwaZulu-Natal is the massive altitudinal gradient between the coastline and the Drakensberg Mountains, an altitudinal range in excess of 3000 m. It is one of the best places in the world to study altitudinal bird migration. This dissertation uses the bird data from the Second Southern African Bird Atlas Project (SABAP2), and altitudinal data from a Digital Elevation Model to try to understand altitudinal migration in a band of KwaZulu-Natal between 29°S and 30°S. The bird atlas provides data on a five minute grid, grid cells with sides of c. 9km, known as pentads. The Digital Elevation Model gives spot heights at 0.5 minute intervals. It therefore provides 100 altitudes in each pentad. There is a description of the data analysis approach used to relate bird species abundance to altitude and selected examples to show how the method works, illustrating the strengths and weakness of the approach. The developed method is then applied to the study area to investigate altitudinal migration. For each of the 304 species which occur with some regularity in the study area, the altitudinal height preferences in summer and winter are plotted and compared. Some species, such as African Dusky Flycatcher*, are definite altitudinal migrants, and some species are definite residents having essentially identical altitudinal distributions in summer and winter, such as Black-bellied Starling. There are also many intermediate strategies. Numerous species have been proposed as altitudinal migrants in KwaZulu-Natal. These claims are evaluated against the results obtains in this dissertation. For some species, the suggestion that they are altitudinal migrants is clearly incorrect, and for other species the hypotheses are confirmed by the bird atlas data. The project attempted to determine if there were common factors that helped explain which species engaged in altitudinal migration. A set of life history characteristics for each species, including aspects such as diet, mass, habitat, etc, was used to evaluate if there was a relationship between the extent of altitudinal migration and these explanatory variables. No meaningful relationships were found. Explanations of altitudinal migrations therefore remain an enigma.

* Scientific names of all species mentioned in the text are provided in Appendix A.

Acknowledgements

This project would not have been possible without my supervisor, Les Underhill, who not only assisted me greatly during the project itself but was the inspiration behind me studying further in the first place. Despite going through personal difficulties of his own, he was always able to encourage me to persevere and conquer all challenges we faced.

Rene Navarro and Michael Brooks contributed hugely by assisting with the presentation of the data used in this project. Thanks also to Caitlin Smith who helped with data capturing and proof reading this dissertation.

Without the funding I received from the Skye Foundation, the National Research Foundation (NRF) and the Animal Demography Unit (ADU) at the University of Cape Town, I would not have been able to complete this dissertation and I am greatly indebted to them.

And lastly, I must thank my coach, James Evans, for his continuing support and belief in me.

Contents

CHAPTER 1

Introduction: Altitudinal migration, bird atlasing, KwaZulu-Natal and the digital elevation model

Introduction

This dissertation sets out to investigate altitudinal bird migration using bird atlas data along a transect of KwaZulu-Natal, South Africa. This introductory chapter provides background information to these topics. It starts with a short overview of the main thrust of this project, altitudinal migration of birds. The data used for this study was obtained from a citizen science bird atlas project, and therefore a history of the development of bird atlasing is relevant. The main focus is on the protocol of the Second Southern African Bird Atlas Project (SABAP2); it is the data from this bird atlas which is used for this analysis. A description of the study area in KwaZulu-Natal is provided. Finally, the statistical analysis of altitudinal migration requires a knowledge of topography in a digital format; thus the Digital Elevation Model used in this study is described. The Introduction ends by providing the aims of the project and overviews the contents of the two chapters which follow.

Global review of altitudinal bird migration

Altitudinal bird migration involves yearly seasonal movements up and down an altitudinal gradient between breeding and non-breeding ranges (Oatley and Arnott 1998). Many bird species living in montane areas worldwide, especially in all the major mountain ranges, engage in altitudinal migration. Altitudinal migration is a vastly understudied topic in ornithology; the first review of the topic was undertaken by Boyle (2017). Her review was focused primarily on North America, but she also provided valuable summaries from a global perspective. Because this is the only full-scale review, and because it is recent, this overview of altitudinal migration refers extensively to Boyle (2017).

Boyle (2017) carried out a systematic survey of the evidence for altitudinal migration among the landbirds of North America. She critically examined the content of the key sections of species accounts in a fully referenced set of life histories of North American bird species (Rodewald 2015). She studied the original sources of references to altitudinal migration. She found that, of the 575 breeding landbirds of North America (USA and Canada), 153 had been reported to undertake altitudinal migration somewhere in their range. She examined 275 original sources of descriptions of altitudinal migration. She noted that less than half (47%) of the sources were in peer-reviewed journals; the remainder were in theses, reports, bird atlases, and other “grey literature” sources. Half of the sources were from 1980 or earlier, and 25% were from 1954 or earlier. The point she was making was that altitudinal migration has been a neglected area of ornithology in North America in recent decades. Of 116 species that undertook altitudinal migration within the USA or Canada, she evaluated the strength of the scientific evidence for this migration; it was strong for only 45 species. For the remainder the evidence was intermediate or weak.

Boyle’s (2017) review cites only three African papers; two from the KwaZulu-Natal study area of this dissertation (Johnson and Maclean 1994, and Brown 2006); and one from the Eastern Arc Mountains of East Africa (Burgess and Mlingwa 2000). Brown (2006), however, did not actually deal directly with altitudinal migration; it is a paper on the lowland birds of KwaZulu-Natal. Burgess and Mlingwa (2000) provided a brief overview of altitudinal migration in Africa, and confirmed that this is not a widely described phenomenon in Africa. They reviewed the information related to altitudinal migration in East Africa, and concluded that the evidence was equivocal, and that more detailed quantitative studies were needed. For example, they considered that the observations of some species at lower altitudes could have alternative explanations. In particular, Burgess and Mlingwa (2000) hypothesised that the low altitude populations could be “sink” populations maintained by “source” populations at high altitudes.

The part of Africa which has largest altitudinal variation over relatively short distances is the Horn of Africa in the north-east; altitudes vary from 110 m below sea level in the Danakil Depression to the Semien Mountains, more than 4000 m in height, both in Ethiopia (Ash and Atkins 2009). This region also has an extensive history of ornithological exploration (Ash 2009) and Ethiopia was the first country in Africa to complete an Important Bird Areas directory (Ethiopian Wildlife and Natural History Society 1996). The avifauna of Ethiopia and Eritrea was comprehensively reviewed, together with the results of a bird atlas project, by Ash and Atkins (2009). This bird atlas project was based on 479 grid cells, 94% of which were visited, and 70% visited by the authors. The book contains an extensive review of bird migration in the region, and summarises both Eurasian-African migration and intra-African migration; it acknowledges the existence of altitudinal migration for many bird bird species, but says that “we are not dealing with these here.” In fact, the term “altitudinal migration” occurs in only one of 872 species texts, for the Olive Thrush, for which it is stated: “There is an unknown degree of altitudinal migration” (Ash and Atkins 2009, page 306). None of the papers cited in the 25-page bibliography in Ash and Atkins (2009) makes mention of altitudinal migration. This paragraph illustrates how poor the knowledge of altitudinal migration is within a region which is likely to be extremely rewarding for the study of this topic.

Boyle (2017) also reviewed the factors explaining altitudinal migration, with a North American emphasis. The obvious hypothesis is that altitudinal migration is a response to variation in food resources in space and time. However, for the few species that have been investigated in detail, she found there was frequently a mismatch between the timing of food availability and the timing of migration. She concluded that altitudinal migration is a complex process shaped by many factors, such as food availability, predation risk and climatic constraints. She described altitudinal migration as “messy.” The conclusions of Burgess and Mlingwa (2000) for East Africa were similar. The observations of altitudinal migration were not consistent with the hypotheses that attempt to explain why birds migrate. In spite of these difficulties, one of the objectives of this thesis is to try to find the explanatory variables which provide insights into which species do and do not undertake altitudinal migration.

Boyle (2017) concluded her paper with the statement that the study of altitudinal migration has “flown under the radar of the ornithological community” and gave four reasons why “this gap in knowledge” should be filled. (1) She encouraged ornithologists to “embrace the messy”. Altitudinal migration is messy because it is a partial migration and quantifying this is difficult and challenging, and there are clearly multiple explanations. (2) Variation is the “fodder” of evolution. By this she meant that massively well-studied long-distance migration can only properly be understood if short-distance migration is understood. (3) From a consideration of research project logistics, it can be efficient to study altitudinal migration. Migration is over a scale of tens or hundreds of kilometres rather than the thousands of kilometres of long-distance migrants, which leads to undertaking research in foreign countries. (4) Because the conservation status of montane bird species is more poorly understood than that of lowland species, it is of conservation importance to understand, for the montane species, their movements and what triggers them. Montane species are especially sensitive to climate change (La Sorte and Jetz 2010).

Prior to this project, there has only been one other attempt to use the data collected by a bird atlas project to investigate altitudinal migration. This was a paper by Harrison and Navarro (1994) which used five altitudinal classes. This project builds on the concept they developed. The next section thus provides an introduction to bird atlasing, the data collection tool which provided the information on which this project is critically based.

History of bird atlasing, especially in South Africa

Bird atlases are standardised surveys, consisting of field observations collected by large numbers of volunteers, usually now referred to as citizen scientists, which describe the distribution of birds (Dunn and Weston 2008). In the briefest possible terms, a bird atlas consists of a set of grid cells, for which citizen scientists are encouraged to visit and generate bird species lists.

The first bird atlases utilising volunteers to gather data took place in Britain and Ireland. Norris (1960) produced one of the earliest attempts to map bird distributions and patterns of abundance using a grid system. He mapped the breeding distribution of 30 bird species in the British Isles using data collected by observers in 1952 onto a regular 25×25 km grid. Observers were requested to indicate, in broad categories, the number of each species in each grid square. This survey was a follow-up project to a trial project which mapped the breeding distribution of 100 selected bird species in a West Midland area in 1950.

The first atlas to attempt to comprehensively map any aspect of biodiversity on a national scale was that of plants in Britain and Ireland by Perring and Walters (1962). The *Atlas of the British Flora* mapped plant distribution on a presence or absence basis of approximately 1700 species using maps with a 10×10 km grid map (Perring and Walters 1962). This publication by the Botanical Society of the British Isles led the way for a similar mapping of the distributions of breeding birds and the first systematic bird atlas was produced by Lord and Munns (1970). It was a regional atlas that described the breeding distribution of birds of the West Midlands region of England between 1966 and 1968. This was followed by the first systematic national atlas, *The Atlas of Breeding Birds in Britain and Ireland* (Sharrock 1976), which mapped the distribution of breeding birds between 1968 and 1972 on a 10×10 km grid (the same scale used in the earlier national botanical atlas). The first French and Danish bird atlases were published in the same year (Dybbro 1976, Yeatman 1976). Before these initial atlases, most descriptions of bird distributions were based on a random accumulation of information of where birds occurred, rather than on systematic structured surveys carried out by volunteers (Dunn and Weston 2008). Since the 1970s there has been a rapid increase in the number of bird atlases worldwide and continued development in atlasing approaches (Gibbons et al. 2007, Dunn and Weston 2008). The atlases map the distributions of breeding, wintering or migrating birds at a wide range of spatial scales and using a variety of atlasing techniques. Some atlas surveys have been repeated to allow temporal changes in bird distributions to be assessed (Gibbons et al. 2007). The first atlas for an entire continent was produced in 1997, and covers Europe; it consisted of a synthesis of all atlases for individual countries (Hagemeijer and Blair 1997). It used a 50×50 km grid. Greenwood (2017) provided an overview of the process of producing the first European bird atlas. A second European bird atlas, also using a 50×50 km grid, but with a statistically modelled maps using a 10×10 km grid, is scheduled for publication in 2020 (Herrando et al. 2017).

Citizen science fieldwork for the first bird atlas project in southern Africa started in KwaZulu-Natal in 1976 (see below) and was published in 1980 as the *Bird Atlas of Natal* (Cyrus and Robson 1980). This was the first of a number of relatively small scale bird atlases to be produced in South Africa before the commencement of the first regional bird atlas project in 1985, which included six countries of southern Africa. Two key books on the birds of KwaZulu-Natal had been published before Cyrus and Robson (1980) and both lacked good information on bird distributions in the province. The first was the book *Natal Birds* which was published in 1899 (Woodward and Woodward 1899). It was a comprehensive description of the birds of Natal and Zululand with the distributions of the species only given in vague narrative form as passing interest within the species descriptions. The nature of ornithological enquiry at the end of the 19th century was mainly taxonomic, and distribution and abundance only became matters of interest and importance with the rise of ecology and the conception of ecosystems. The second book was a 509 page catalogue of birds of Natal and Zululand published in 1964 by the well-known ornithologist-taxonomist Philip Alexander Clancey (Clancey 1964). This provides feather-by-feather descriptions of 574 species. The distribution of species is obscurely described and species abundance is vague. These two books are highlighted because they deal with the birds of the study area of this project.

Digby Cyrus, one of the authors of the *Bird Atlas of Natal*, spent time in the United Kingdom as a summer vacation assistant at bird observatories in 1971 and 1972

(Cyrus and Robson 1980). During his second summer as vacation assistant he participated in fieldwork for *The Atlas of Breeding Birds in Britain and Ireland* which was published in 1976 (Sharrock 1976). Towards the end of 1975 Cyrus suggested a project to record the distribution of birds in KwaZulu-Natal. The project began in early 1976. Thus the history of bird atlasing in southern Africa can be traced back to this visit by Digby Cyrus to the United Kingdom.

The atlas project which Cyrus observed in the United Kingdom collected data in only one period of the year, the breeding season. His innovation for the Natal atlas in comparison with the United Kingdom atlas was to collect data throughout the year and on a monthly basis. This is a significant piece of lateral thinking, and this pattern of through-the-year fieldwork has been adopted by all atlas projects in the region. It is this development, fieldwork throughout the year, which makes this study of altitudinal migration feasible. The Natal atlas however adopted the same presence-absence approach as was used in the United Kingdom atlas, on which it was modelled.

The *Bird Atlas of Natal* mapped the distributions, by monthly presence or absence, of 530 bird species occurring in KwaZulu-Natal from January 1970 to December 1979. Most of the data however was collected from 1976 through to the end of 1979. The quarter degree grid cell (QDGC) was used as the sampling unit. There is no discussion of how this choice of sampling unit was made, but this scale became the gold standard for biodiversity atlasing in southern Africa for several decades. No indication of abundance was provided in Cyrus and Robson (1980). The aim of the atlas was to provide the distributions which could serve as baseline data against which future changes could be compared (Cyrus and Robson 1980).

Following the *Bird Atlas of Natal*, the *First atlas of bird distribution in the Orange Free State* (Earlé and Grobler 1987) and *Birds of the Transvaal* (Tarboton et al. 1987) were published in 1987. They covered the atlas period January 1983 to December 1986 (Earlé and Grobler 1987) and 1960 to 1986 respectively (Tarboton et al. 1987). *First atlas of bird distribution in the Orange Free State* recorded the monthly presence or absence of species using QDGC grid reference (Earlé and Grobler 1987). *Birds of the Transvaal* recorded presence or absence of species and also recorded the breeding status of species present using QDGC format (Tarboton et al. 1987). This was the first atlas in southern Africa to include breeding information.

The next innovation in atlasing was to provide an index of relative abundance. This was tackled by the *Atlas of the Birds of the Southwestern Cape* (Hockey et al. 1989) and *The New Atlas of Breeding Birds in Britian and Ireland: 1988–1991* (Gibbons et al. 1993), and subsequently by the First Southern African Bird Atlas Project (SABAP1) which produced the two-volume set of books, *The Atlas of Southern African Birds* (Harrison et al. 1997).

The *Atlas of the Birds of the Southwestern Cape* (Hockey et al. 1989) was the first bird atlas globally to attempt to indicate presence and abundance of bird species. The index of relative abundance used is called the reporting rate. The reporting rate is the proportion of checklists submitted for each QDGC that recorded the species in question as present. This atlas provided reporting rates calculated over the entire five-year period of the project; for selected species, especially the migrants, it presented monthly reporting rates, which provided a measure of the time of arrival and departure of species. The reporting rate is a non-linear measure of abundance; an increase from 10% to 20% does not imply the same relative increase in numbers of birds as an increase from 80% to 90%. Reporting rates are described in more detail below. On the geographical distribution maps in Hockey et al. 1989, the innovation was to represent reporting rates graphically by circles in the QDGC of different diameters. Smaller circles were used for less abundant species with the circles growing larger to indicate increase in abundance. The areas of the circles, rather than the diameters, were used to represent reporting rates.

The measure of relative abundance or "frequency index" adopted by *The New Atlas of Breeding Birds in Britian and Ireland: 1988–1991* (Gibbons et al. 1993) was similar to that used by Hockey et al. (1989) and is essentially a reporting rate. Distribution and abundance were plotted on a 10x10 km grid. Each of these grid squares consisted of 25 tetrads (2×2 km squares) (Gibbons et al. 1993). Their "frequency index" is the proportion of tetrads visited in each 10×10 km grid square which recorded the species in question as present (Gibbons et al. 1993).

The First Southern African Bird Atlas Project (SABAP1) was launched in southern Africa in 1986 (Harrison et al. 1997). Within southern African ornithology there is a tradition of defining the subcontinent as the geographical region that includes Botswana, Lesotho, Mozambique (south of the Zambezi River), Namibia, South Africa, Swaziland and Zimbabwe. SABAP1 aimed to cover the same region but Mozambique had to be excluded due to civil war in that country (Harrison et al. 1997). Although SABAP1 started in 1986, it officially collected data from the beginning of 1987 to the end of 1991, a five-year period, but included data collected using the same protocol since 1980 (Harrison et al. 2008). SABAP1 provided a ‘snapshot’ of the distribution and relative abundance of birds in southern Africa during this time period. It improved public understanding of science and played an important role in science education by encouraging public participation in the project (Harebottle et al. 2007). More than 5000 citizen scientists (bird atlasers) collected data across six southern African countries on the distribution of 932 bird species using the QDGC as the sampling unit. The project culminated in a database of seven million peer-reviewed bird distribution records and the publication of *The Atlas of Southern African Birds* (Harrison et al. 1997, 2008). The atlas did not only provide information on bird distribution and abundance but also information on the seasonality of breeding and the direction and seasonality of migration (Harrison et al. 2008).

Patrick Osborne and Barbara Tigar undertook a bird survey in Lesotho from 1986 to 1989 and produced a bird atlas for the country (Osborne and Tigar 1990), and contributed these valuable data to SABAP1. The 31-month bird survey collected data for 55 of the 62 QDGCs in the country, with 504 checklists collected remarkably evenly throughout the year; their species texts make frequent, but not consistent, references to altitudinal migration and have proved invaluable for providing context to the study area for this project, which was adjacent to theirs.

The second bird atlas project, SABAP2, was launched on 1 July 2007 and is a follow-up project to SABAP1 with data being collected on the finer pentad scale (Harrison et al. 2008, Harebottle et al. 2007). The atlas region for the second project is limited to South Africa, Lesotho and Swaziland (Harebottle et al. 2007). Data collection for SABAP2 is ongoing. It is the subset of data from this project that is used in this study of altitudinal migration in KwaZulu-Natal. The project is described in more detail in the next section.

The data – Second Southern African Bird Atlas Project

The project makes use of the database collected by Second Southern African Bird Atlas Project (SABAP2). SABAP2 builds on the results and feedback of SABAP1 to produce an improved atlas and thus contribute in a greater way to the conservation of avian biodiversity in South Africa, Lesotho and Swaziland (Harebottle et al. 2007).

The concept which underpins SABAP2 is slowly shifting. The initial concept was to create a new set of bird distribution maps for South Africa, Lesotho and Swaziland. The realisation that SABAP2 represents a powerful tool for monitoring changes in bird communities through time has led to a paradigm shift. In parts of the SABAP2 region where there is comprehensive coverage, this paradigm shift has already taken place and monitoring is the main objective. However, in regions where there are still gaps in basic coverage, mapping bird distributions remains the primary focus (Underhill and Brooks 2016a).

The objective of both Southern African Bird Atlas Projects is to provide a more accurate and deeper understanding of how bird population densities and distributions in southern Africa are changing over time (Harrison and Underhill 1997). More specifically, SABAP2 aims to measure the impact environmental change is having on southern African birds through a scientifically sound and repeatable platform that uses standardised data collection on bird distribution and abundance. SABAP2 aims to increase public participation in the collection of biodiversity data and increase public awareness of birds. This is done via the mobilisation of citizen scientists (volunteer bird atlasers) throughout southern Africa. Lastly, SABAP2 aims to provide information that can be used to establish changes in the distribution and abundance of birds since SABAP1 (Harebottle et al. 2007, Underhill 2016, Underhill and Brooks 2016a, Ainsley and Underhill 2017, Underhill et al. 2017).

SABAP2 protocol

The SABAP2 protocol has the following features, as outlined by Harebottle et al. (2008), Underhill (2016) and Underhill et al. (2017):

(1) The geographical sampling unit is pentad grid cells. These grid cells cover 5 minutes of latitude by 5 minutes of longitude (5’ x 5’). Within the context of South Africa, each pentad is approximately 9.2 km north to south and 8.3 km east to west (this length gets narrower southwards because the planet is a sphere, but within the southern Africa study area this change is small). There are nine pentads in a quarter degree grid cell.

(2) The participants in the project try to cover all the different major habitats in the pentad during the observation period. They aim to make as complete a list as possible of all the species present in the pentad. This maximises information on species diversity in the pentad.

(3) The bird atlasers record as many different bird species as possible for a minimum observation time period of two hours in their pentad. The two-hour minimum is thought to be enough time to locate most species in a pentad with uniform habitat and low avian diversity. Atlasers can continue atlasing for longer than two hours and are encouraged to do so, especially if their pentad contains many diverse habitats, has high avian diversity and they are still regularly adding species to their list.

(4) Bird atlasers list the species in the order in which they observe the species. I do not make use of this information in this project.

(5) Atlasers can continue to add “additional species” to their list for five days, which is the maximum observation time period. The five-day maximum observation time period enables researchers to accurately map seasonal patterns of resident and migrant species.

(6) After the five-day period, atlasers can start a new list for the pentad. The five-day gap helps to ensure that each successive list submitted by the same participant for the same pentad is not simply a replica of the previous list.

Reporting rates

Reporting rates provide a way of obtaining quantitative information from presence/absence data, such as that provided by the bird atlas project. The observers did not count the birds, but merely recorded the presence of identified species on checklists (Harrison and Underhill 1997). As used in previous atlas projects in southern Africa, the reporting rate is defined as the proportion of checklists on which a species is recorded. So, if a species was recorded on 10% of the checklists, then it has a reporting rate equal to 10% for a specific pentad. Differences in reporting rates between different geographical areas and different times of the year may be interpreted as indicating possible changes in abundance (or density) of birds (Harrison and Underhill 1997). Reporting rates are however, not proportional to density, but they provide an index which varies with changes in density (Harrison and Underhill 1997).

Reporting rate can be viewed as a measure of conspicuousness of a species, which is how easily a bird is observed (seen or heard). It can be roughly defined as the likelihood that the average observer spending an average amount of time searching for a species, records a species as present (Harrison and Underhill 1997). There are many factors which influence reporting rate. Relative abundance is only one of the factors. The other factors can be categorised into species, geographic, observer and arithmetic effects (Harrison and Underhill 1997):

(1) Species effects: Some bird species are more easily observed than others. Given species of equal abundance, the more conspicuous species is likely to be recorded more often than the inconspicuous, secretive species. For some species, conspicuousness changes between seasons with no change in abundance due to seasonal changes in plumage and behaviour. Bright breeding plumage makes birds easy to identify while drab non-breeding plumage does the opposite. Some species call more frequently during the breeding season, increasing their conspicuousness.

(2) Geographic effects: Some areas are easier to access than others. Species that are habitat specific will only be encountered if the observer visits this specific habitat. Some pentads have good road systems allowing access to all

parts, while others have few or no roads making access to difficult e.g. mountain tops, isolated wetlands, forest patches.

(3) Observer effects: Some species are easier for observers identify and are subsequently recorded more frequently than those which are more difficult to identify. The level of observer skill and experience can also affect the reporting rate.

(4) Arithmetic effects: The number of checklists presented for a given pentad can influence the reporting rate. If there is one checklist, then the reporting rate can only be 0% or 100%. If there are two checklists, then the reporting rate can be 0%, 50% or 100%. If there are 100 checklists, then the reporting rate can be any integer value from 0% to 100%. For this reason observers were encouraged to revisit pentads as often as possible and to complete as many checklists as possible. For SABAP2, reporting rates are being shown for pentads with four or more checklists (Underhill and Brooks 2016b).

Given the factors that influence reporting rates, does the reporting rate statistic have any value at all? The usefulness of the reporting rate statistic might be less for certain species (e.g. rare or secretive species) and certain field conditions (e.g. inaccessible areas), but its value has been demonstrated in several ways (Harrison and Underhill 1997). Reporting rates have proven to be valuable in describing the phenology of migratory species. The reporting rates show a clear increase and decrease with the arrival and departure of migrants (Harrison and Underhill 1997). Reporting rates vary over geographical space and this agrees with what is predicted for species' distributions. For example, reporting rates are usually highest in the centre of the species' distribution and decreases towards the edge (Harrison and Underhill 1997). Similarly, reporting rates for different vegetation types frequently corresponds to the known habitat preferences of species (Harrison and Underhill 1997). Changes in the timing of migration in the two decades between the first and second bird atlas projects in southern Africa have been detected through analysis of the reporting rates in the arrival and departure periods (Altwegg et al. 2012, Bussière et al. 2015).

When explaining seasonal variations in reporting rate, it is important to first consider all factors that might influence the reporting rate throughout the year. If change in relative abundance is the only factor that cannot be rejected, then movement or migration can be reasoned to be the likely explanation (Harrison and Underhill 1997).

The study area – KwaZulu-Natal between 29°S and 30°S

The study area for this project is in the south-eastern portion of southern Africa. It lies within the KwaZulu-Natal province of South Africa between lines of latitude 29°S and 30°S. It encompasses a small fraction of the total area covered by SABAP2. The special ornithological advantage of this region is the massive altitudinal gradient between the coastline and the Drakensberg Mountains. It is one of the best places in the world to study altitudinal migration (Underhill and Brooks 2016a).The altitudinal range is from sea-level to an elevation in excess of 3385 m. At the latitude of 30°S, the distance from the shoreline to the 3000 m contour is only 160 km. This altitudinal gradient is modified by a series of terraces or scarps (Oatley and Arnott 1998, Oatley 2017). Deep river valleys run from northwest to southeast. Evergreen forest often grows on the shaded south-facing slopes of these river valleys, while thornveld and thickets usually cover the sunny north-facing slopes. Dense vegetation lines in the river channels (Oatley and Arnott 1992). This specific transect from the sea to the Drakensberg was chosen because it has large volumes of SABAP2 checklists (Underhill and Brooks 2016a).

Climatically, the province of KwaZulu-Natal is subject to summer rainfall, with the main portion of the annual precipitation falling in the six summer months (October to March). This general pattern is susceptible to modification by topographic features and proximity to the coast (Oatley 2017). The minimum temperatures of the region are important when considering bird migration. In this regard, frost does not occur on the KwaZulu-Natal coast, but may be expected during the winter months in the highland regions. The frequency of severe frosts and snow increases significantly above 1800 m (Oatley 2017).

The natural vegetation ranges from Coastal Evergreen Bush at the coast, through Dry Thornveld and Open Bush to Mistbelt Evergreen Forest up to an altitude of 1225 m. Sourveld grassland occurs above this in the highlands (Cyrus and Robson

1980) with Alpine grassland on the uppermost slopes of the Drakensberg Mountains just below the edge of the highland plateau (Mucina and Rutherford 2010).

KwaZulu-Natal Coastal Belt forms a long, and in some places broad, vegetation strip running along the coastline. The landscape consists of undulating coastal plains (Mucina and Rutherford 2010). Coastal Evergreen Bush occurs from sea-level to an altitude ranging from 300–450 m. In river valleys there is a change from Coastal Evergreen Bush to coastal thornveld (Cyrus and Robson 1980). Annual rainfall is fairly evenly distributed and increases from south to north. Remnants of previously widespread subtropical coastal forest occur in patches mainly along streams and on steep slopes. The species-rich forest is low and dense, with a shrubby understorey, near the coast and in more exposed areas. In valleys and against mountainsides farther away from the coast, there is a change to closed, high forest with well-developed canopy and understorey tree layers (Cyrus and Robson 1980, Mucina and Rutherford 2010). Some primary grassland still occurs in hilly, high-rainfall areas. The region is currently affected by widespread sugarcane farming, timber plantations and holiday resorts (Mucina and Rutherford 2010).

Dry Thornveld is recognisably different from coastal thornveld and, in the study area, it is largely restricted to following the rivers from the coast to an altitude of just over 900 m. A number of different veld types are grouped together as Dry Thornveld. It is very species rich, with the most common being *Euphorbia, Aloe* and *Acacia* species. The annual rainfall is low and sporadic, occurring in heavy storms (Cyrus and Robson 1980, Mucina and Rutherford 2010).

Open Bush occurs between 600 and 900 m. It lies between Coastal Evergreen Bush and Mistbelt Evergreen Forest areas and occurs in patches. The annual rainfall is modest at 500–750 mm per annum and is fairly evenly distributed throughout the summer months. Closed forest is present in the kloofs in this vegetation type, while on the more exposed undulating countryside, bush is mixed with grass. Thornbush is dominant. Some of the most common grass species include *Aristida juniformis, Sporobolus* spp., *Aristida* spp. and *Digitaria tricholaenoides* (Cyrus and Robson 1980, Mucina and Rutherford 2010). Proteaceae trees and shrubs (*Protea, Leucospermum, Faurea*) can be locally common (Mucina and Rutherford 2010).

Mistbelt Evergreen Forest runs in a narrow belt at an altitude of 900–1225 m. The annual rainfall ranges from 750–1125 mm and is uniformly distributed. Heavy mists are a common occurrence in this region. A large portion of this area is cultivated. Where it is not cultivated, original bush or forest occurs in deep kloofs and on hillsides (Cyrus and Robson 1980). These forests are species-rich, tall (15–20 m) and multilayered. They have a dense shrubby understorey and a well-developed herb layer (Mucina and Rutherford 2010). Some of the main tree species found in the area include: *Podocarpus* spp., *Apodytes dimidiata, Rapanea melanophloeos* and *Trimeria grandifolia*. The remainder of the undulating land is covered with grassveld (Cyrus and Robson 1980, Mucina and Rutherford 2010).

Highland Sourveld grassland occurs at an altitude of 1375–1825 m. In the study area it forms a broad band at the foot of the Drakensberg mountain range and the country is undulating. Some of the typical species in this veld type include: *Tristachya leucothrix, Themeda triandra, Monocymbium cerisaeforme, Andropogon appendiculatus, Harpechloa falx, Eragrostis plana, Trachypogon spicatus Elionurus argenteus* and *Alloteropsis semialata*. Relatively species-poor *Podocarpus,* temperate forest and *Leucosidea* scrub-forest occur patchily in kloofs (Cyrus and Robson 1980, Mucina and Rutherford 2010). This region experiences a cooler version of a warm-temperate climate (Mucina and Rutherford 2010). The annual rainfall is high (875–1250 mm per annum) and is evenly distributed, although most rain occurs during the summer months. Mists frequently occur (Cyrus and Robson 1980).

Basalt grassland occurs on the uppermost slopes of the Drakensberg Mountains at an altitude of 1820–3300 m (Mucina and Rutherford 2010). Basaltic lava flow lines form ledges in the Drakensberg escarpment, which are used by raptors and other birds as breeding or roosting sites (Little and Bainbridge 1992). The grasslands in this region are species-rich and grow at varying degrees of density, forming tussocks on terraces as a result of the steepness of the slopes. *Bromus speciosus, Pentaschistis tysoniana, Cymbopogo nardus, Festuca caprina, Rendlia altera* and *Themeda triandra* are some of the dominant species. In some places herbs (*Agapanthus, Merwilla, Helichrysum*) and shrubs (*Erica*, *Helichrysum*, *Euryops*) grow alongside the grasses (Little and Bainbridge 1992, Mucina and Rutherford 2010). Deep ravines on basalt support lush, tall-herb vegetation. The landscape is characterised by steep basalt rock faces and terraces (Mucina and Rutherford 2010). There is a large temperature difference between summer (some days temperatures exceed 30°C) and winter. Morning summer mists are common. Winter is characterised by snow and frequent frost (Mucina and Rutherford 2010).

The climatic regimes of the KwaZulu-Natal province involve wet summers and dry winters. For most species, the breeding season coincides with the summer rainfall season.

The digital elevation model

The CGIAR Consortium for Spatial Information (CGIAR-CSI) Geoportal provides access to the global Shuttle Radar Topographic Mission (SRTM) at a resolution of three arc seconds (c. 90 m). This open access digital elevation model (DEM) provides a database containing high quality elevation (spot height) data (Reuter et al. 2007, Jarvis et al. 2008). The global SRTM 90 m digital elevation models (DEMs) are considered to have a vertical error of less than 16 m. The source of the digital elevation data was the NASA Shuttle Radar Topographic Mission which covered more than 80 % of the land surface of the earth. The DEM was downloaded from the CGAIR-CSI website (http://srtm.csi.cgiar.org/).

The digital elevation model downloaded for this project gave spot heights at 0.5 minute (30 arc second) intervals. It therefore provides 100 altitudes in each SABAP2 pentad, five minutes of latitude by five minutes of longitude. The pentad is the spatial unit of bird data collection for the bird atlas.

Overview of this project

The primary objective of this project was to devise a quantitative method to objectively examine the altitudinal preferences of bird species, and to illustrate this using the KwaZulu-Natal study area. The final step was to examine these preferences seasonally, in summer and winter. In this way, I aimed to explore the altitudinal seasonal movements of birds using the devised method to infer the extent of altitudinal migration. Clearly, no birds were actually observed moving; the objective was to investigate whether the bird atlas data from SABAP2 were “strong enough” to provide solid inferences of the extent of migration.

Several studies in KwaZulu-Natal have made suggestions as to which species were thought to show altitudinal movement. In many instances, these suggestions were made on limited and anecdotal evidence. Nevertheless, all these species were considered in more detail.

I also set out to explore possible explanations for the observed movement patterns. In particular, it would be extremely satisfying to be able to answer the question: “Why are some species residing at higher elevations in the Drakensberg altitudinal migrants and other species are not?”

Chapter 2 describes the data analysis approach used in this project. The algorithm can be classified as an example of exploratory data analysis (in contrast to confirmatory data analysis). A small but taxonomically varied selection of species is used to illustrate the method, and then a case study is performed on a single family, to investigate the outcomes of the algorithm at this level.

Chapter 3 applies the algorithm described in Chapter 2 to 304 bird species which occur with some regularity within the study area, estimates their altitudinal preferences in summer and winter, measures the distance apart of these curves and classifies each species into a series of categories. A small set of species are used to illustrate the results. The detailed results for a large set of species, suggested by other authors as potentially being altitudinal migrants, are included in an Appendix. A set of life history characteristics for each species, including aspects such as diet, mass, habitat, etc, was used to evaluate if there was a relationship between the extent of altitudinal migration and these explanatory variables. Apart from an apparent correlation which suggested that frugivory was a predictor of not being an altitudinal migrant, no meaningful relationships were found. Explanations of altitudinal migrations remain an enigma.

CHAPTER 2

Quantifying altitude preferences of birds: case study of a transect in KwaZulu-Natal

Introduction

This chapter is primarily methodological and addresses the problem of how one relates bird species distribution and abundance, as measured by reporting rate, to an explanatory variable. The chosen explanatory variable is altitude but this method could also be applied to any explanatory variable e.g. vegetation type, rainfall, temperature, season, geology. The two sets of data used to address the problem are the occurrence of bird species using the pentad-scale atlas data from SABAP2, and the data from the digital elevation model which provides multiple altitude values per pentad. The two sets of data are for a region of southern Africa with a steep altitudinal gradient.

A first attempt at developing methods to relate bird atlas distribution data to altitude and season was made by Harrison and Navarro (1994), in a paper first presented at a conference in 1992. Checklist data, on a quarter degree grid cell (QDGC) scale, collected for the First Southern Africa Bird Atlas Project (SABAP1) were used. Their analysis made use of a generalised linear model to relate changes in relative abundance of a species to altitude and season and to detect interactions between the explanatory variables. Each QDGC was classified into one of five height classes, determined by which height class was dominant in the QDGC. The method of Harrison and Navarro (1994) was re-applied by Berruti et al. (1994) in a paper which focused mainly on coastal migration along the south-eastern coast of South Africa, than on altitudinal migration within KwaZulu-Natal. However, the approach developed by James Harrison and Rene Navarro is the primary starting point for this project.

The aim of this chapter is to develop a graphical method which can relate multiple values of the explanatory variable per grid cell to the occurrence of bird species in the grid cells. In this case study the explanatory variable is altitude, which is a continuous variable, converted into a set of ordered categorical variables using 100 m class intervals. The output is a measure of the extent of preference/avoidance for each height class.

Methods

In the terms championed by Tukey (1977), the approach to data analysis used in this chapter (and in Chapter 3) is classified as an “exploratory data analysis”. Exploratory data analysis is defined as calculations which highlight the main features of sets of data, and which often depend on visual interpretation of the graphical display (Tukey 1977). Five-number-summaries, stem-and-leaf plots and box-and-whisker plots are three of the many methods in exploratory data analysis invented by John Tukey, over a career spanning six decades (McCullagh 2003). The evaluation of the success of these exploratory methods is fairly subjective. McCullagh (2003), described the domain of exploratory data analysis, developed by John Tukey, as “a world rich in examples, where the rules are unclear, and the guiding principles are as likely to be found in psychology as in mathematics or probability.” Two key considerations help to evaluate the product of the exploratory data analysis: (1) Is it a reliable summary of the raw data? (2) Does it communicate the essential features of the data faithfully? These issues will be addressed in the Discussion.

The altitude analysis developed here draws on a broadly similar approach used successfully for the “habitat-type” analysis in the First Southern African Bird Atlas Project (SABAP1) (Harrison and Underhill 1997, see especially the section on “Vegetation analysis”). This was also an exploratory data analysis, and was used to describe some of the fundamental patterns in the data.

Harrison and Underhill (1997) pointed out a bias in this approach, and that bias applies to the analysis presented here as well. The bias is a consequence of the unit of data collection being the grid cell, and not the height class. This results in species being potentially associated with height classes in which they do not occur. The bias is most conspicuous in species that are restricted to the coastline, but because the coastal pentad also includes areas with altitudes of, for example, 100–200 m, a proportion of the coastal birds are assigned to this altitude.

The study area chosen for this analysis consisted of a transect through central KwaZulu-Natal and potentially into Lesotho (Figure 2.1). The study area consisted of three degree cells, 2929, 2930 and 2931, in the standard South African nomenclature. This is the area between 29°S and 30°S, and east of 29°E to the coastline of KwaZulu-Natal. This transect was selected because it had large volumes of SABAP2 atlas checklists (Underhill and Brooks 2017b). The potential transects immediately to the north and the south had far less data. Even within the study transect, the big weakness was a lack of bird checklists for the highest altitudes, in the Drakensberg itself and in Lesotho. As a result, it was not possible to create equal-interval height classes all the way to 3,000 m, and the highest height class that could be used was 2000 m and above.

Two datasets were used in the altitude analysis: the SABAP2 dataset and an altitude dataset. The latter contained spot heights on a grid of 30 seconds (half a minute); this generates 100 altitude points per pentad. The percentage of each pentad in each height class was estimated based on these 100 altitude points per pentad. Height class intervals of 100 m were used from sea-level to the Drakensberg. The highest class was taken as 2000 m and above, so there were 21 height classes: 0–100 m, 100–200 m,…, 1900–2000 m, 2000 m+ above sea-level. Algebraically, let the proportion of height class k in pentad j be h_{jk}. The percentage of the study area in height class k is denoted s_k and is found by summing over the pentads: $s_k = \sum_j h_{jk}$. Table 2.1 shows the proportions, expressed as percentages, of the study area in each of the 21 height classes. All except six of the height classes have percentages between 3% and 6%.

The second set of data to be used was the SABAP2 data for the study transect. For each target species, the raw data consists of the number of checklists for each pentad, and the number of times that species was recorded. The ratio of these two numbers provides the reporting rates for the species in each pentad in the study area. The next objective is to estimate the percentage of the total population of the target species which is in each pentad. This percentage needs to be calculated relative to the study transect. The available data consists of the reporting rates for the species in each pentad. The so-called “Griffioen transformation” enables a first estimate of these proportions to be made (Griffioen 2001, Underhill 2016, Underhill and Brooks 2016c). Peter Griffioen, in an unpublished PhD thesis, based his analysis on mathematical ecology developed by Nachman (1984).

In algebraic terms, the approach is described here. For each species and for each pentad, define m_{ij} and n_j, where m_{ij} is the number of checklists that report species i as present in pentad j and n_j is the number of checklists in pentad j. Then $r_{ij} = \frac{m_{ij}}{nj}$ is the reporting rate for species i in pentad j. Let d_{ij} be the density or relative abundance of the species i in pentad j. Then, using Griffioen’s (2001) transformation, define $d_{ij} = K_i\left(-\ln\left(1 - r_{ij}\right)\right)$, where K_i is a species specific constant of proportionality. The value of K_i depends on the conspicuousness of the species, also known as its detection probability. Let $D_i = \sum d_{ij}$. Next, let $g_{ij} = \frac{d_{ij}}{D_i}$. Then g_{ij} provides an estimate of the proportion of the total population of species i which is in pentad j. The actual value of K_i is irrelevant, because it is only an estimate of the proportions of the species in each pentad that are needed in this analysis. At this point, the relative abundance of species i across all pentads in the study transect is estimated. This proportion g_{ij} is further subdivided into the proportion in height class k in pentad j: $f_{ijk} = g_{ij} h_{jk}$. We now sum across the pentads to estimate the proportion of the population of species i in height class k, denoted b_{ik}, in the study area: $b_{ik} =$

$_j f_{ijk}$. This makes the assumption that the birds are uniformly distributed across the pentad, and this is where the bias mentioned in the second paragraph of Methods is introduced.

At this point, I have related the bird data and the altitudinal data for each pentad, and estimated the proportion of the population of the species at each height class. The estimated proportion of birds in each height class per species and the proportion of the study area that consists of that height class now need to be compared to calculate a measure of preference. Because the areas of the height classes varied, a preference index was needed which removed the effect of varying areas of the height classes. The index of choice was Jacobs Index, described in the next section.

Jacobs Index

Jacobs Index is a modification of the forage ratio and Ivlev’s electivity index and is a measure of relation between resource use and resource availability (Jacobs 1974). This index has the following properties: it is independent of resource relative abundance; takes a value of zero under random selection (no preference) and deviates symmetrically from zero between –1 and +1; negative values indicate avoidance and positive values indicate preference (Jacobs 1974, Lechowicz 1982, Tjørve et al. 2005). Jacobs (1974) gives the expression for Jacobs Index (D), where r is resource selection and p is resource availability, as follows:

$$D = \frac{r - p}{r + p - 2rp}$$

The range of values for D is restricted to lie between –1 and +1; negative values indicate avoidance, positive values indicate preference and a value of zero indicates no preference (Jacobs 1974, Tjørve et al. 2005).

In the context of this study, we have analogous values: r becomes the relative proportion of the total population of the birds of a species in a particular height class, denoted b_{ik} above, and simplified here to b and p becomes the proportion of the total area that is in that particular height class, denoted s_k above, simplified here to s. This generates the expression for Jacobs Index in this context:

$$D = \frac{b - s}{b + s - 2bs}$$

Other measures of preference also exist (Jacobs 1974). However, as Jacobs (1974) pointed out, they are “useless” when resource availability varies, as it does in this study (Table 2.1). Jacobs (1974) demonstrated that the index he proposed is independent of the relative abundance of the resource; this is achieved by the introduction of the term $-2rp$ in the denominator of his original index (and the term $-2bs$ in the formulation used here).

Table 2.1. Percentages of the KwaZulu-Natal study area, between 29°S and 30°S, which fall within each of the 21 height classes

Height class (m)	Percentage of total area (%)
0–100	5.65
100–200	3.57
200–300	3.25
300–400	3.16
400–500	3.37
500–600	3.70
600–700	4.96
700–800	4.76
800–900	4.80
900–1000	4.75
1000–1100	5.30
1100–1200	5.21
1200–1300	5.31
1300–1400	5.92
1400–1500	7.78
1500–1600	7.72
1600–1700	4.52
1700–1800	2.81
1800–1900	2.18
1900–2000	1.73
2000+	9.55

Table 2.2. Interpretation of Jacobs Index values in terms of the relative abundance of birds that generate those values when area available in a height class is 3%, 5% and 7% of the total area.

	Value of b for birds (%)		
Jacobs Index	for s=3%	for s=5%	for s=7%
–1	0.00	0.00	0.00
–0.9	0.16	0.28	0.39
–0.8	0.34	0.58	0.83
–0.7	0.54	0.92	1.31
–0.6	0.77	1.30	1.85
–0.5	1.02	1.72	2.45
–0.4	1.31	2.21	3.13
–0.3	1.64	2.76	3.90
–0.2	2.02	3.39	4.78
–0.1	2.47	4.13	5.80
0	3.00	5.00	7.00
0.1	3.64	6.04	8.42
0.2	4.43	7.32	10.14
0.3	5.43	8.90	12.26
0.4	6.73	10.94	14.94
0.5	8.49	13.64	18.42
0.6	11.01	17.39	23.14
0.7	14.91	22.97	29.90
0.8	21.77	32.14	40.38
0.9	37.01	50.00	58.85
1	100.00	100.00	100.00

It is valuable to develop an understanding of Jacobs Index. Clearly, and intuitively correctly, Jacobs Index is zero when $b = s$. There is no preference for a particular height class when the percentage of the population in that height class is equal to the percentage of the area in that height class (ie when $b = s$). The mathematical theory that underpins Jacobs Index, and fully discussed in Jacobs (1974), introduces subtle non-linearities into the calculations when $b \neq s$. There are, for example, multiple ways in which a Jacobs Index of, say, 0.5 arises. Table 2.2 shows some of the combinations to achieve this value: when 3% of the area is in the height class and 8.49% of the birds are in this height class; 5% of the area and 13.64% of the birds; and 7% of the area and 18.42% of the birds. In these three cases, the ratios b/s are 2.83, 2.73 and 2.63 respectively.

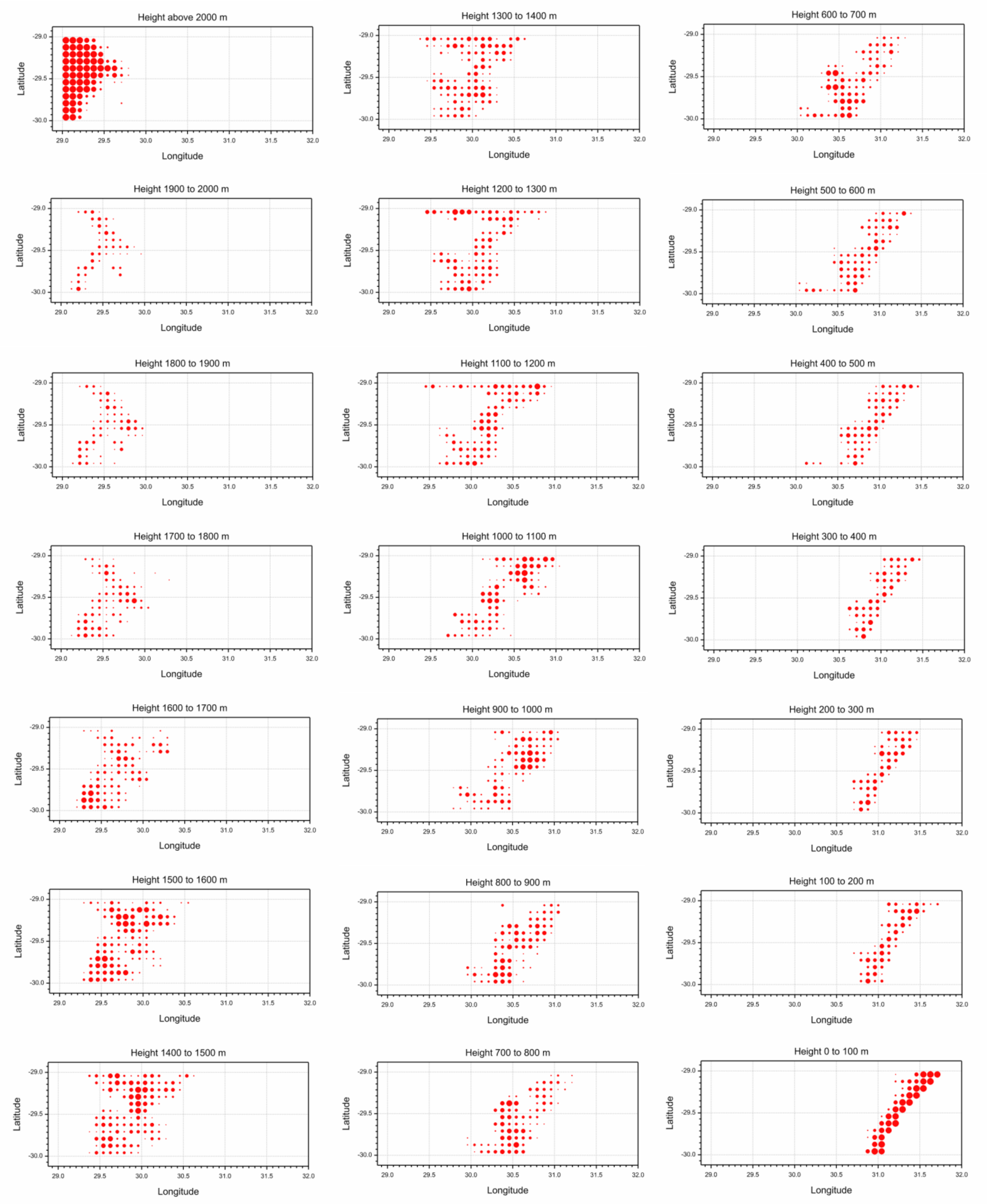
For Jacobs Index to be larger than 0.9, indicating strong preference, 37.01% of the population of a species need to be concentrated into the height class if the height class only consists of 3% of the total area, 50% if the height class consists of 5% of the total area, and 58.85% if the height class consists of 7% of the total area (Table 2.2). For Jacobs Index to be –0.9, indicating strong avoidance, the analogous percentages of the population are 0.16%, 0.28% and 0.39% at 3%, 5% and 7% of the total area, respectively (Table 2.2).

All calculations were programmed in GenStat Seventeenth Edition (2014). This software also generated the plots used throughout this dissertation.

Results

For the study area, the transect across KwaZulu-Natal between 29°S and 30°S, Figure 2.1 provides a representation of the percentage of each pentad which is in each height class. The area of the circle is proportional to the area in the height class. Appendix B provides the percentages of each height class in each pentad. The median number of height classes per pentad is five, with three and six as the lower and upper quartiles. The minimum number of height classes is one, when the entire pentad falls into a single height class, and the maximum is ten, which occurred twice, in pentads 2930_2935 and 2930_2940, both of which had height classes ranging from 1100 m upwards. Pentads which had only one height class were either at the coast (0–100 m height class) or in the uppermost height class (2000+ m) (Appendix B).

Results for species are presented in two sections. The first section discusses a selection of species, chosen to illustrate the range of variation generated by the approach. The second section takes a different approach, and is a case study focusing on six species in one family which occur in the study transect. The family is the Phasianidae, the spurfowls and francolins, and the maps explore the extent to which their altitude preferences overlap.



Height above 2000 m

Height 1300 to 1400 m

Height 600 to 700 m

Height 1900 to 2000 m

Height 1200 to 1300 m

Height 500 to 600 m

Height 1800 to 1900 m

Height 1100 to 1200 m

Height 400 to 500 m

Height 1700 to 1800 m

Height 1000 to 1100 m

Height 300 to 400 m

Height 1600 to 1700 m

Height 900 to 1000 m

Height 200 to 300 m

Height 1500 to 1600 m

Height 800 to 900 m

Height 100 to 200 m

Height 1400 to 1500 m

Height 700 to 800 m

Height 0 to 100 m

Figure 2.1. The study area is a transect across KwaZulu-Natal between 29°S and 30°S. Each of the 21 plots relates to a particular height class. Pentads with circles containing the height class have the circle, with area proportional to the area in the height class in the pentad.

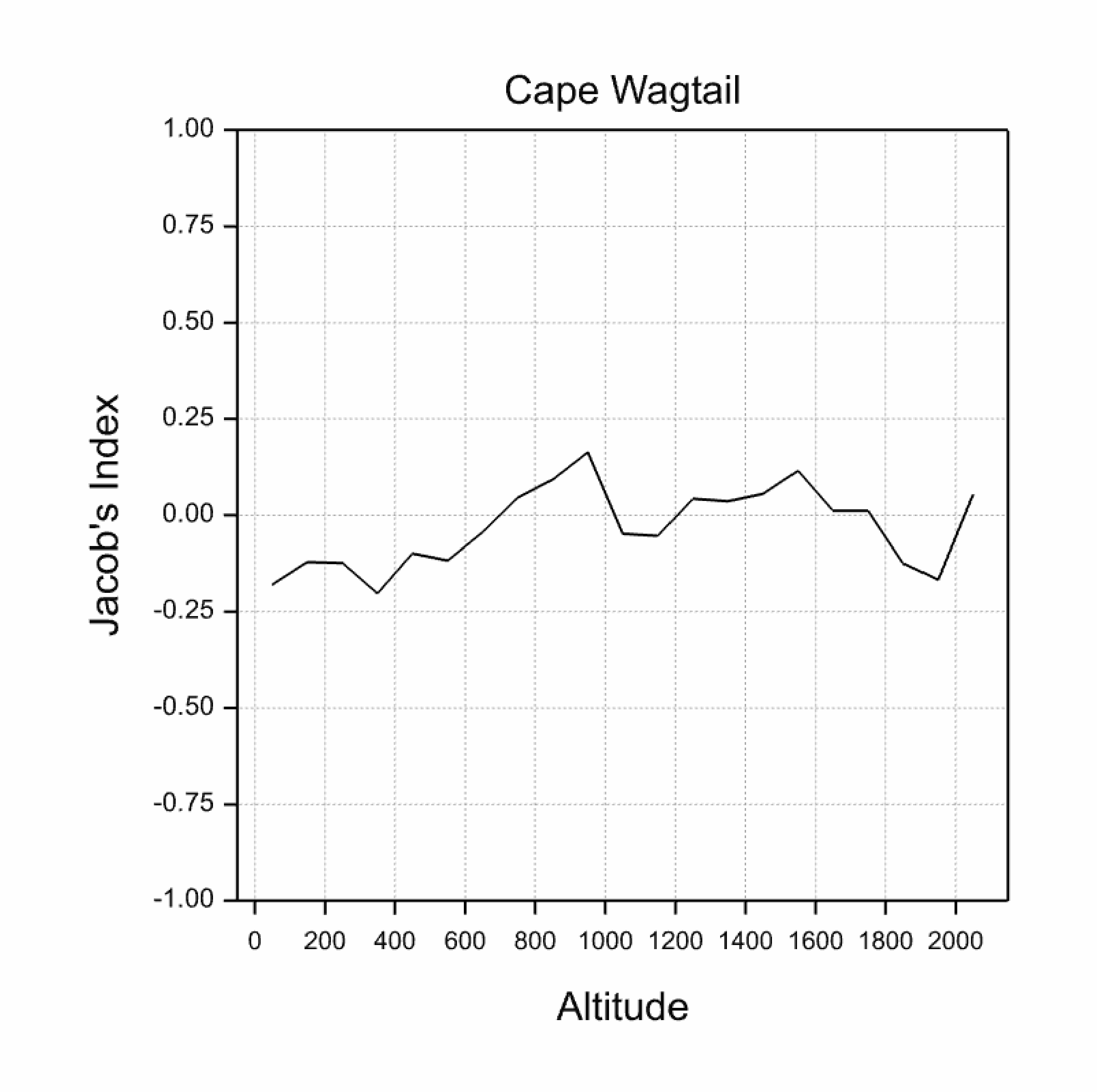
Examples of species to illustrate the method

This section contains a selection of species which illustrate the output of this exploratory data analysis algorithm. The selection is designed to display the full variety of outcomes. I chose not only to present species which had clear preferences for particular height classes, but also species which had weak preferences for height classes. Also included are species for which height class is not a factor determining distribution. For certain species their distribution is known to depend on features in the landscape, which occur at a variety of altitudes. For example, the analysis for most waterbirds reveals the height classes at which wetlands occur, and cannot be interpreted as a height class preference by the species. The species selected illustrate these considerations. This section posed a particular challenge for presentation; each species starts on a new page, resulting in a page layout with large amounts of blank space.

For each species, an altitudinal preference plot is presented. Along the x-axis, the height classes are shown. The y-axis for each species is scaled from –1 to +1, which is the range of possible values for Jacobs Index. For each species (i.e. in each plot), the Jacobs Index value is plotted at the centre of each height class. Successive points are linked by straight lines. In terms of interpretation, first examine the height classes where the line passes through zero on the y-axis; these reveal the preferred and avoided height classes. Secondly, examine whether the line has a single peak; the peakedness of the line reveals the strength of the height-class preference. More subtle interpretations will emerge through the series of examples.

The SABAP2 distribution map for the study transect, and a few rows of pentads to the north and south is presented. These aid interpretation of the altitudinal preference plots. Colour shades represent the reporting rates, as described by Underhill and Brooks (2016a). The shading is graded from yellow (lowest reporting rates) to dark blue (highest reporting rates).

Cape Wagtail, *Motacilla capensis*



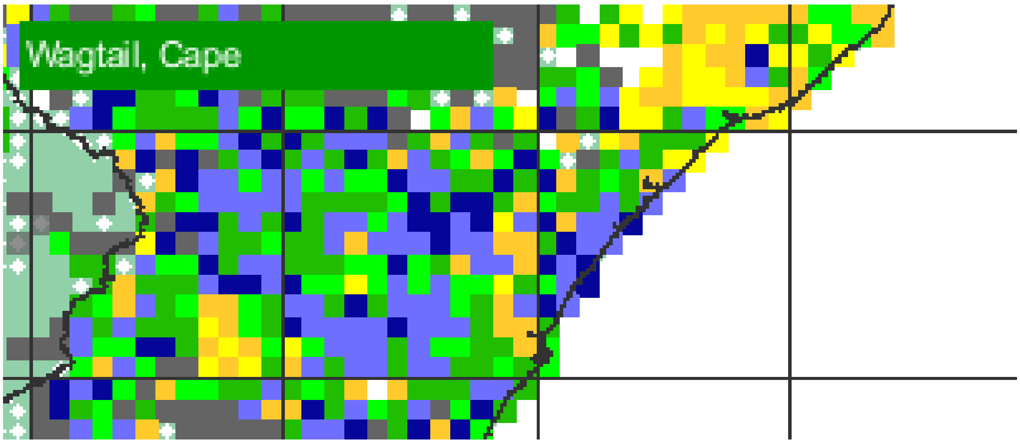
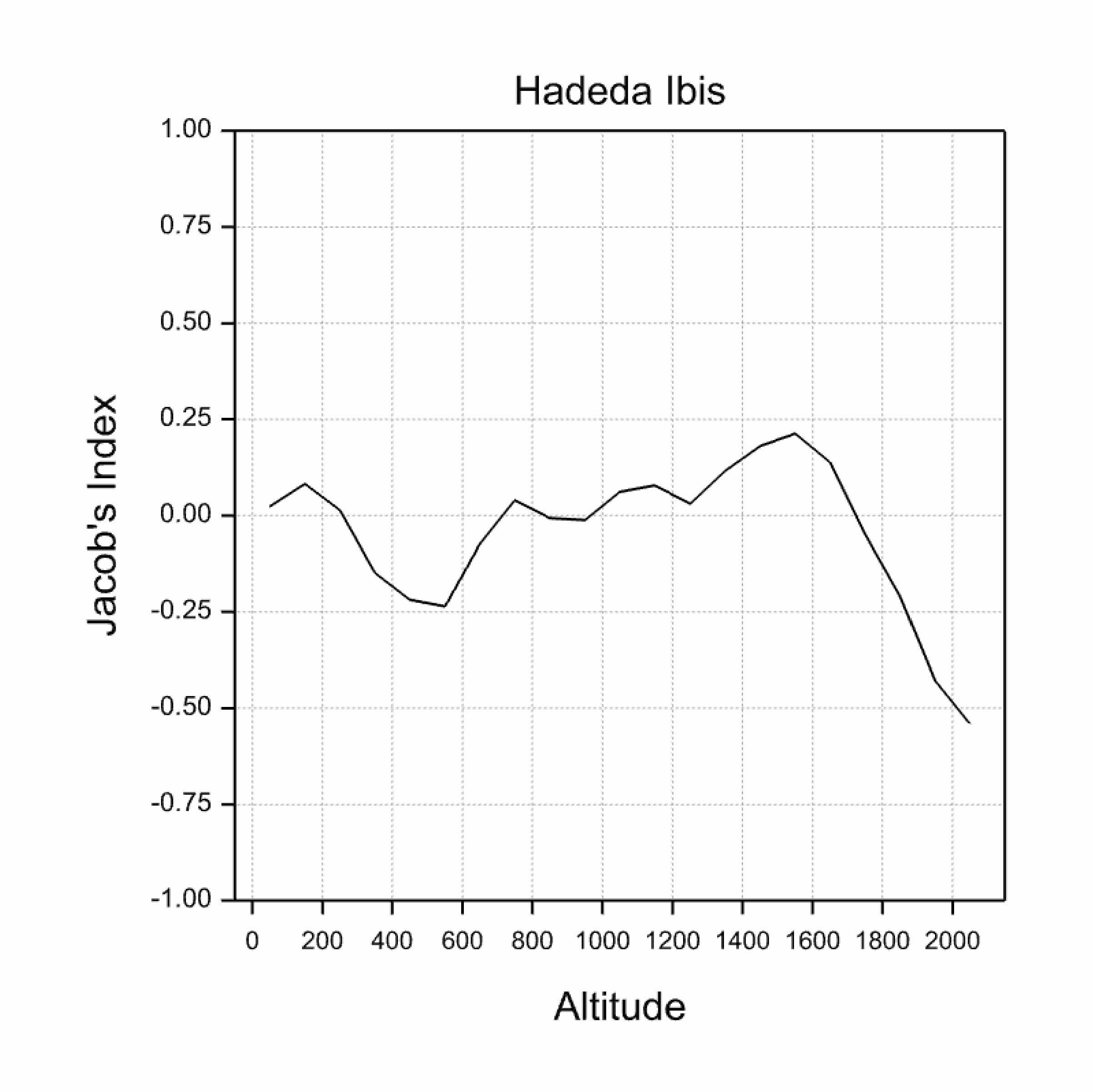


Figure 2.2. The altitudinal preference curve for the Cape Wagtail and the distribution map for study transect in KwaZulu-Natal.

The altitudinal preference curve for the Cape Wagtail is almost horizontal (Figure 2.2). The estimated relative abundance of the species in each height class is close to proportional to the area of the height class. In other words, at each altitude the term *b-s* in equation (2), for the Jacobs Index, is close to zero. The Cape Wagtail does not have a preference for any particular altitude. The distribution map of the Cape Wagtail for the study transect shows some patterning of reporting rates, but there is clearly no altitudinal trend (Figure 2.2).

Hadeda Ibis, *Bostrychia hagedash*



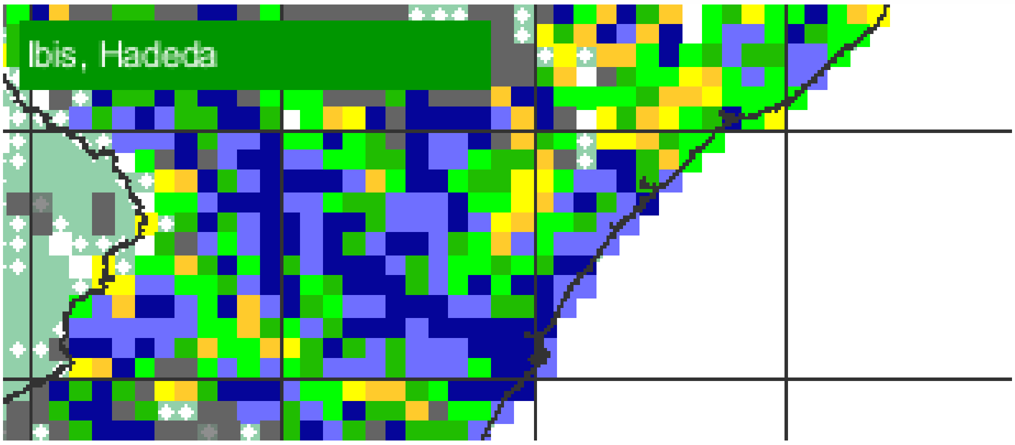
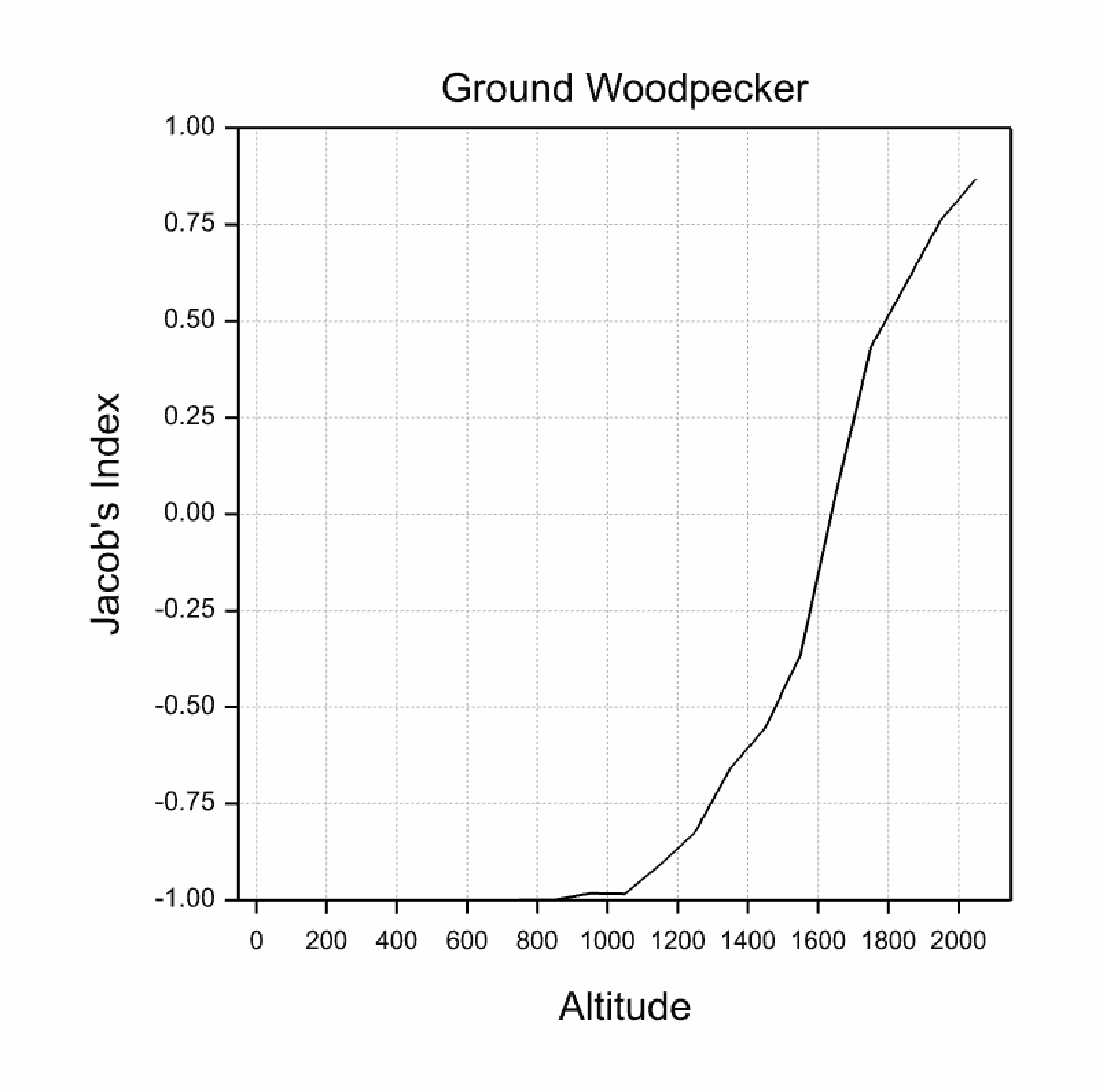


Figure 2.3. The altitudinal preference curve for the Hadeda Ibis and the distribution map for study transect in KwaZulu-Natal.

The Hadeda Ibis shows a similar pattern as the Cape Wagtail, with relative abundance at each height class approximately proportional of the area of the height class, except that for altitudes above 1600 m. At altitudes in excess of 1600 m there are disproportionately few Hadeda Ibises, and the preference curve lies below the zero line (Figure 2.3). However, the curve does not decrease to minus one, indicating that there are still some Hadeda Ibises even at the highest height classes (Figure 2.3).

Ground Woodpecker, *Geocolaptes olivaceus*



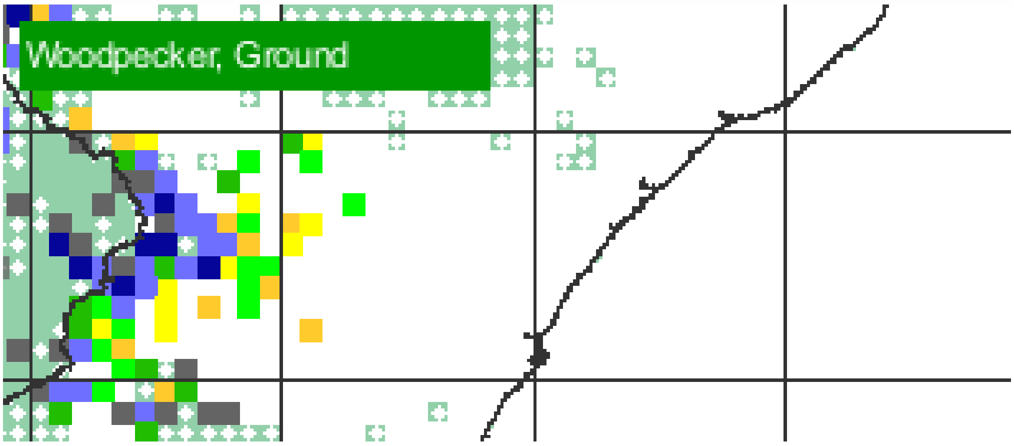
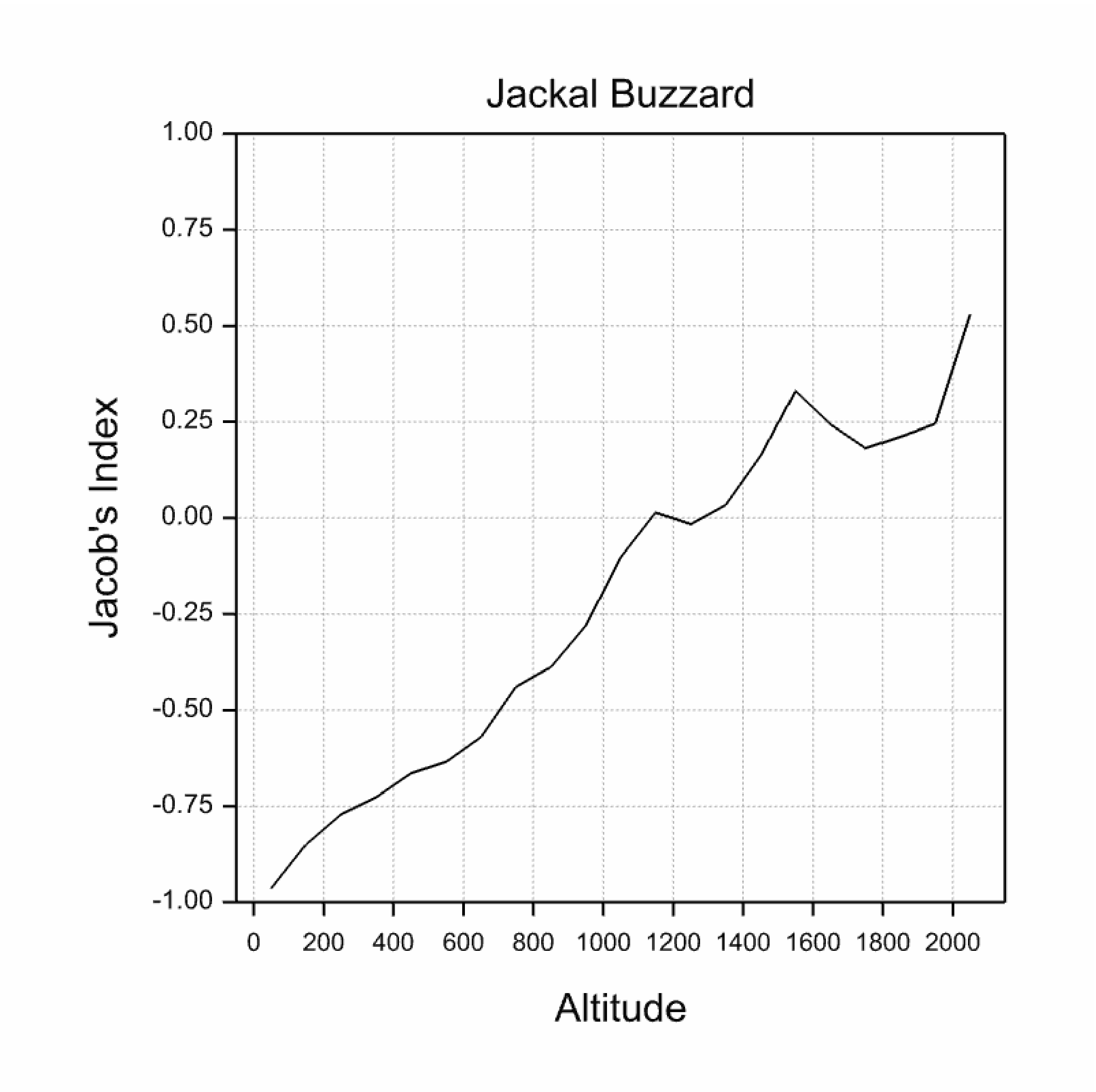


Figure 2.4. The altitudinal preference curve for the Ground Woodpecker and the distribution map for study transect in KwaZulu-Natal.

Preference curve for Ground Woodpecker reaches minus one, indicating complete avoidance of altitudes below 900 m; the small value at 1000 m indicates that a minute fraction of the population occurred in this height class. The preference curve was positive from 1600 m and above, indicating that the proportion of Ground Woodpeckers in these height classes was larger than the proportion of area (Figure 2.4).

Jackal Buzzard, *Buteo rufofuscus*



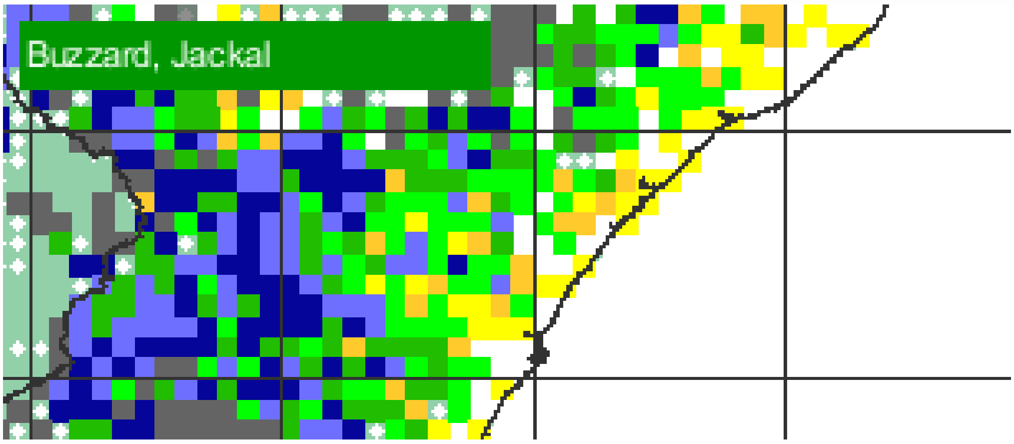
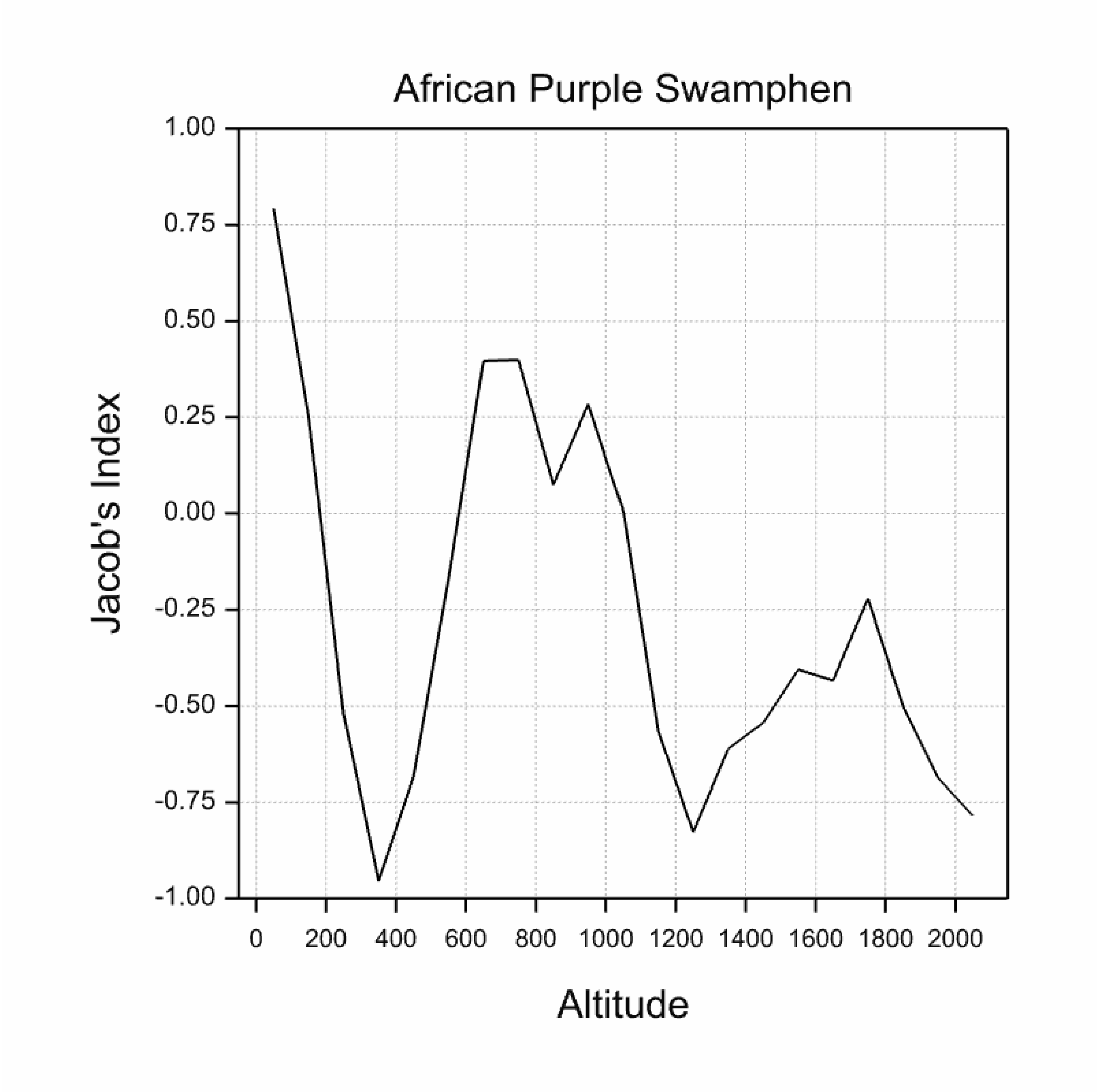


Figure 2.5. The altitudinal preference curve for the Jackal Buzzard and the distribution map for study transect in KwaZulu-Natal.

The preference curve for the Jackal Buzzard appears nearly linear, but is above minus one even in the lowest height class. This indicates that Jackal Buzzards do occur right down to the coast, unlike the Ground Woodpecker which completely avoided areas below 900 m. This pattern is borne out by the distribution map for the species, which shows gradually increasing reporting rates from the coastal plain to the highest elevations in the Drakensberg (Figure 2.5)

African Purple Swamphen, *Porphyrio porphyrio*



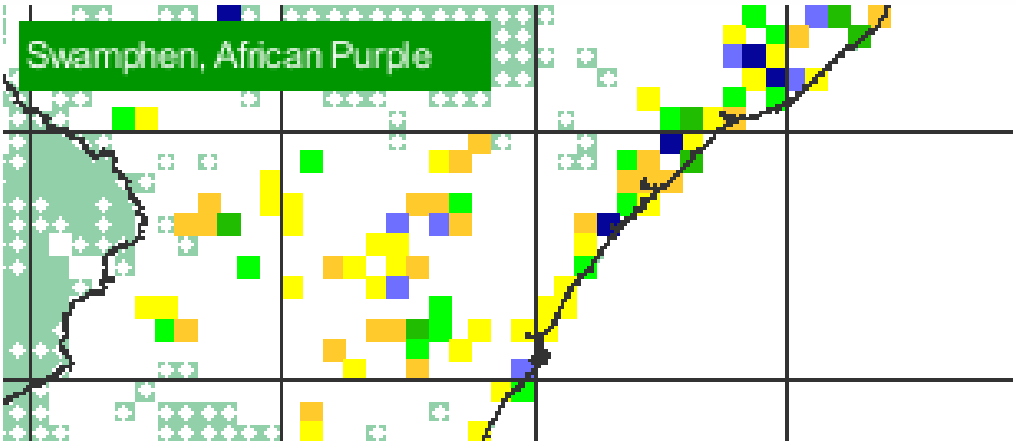
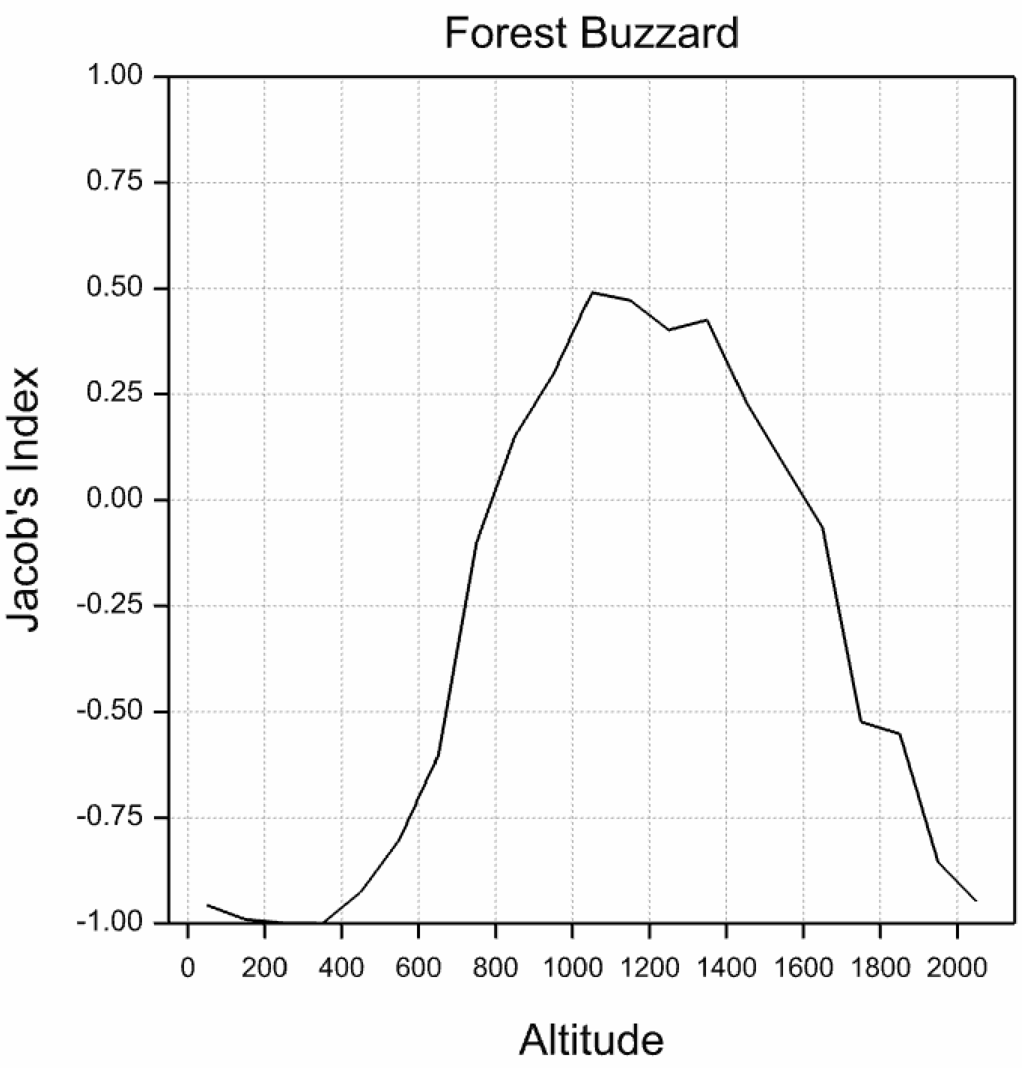


Figure 2.6. The altitudinal preference curve for the African Purple Swamphen and the distribution map for study transect in KwaZulu-Natal.

In relation to altitude, the distribution of African Purple Swamphen is erratic (Figure 2.6). This is a species which occurs at suitable wetlands, which may occur at any altitude. It turns out that in KwaZulu-Natal, the distribution of wetlands is not random, but there are height classes in which wetlands tend to occur. This erratic pattern is characteristic of altitude preference plot of all waterbirds. The occurrence of wetlands across the study transect of KwaZulu-Natal is concentrated along a subset of the height classes (Hiestermann and Rivers-Moore 2015).

Forest Buzzard, *Buteo trizonatus*



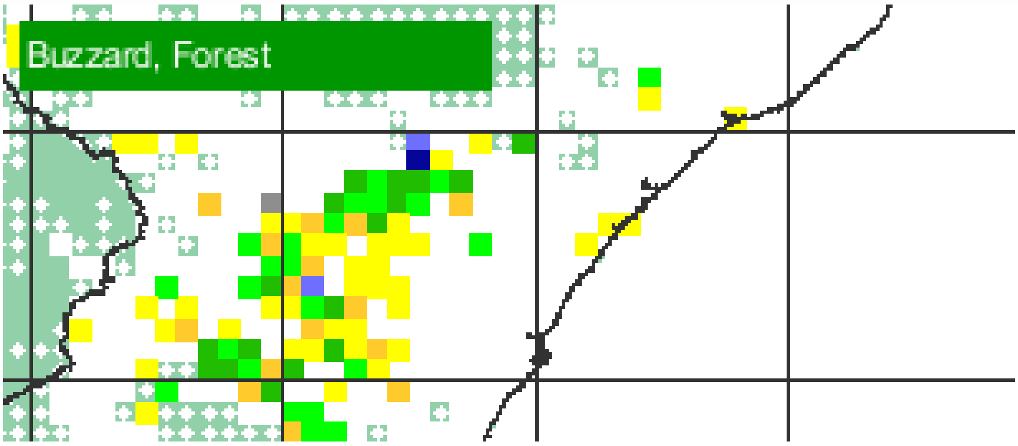


Figure 2.7. The altitudinal preference curve for the Forest Buzzard and the distribution map for study transect in KwaZulu-Natal.

Forest Buzzard illustrates preference for an intermediate altitude. The preference curve reaches minus one, indicating complete avoidance of altitudes 200–300 m; the small value at 100 m and 400 m indicates that a minute fraction of the population occurred in these height classes. The preference curve was positive from 800 m to 1600 m, indicating that the proportion of Forest Buzzards in these intermediate height classes was larger than the proportion of area (Figure 2.6). At altitudes above 1600 m there are disproportionately few Forest Buzzards, and the preference curve lies below the zero line (Figure 2.7). However, the curve does not decrease to minus one, indicating that there are still some Forest Buzzards even at the highest height classes (Figure 2.7).

Altitude preference plots for six species of gamebirds (Phasianidae), occurring in KwaZulu-Natal

In this section, I explore the altitude preference plots for the six species of spurfowl and francolin that occur within the study area; these are “gamebirds” in the sense of Little and Crowe (2000). This section provides a case study on altitude preferences of a group of closely related species. Clearly, altitude in itself is not the factor determining the distribution of each species, but it is nonetheless interesting to examine the outworking of the actual factors on altitude choice. The altitudinal preferences of these species are summarised in Figure 2.8 and Table 2.3. The full size altitudinal preference curves and distribution maps, using the same format as in Figures 2.2 to 2.7 are contained in Appendix C.

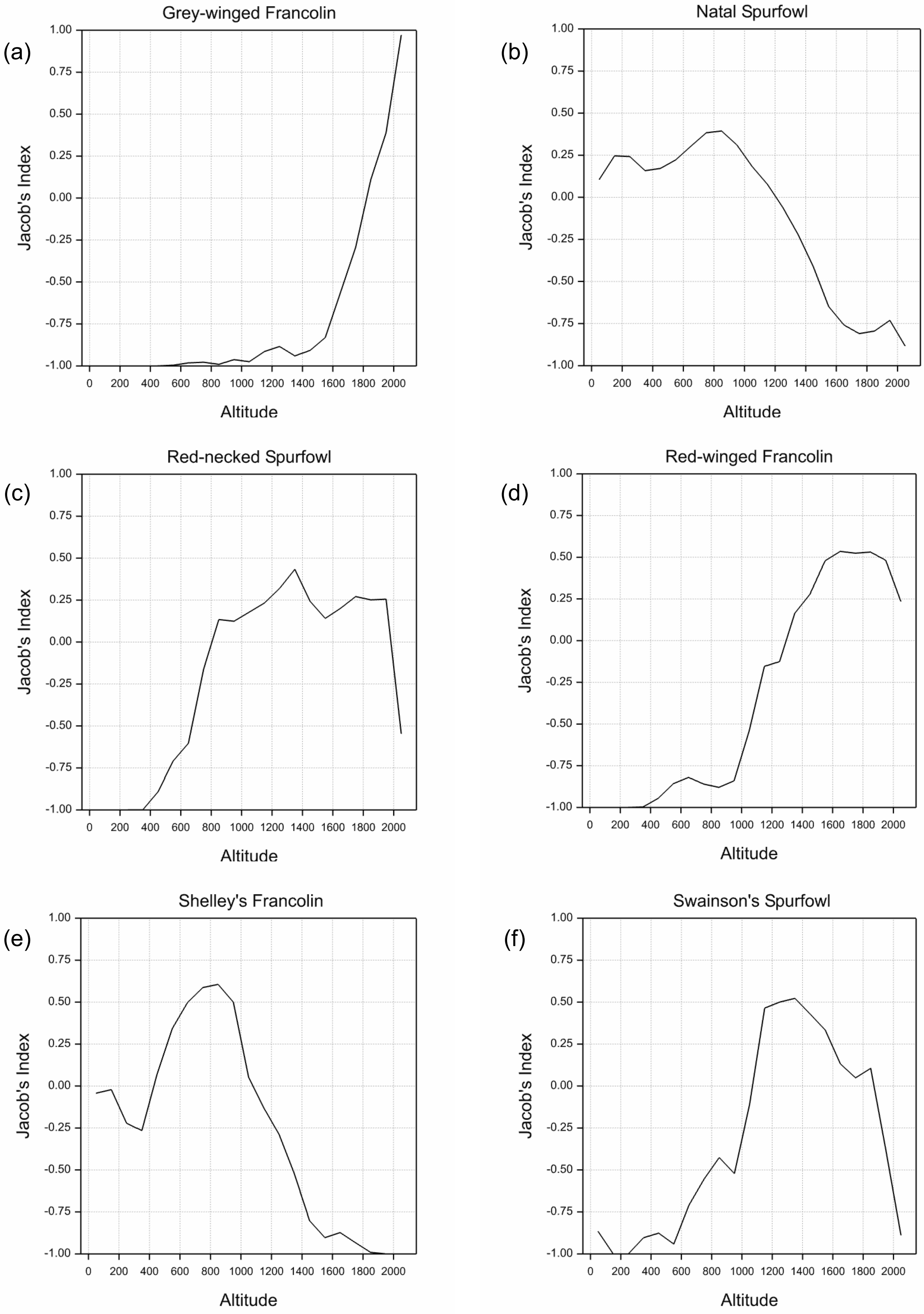


Figure 2.8. The altitudinal preference curves for (a) Grey-winged Francolin *Francolinus africanus*, (b) Natal Spurfowl *Pternistis natalensis*, (c) Red-necked Spurfowl *Pternistis afer*, (d) Red-winged Francolin *Francolinus levaillantii*, (e) Shelley's Francolin *Francolinus shelleyi* and (f) Swainson's Spurfowl *Pternistis swainsonii* for study transect in KwaZulu-Natal.

Grey-winged Francolin has a strong preference for altitudes above 2000 m. The preference curve reaches minus one, indicating complete avoidance of altitudes below 500 m; the small values at 600–1000 m indicates that a minute fraction of the population occurs in these height classes (Figure 2.8a). The altitude preference curve is positive from just over 1800 m and above, indicating that the proportion of Grey-winged Francolins in these height classes is larger than the proportion of area (Figure 2.8a). Grey-winged Francolin, however, occurred in only 15 pentads in the study transect. It is a species that used to be fairly common in KwaZulu-Natal (Cyrus and Robson 1980) so has been included here for completeness sake of spurfowls and francolins.

Natal Spurfowl preferentially chooses suitable habitats in low-to-mid altitude areas. The altitudinal preference curve is positive from sea-level to 1200 m, indicating that the proportion of Natal Spurfowls in these height classes is larger than the proportion of area (Figure 2.8b). At altitudes above 1200 m there are disproportionately few Natal Spurfowls, and the preference curve lies below the zero line (Figure 2.8b). However, the curve does not decrease to –1, indicating that there are still some Natal Spurfowls even at the height classes above 1500 m (Figure 2.8b).

Red-necked Spurfowl illustrates preference for intermediate to high altitudes. The altitudinal preference curve reaches minus one, indicating total avoidance of altitudes below 300 m. The preference curve was positive from 800 m to just below 2000 m, indicating that the proportion of Red-necked Spurfowls in these height classes in larger than the proportion of area in these height classes (Figure 2.8c). At altitudes above 2000 m there are disproportionately few Red-necked Spurfowls and the preference curve lies below the zero line (Figure 2.8c). The curve however, does not decrease to minus one, indicating that there are still some Red-necked Spurfowls even at this highest height class (Figure 2.8c).

Similar to Grey-winged Francolin (Figure 2.8a), Red-winged Francolin has preference for high altitudes. Red-winged Francolin has a main preference for slightly lower altitudes (1600–1900 m) than that of Grey-winged Francolin (2000+ m). The preference curve for Red-winged Francolin reaches minus one, indicating complete avoidance of altitudes below 300 m; the small value at 400 m indicates that a minute fraction of the population occurs in this height class (Figure 2.8d). The preference curve is positive from 1300 m and above, indicating that the proportion of Red-winged Francolins in these height classes is larger than the proportion of area (Figure 2.8d).

Shelley's Francolin has a preference for intermediate altitudes. From the coast to 400 m, the estimated relative abundance of Shelley's Francolins in each height class is close to proportional to the area of the height class (Figure 2.8e). At preference curve is positive between 400 m and 1100 m indicating that the proportion of Shelley's Francolins in these height classes is larger than the proportion of area (Figure 2.8e). At altitudes in excess of 1100 m there are disproportionately few Shelley's Francolins, and the preference curve lies below the zero line (Figure 2.8e). The curve decreases to minus one, indicating complete avoidance of altitudes above 1900 m; the small value at 1800 m indicates that a minute fraction of the population occurs in this height class (Figure 2.8e).

Swainson's Spurfowl illustrates preference for intermediate to high altitudes. The preference curve reaches minus one, indicating complete avoidance of altitudes around 200 m; the small values on either immediate side of this height class indicate that a minute fraction of the population occurs in these neighbouring height classes. The preference curve is positive from 1100 m to 1900 m, indicating that the proportion of Swainson's Spurfowls in these height classes is larger than the proportion of area (Figure 2.8f). At altitudes above 1900 m there are disproportionately few Swainson's Spurfowls, and the preference curve lies below the zero line (Figure 2.8f). However, the curve does not decrease to minus one, indicating that there are still some Swainson's Spurfowls even at the highest height classes (Figure 2.8f).

Figure 2.8 enables a visual comparison of the height class preferences of these six species belonging to one family, and therefore closely related. They provide an aid to understanding the spatial partitioning of the landscape between the species. The Natal Spurfowl has the widest altitudinal preference of the six species (Figure 2.8). It is also of interest to note that Shelley's Francolin shows decreasing preference in the altitudinal range 1000 m to 1500 m whereas, within this range, Red-winged Francolin is showing increasing preference (Figures 2.8d and e). Likewise, the ordered altitudinal preferences (Table 2.3) provide a useful, and hopefully suggestive, summary of the spatial partitioning of these species.

Table 2.3. Summary of the altitudinal preferences of the spurfowl and francolin of the study area in KwaZulu-Natal. The species are ordered, firstly, by the maximum altitudinal preference in the third column and, secondly, by the midpoint of the altitude preference in the second column.

Species	Altitude preference	Maximum altitudinal preference
Natal Spurfowl	0–1000 m	800–900 m
Shelley’s Francolin	400–1100 m	800–900 m
Red-necked Spurfowl	800–2000 m	1300–1400 m
Swainson’s Spurfowl	1100–1900 m	1300–1400 m
Red-winged Francolin	1300+ m	1600–1800 m
Grey-winged Francolin	1800+ m	2000+ m

Discussion

The Discussion is presented in two sections. Firstly, an assessment of the algorithm itself; secondly, an assessment of the results obtained for the six gamebirds in relation to the published literature.

Assessment of the algorithm which generates the altitude curves

Because there are no alternative methods to make comparisons with, the discussion presented here is based on an internal discussion of the method proposed to visualise altitudinal preferences, especially the choices which were made for this case study. The method could similarly be applied to “explanatory variables” other than altitude, and much of the discussion applies to these as well.

Given that this is an exercise in exploratory data analysis, the key decision point is to discuss the question of visual communication: “Does this method succinctly provide a visual display of the altitudinal preferences?” Intuitively, the answer has to be “yes”. The plots which emerge from what appears to be a complex algorithm, are remarkably simple. Preference is scaled between –1 and +1, with “no preference” set at zero, a scale which is immediately familiar to anyone who has encountered and mastered the correlation coefficient. The length of the avoidance section of the axis is one unit, the same as the length of the preference section, so there is a symmetry. The value of –1 communicates that the species completely avoids the height class, and a value of +1 communicates that the species has a particularly strong preference for this height class that it occurs exclusively in this height class. The position of the maximum value of the preference curve along the x-axis unambiguously indicates the preferred height category. The maximum value itself, along the y-axis, indicates the strength of the association with that height class. The larger this value, the more exclusively the species chooses this height class. The answer to the communication question posed at the start of this paragraph is that interpretation is so simple that the altitudinal preference plot (or a plot for any other explanatory variable of interest) could easily become a feature not only of reference handbooks, but also be incorporated into the fieldguides.

As with any data analytic method, small sample sizes can be misleading. In this context, the approach is more likely to produce unsatisfactory results when it is applied to species which occur in only a small numbers of pentads. For this reason, a cut off of occurrence in a minimum of 15 pentads was used, and all the altitude preference plots had records from at least 15 pentads. In this context, an unsatisfactory result consists of the plot showing a saw-tooth pattern with a random scatter of height classes from which it is absent (preference values of –1).

The Griffioen transformation (Griffioen 2001, Underhill and Brooks 2016b) from reporting rate to relative abundance appears to work best for species that occur at random across the landscape, and to be less reliable for species that occur in large flocks (Griffioen 2001). Whatever its shortcomings, this transformation is likely to be better than the alternative, which consists of doing arithmetic, such as taking averages, on reporting rates. These are known to be non-linearly related to abundance (Harrison and Underhill 1997). The Griffioen transformation is based on data collected on Australian bird species, under field conditions which are likely to be broadly similar to those in South Africa. The results presented here would, however, be stronger if the Griffioen transformation could be field-tested in relation to the

SABAP2 protocol, in other words, if estimates could be made of actual bird numbers per species in a sample of pentads. The relationship between atlas reporting rates and relative abundance is a topic of importance for further research.

The choice of classifying the continuous variable, altitude, into 21 categories with a class width (except for the final class) of 100 m, needs consideration. The competing alternatives would have been 50 m and 200 m. Given that the median number of height classes per pentad, using the 100 m interval was five, it seems unwise to attempt a finer scale, because this would have increased this value. Using class intervals of 200 m would generate only 11 categories, and this seems unattractively coarse. As a tool of exploratory data analysis, the 100 m class interval was successful. Finer altitudinal classes will require a smaller spatial grid for the bird atlas data. It seems that the 100 m height classes are appropriate for the five-minute grid, which generates the pentads used by SABAP2.

“Altitude creep” occurs because species are potentially shown to occur in a broader range of height classes than is really true. This is a consequence of the assumption that the population of a species present in a pentad is uniformly distributed over the entire pentad. In the analogous analyses performed for habitats in Harrison et al. (1997), the same problem occurred, and for the same reason (Harrison and Underhill 1997). However, the bias is unlikely to be serious. For most pentads, two or three height classes account for 50%–80% of the area of the pentad (Appendix B). Thus the effective spread of height classes in a single pentad is relatively small. If a species does not occur at a particular height class, then this will primarily be reflected in the arithmetic for pentads in which that height class is dominant. These pentads have the largest influence in the calculations for that height class. If altitude creep were to prove a serious issue, then one strategy would be to exclude pentads from the calculations if they spread over more than a predetermined number of height classes.

One strategy for investigating the usefulness of a new approach such as this is to apply it in a practical context, and see how it performs. This particular study area in KwaZulu-Natal was chosen because altitudinal migration is of noteworthy interest in this region (e.g. Berruti et al. 1994, Johnson and Maclean 1994, chapter 4 of Oatley and Arnott 1998). In these studies, many species have either been demonstrated (or conjectured) to be altitudinal migrants. Species such as the Cape Robin-chat *Cossypha caffra* are considered by Oatley and Arnott (1998) to be short distance partial altitudinal migrants, and potentially provide a stringent test of the approach described here. Chapter 3 of this dissertation aims to provide a demonstration of the ability of the algorithm to investigate altitudinal migration by comparing the altitude preference curves in summer and in winter in the study area.

Assessment of the results for francolin and spurfowl

The six species of gamebird (Grey-winged Francolin, Red-winged Francolin, Red-neck Spurfowl, Swainson's Spurfowl, Natal Spurfowl and Shelley's Francolin) each had a clearly preferred altitudinal range but they did show altitudinal overlap, and thus potential habitat overlap (Table 2.3, Figure 2.8, Appendix C). This result is supported by the literature; which has been critically reviewed by Little and Crowe (2000). The choice of the gamebirds for detailed study was, in part, motivated by the detailed species accounts provided by Little and Crowe (2000). The six species are regarded as resident or sedentary species exhibiting no seasonal movements (Little 1997a, b, c, d, e, Little and Allan 1997, Little and Crowe 2000). For the specialist ornithologist researching these species, the exploratory data analysis summarised into Table 2.3 and Figure 2.8 will suggest hypotheses worth following up relating to the boundaries of the distributions between these species, and how they partition the landscape between them.

Grey-winged Francolin is a montane species most commonly occurring in highland Alpine Grasslands of the Drakensberg at altitudes of 1800–2750 m (Little 1997a); the lower altitude is precisely that given by the altitudinal preference curve (Figure 2.8a, Table 2.3). The distributions of the Grey-winged Francolin and Red-winged Francolin overlap in the highland grasslands of the study area, with the former generally occurring at higher altitudes than the latter (Cyrus and Robson 1980, Little 1997, Little and Allan 1997, Little and Crowe 2000). This study helps quantify this relationship: the limit of preference of Grey-winged Francolin is at 1800 m and of Red-winged Francolin at 1300 m (Figures 2.8a and 2.8d, Table 2.3). Grey-winged Francolin favours sparse, short grass on shallow soils whereas Red-winged

Francolin generally prefers longer, rank grasslands with deeper soils, particularly highland *Themeda* grassland (Little and Crowe 2000). Grey-winged Francolin is thus more tolerant of grasslands that are frequently burnt and moderately grazed (Little 1997a, Little and Allan 1997, Little and Crowe 2000) whereas Red-winged Francolin is more tolerant of the prolonged absence of fire (Little and Allan 1997). Where the two species do occur together, they are not isolated ecologically and are thus potentially in competition (Little and Crowe 2000). In the Drakensberg of KwaZulu-Natal, where previously farmed areas have been protected from heavy grazing and frequent burning, long, rank grassland habitat has been able to return. This grassland recovery has caused a partial displacement of the Grey-winged Francolin by Red-winged Francolin (Little and Crowe 2000). A comparison of the Grey-winged Francolin distribution map in Little and Allan (1997) with the map shown in Appendix C, demonstrates the extent to which the range of the Grey-winged Francolin has shrunk between the two atlas projects.

The literature on the next pair of species, Red-necked Spurfowl and Swainson's Francolin, makes little mention of altitude preferences. Red-necked Spurfowl is described as inhabiting dense, moist habitats in the KwaZulu-Natal Midlands and is mainly found on the edges of evergreen forests above 1000 m, or in riparian thickets or marsh edges (Cyrus and Robson 1980, Little 1997d, Little and Crowe 2000). In KwaZulu-Natal it feeds in cultivated land adjoining its thicket habitat. Here it can occur together with Swainson's Spurfowl (Little 1997d, Little and Crowe 2000). Red-necked Spurfowl is thus partially sympatric with Swainson's Spurfowl, although the former tends to prefer denser vegetation cover in moister areas than that favoured by the latter (Little 1997d, e). Swainson's Spurfowl occurs in open grassland and woodland provided there is tall grass. It also occurs in cultivated areas, particularly maize-growing areas, and close to water (Cyrus and Robson 1980, Little 1997e, Little and Crowe 2000). Swainson's Spurfowl is largely absent from the highland Alpine Grasslands of the Drakensberg (Little and Crowe 2000) above 2000 m (Figure 2.8f).

Natal Spurfowl is described as commonest at lower altitudes in KwaZulu-Natal but does also venture into riverine bush among the Drakensberg escarpment grasslands, especially in the foothills of KwaZulu-Natal Drakensberg (Little and

Crowe 2000). Natal Spurfowl inhabits dense vegetation in a wide range of woodland habitats. Its habitat ranges from savanna with scrub understorey (especially along rivers), to thickets and coastal forest and bush. Preferred habitats are dry riparian vegetation and wooded hills (Cyrus and Robson 1980, Little 1997c, Little and Crowe 2000). Natal Spurfowl regularly utilises the edges of agricultural lands, where it is often seen alongside Swainson's Spurfowl, provided the fields are adjacent to dense vegetation cover (Little 1997c, Little and Crowe 2000). Natal Spurfowl can also be found alongside Red-necked Spurfowl. The two species cohabit in forest edges and moister sites (Little and Crowe 2000).

Shelley's Francolin occurs in open montane and other grasslands, wooded savanna, thornveld and open areas in woodland, often in stony terrain or among rocky outcrops (Cyrus and Robson 1980, Little 1997b, Little and Crowe 2000). Shelley's Francolin occurs in more open habitat towards the coast and can also be found in cultivated lands (Cyrus and Robson 1980).Shelley's Francolin has a preference for taller sweetveld, whereas Red-winged Francolin prefers shorter sourveld, resulting in a distinct habitat separation between the two species (Little and Crowe 2000). Shelley's Francolin can occur alongside Swainson's Spurfowl and Natal Spurfowl, but these two latter species tend to prefer denser, woodier cover than Shelley's Francolin (Little and Crowe 2000).

This case study provides valuable new insights into the distributions of this group of species, the gamebirds. These species are particularly well studied, with sufficient information about them to produce a book, with several pages of text for each species (Little and Crowe 2000). If the information relating to altitudinal preference had been available to the authors, it would have helped to strengthen and improve the sections on distribution in the book. The authors might well have chosen to include the altitude preference plots within the species accounts.

CHAPTER 3

Altitudinal bird migration in a transect across KwaZulu-Natal

Introduction

One of the ornithological opportunities of KwaZulu-Natal is the study of altitudinal migration and this provides an excellent opportunity to use the methods developed in Chapter 2 to study this seasonal movement of birds. Migration is defined as a cyclical movement between two or more areas (Oatley and Arnott 1998). Altitudinal migration is defined as the cyclical seasonal movement of birds from high level breeding grounds to lower levels during winter (Oatley and Arnott 1998). The geographical landscape of KwaZulu-Natal province is a steep altitudinal gradient from the coast up the Drakensberg escarpment to the summit of the Drakensberg Mountains. There is an altitudinal range from sea-level to an elevation in excess of 3385 m over a distance of only 160 km (Oatley and Arnott 1998). This means that the seasonal movements by many species of birds are characterised by large altitudinal changes over relatively short distances (Oatley 2017).

The foundation of the study of birds in KwaZulu-Natal is provided by two books: the systematic handbook by Clancey (1964) and the bird atlas by Cyrus and Robson (1980). Both made mention of altitudinal migration in the province. There is extensive literature on the species thought to be involved in altitudinal migration in KwaZulu-Natal. Johnson and Maclean (1994) listed 75 species as altitudinal migrants in KwaZulu-Natal. Their selection of species was based on evidence from the literature, ringing data and personal observation resulting in a substantial portion being anecdotal evidence. The review by Johnson and Maclean (1994) and a novel analysis by Berruti et al. (1994) are the most recent studies of altitudinal migration in KwaZulu-Natal, and this topic has not been addressed for two decades.

Berruti et al. (1994) made use of data from the First Southern African Bird Atlas Project (SABAP1) and the reporting rate as an index of relative abundance. The study focused both on coastal migration, dividing the coastal region of the Western Cape, Eastern Cape and KwaZulu-Natal into six sections, and on altitudinal migration in KwaZulu-Natal, dividing the province into three altitudinal bands (0–300 m, 300–900 m and 900–1500 m a.s.l.). They considered only a small subset of species.

In this chapter I will apply the method devised in Chapter 2 to the summer and winter distributions of the more common species across the study area. The outcome will be a comprehensive data-based analysis of altitudinal migration in this region. A preliminary analysis of variables that might explain altitudinal migration is undertaken, using diet, habitat and body size, as measured by mass, was undertaken.

Methods

The method developed in Chapter 2 was applied to the distributions in summer (defined as the months from October to March) and in winter (April to September) separately. For each species, I plotted its altitudinal height choices in summer and winter on a single plot and compared them. The comparison was both visual and quantitative. If the distribution of a species was the same in summer and in winter, then the expectation of the qualitative visual comparison was that the altitudinal height choice lines for summer (displayed in red) would closely coincide with the line for winter (displayed in blue). If the species was a downward altitudinal migrant then the blue line for winter would be to the left of the red line for summer, indicating a preference for lower altitudes in winter than in summer. Other movement strategies potentially exist for some species, such as upward migration in winter, or other unexpected patterns, and these were searched for visually.

To compare the difference between the summer and winter distributions quantitatively, various metrics were available. The standard metric would be the Euclidean distance between the values at each height class for summer and winter, but this consisted of the sum or squares of the differences, but this measure was found to exaggerate the contributions of the large differences between the summer and winter lines. To compensate for this, the sum of absolute differences (SAD) was computed. The results were then sorted on the SAD. This provided an ordered table of species. It is clear that those with small values for the SAD had nearly identical summer and winter distributions. As the SAD value increased, the difference between the summer and winter distributions increased, but visual inspection of the summer and winter curves was needed to determine whether the species was a downward altitudinal migrant or not.

As in Chapter 2, the approach to data analysis used in this chapter is classified as an “exploratory data analysis” Tukey (1977). This chapter expands on the algorithm developed in Chapter 2 by presenting two altitude preference curves in each graph, and measuring the “distance” between the curves. In this chapter, the display of the summer and winter curves, colour-coded, and on a single pair of axes, represents the output of the exploratory data analysis, and provides the visual summary for interpretation.

If the summer and winter curves are coincident, then the altitudinal preferences of the species are identical in summer and winter, and altitudinal migration does not occur. Clearly, what is needed is a measure of the distance apart of the summer and winter curves. Of the alternative measures available, I chose to use the Sum of Absolute Differences (SAD). The SAD consists of the sum, over the 21 height classes, of the absolute differences of the summer and winter values of the Jacobs Index in each height class. If the SAD is close to zero for a species, then altitudinal migration does not take place. If the SAD is large, then visual inspection of the plots is needed. If the winter line (blue) is displaced to the left (i.e. towards lower altitudes) of the summer line (red), then altitudinal migration from higher altitudes in summer to lower altitudes in winter is the most likely interpretation. The SAD represents the first step towards producing a formal test statistic, for which the null hypothesis would be that the summer and winter distributions are identical. The development of that statistical test lies in the discipline of mathematical statistics and is beyond the scope of this study. Even when the null hypothesis of identical summer and winter distributions is rejected, it will still require the qualitative visual methods developed here to explain the direction of the change which the formal confirmatory data analysis has detected. I classified the species with SAD scores into five categories: definite residents, definite altitudinal migrants, possible residents, possible altitudinal migrants and an intermediate category in the middle, for species which showed no clear preference. The cutpoints for the categories were chosen from a visual analysis of the altitude preference plots.

Without a formal statistical hypothesis testing strategy, a methodological difficulty faced at present are the magnitudes of the differences between the summer and winter lines which are interpretable. Even so, with the large sample sizes of atlas data, it is likely that even minor differences between the lines will turn out to be formally statistically significant. Thus the focus of interpretation will turn to differences which are biologically meaningful, as opposed to statistically significant (Underhill 1999). The species accounts below help engage this interpretation process. The lessons learnt are considered again in the Discussion.

Statistical analysis in search of explanatory variables for altitudinal migration

A spreadsheet summarising life history information for all species in Hockey et al. (2005) has been used in several studies (e.g. Okes et al. 2008, Loftie-Eaton 2014). The table was compiled from the species texts in Hockey et al. (2005). This analysis made use of three of the available variables: Diet, Habitat and Mass, selected because they had been suggested as likely candidates by Boyle (2017) in her review of altitudinal migration. For Diet and Habitat, a chi-squared test was performed with a 2×5 table; the rows indicating whether the Diet or Habitat category was present or absent, and columns indicating the migration category of the species, based on the SAD scores. Average masses for each species were obtained from Hockey et al. (2005). Mass was split into four classes, at the quartiles of mass (19 g, 46 g and 285 g), creating groups of almost equal numbers of species in each mass class. A chi-square test of association between migrant class and mass class was performed.

Results

There were 6,038 and 3,552 checklists for the study area in KwaZulu-Natal in summer (October to March) and winter (April to September) respectively. These contained a total of 373,540 records in summer and 190,938 winter. 304 species occurred in at least 15 pentads. Altitudinal analyses for both summer and winter were restricted to 285 (304 – 19) species which had records from at least 15 pentads in both summer and winter (Table 3.1). There were 19 species with altitudinal analyses for summer only because they were not recorded in at least 15 pentads in winter: eight Palearctic migrants, 10 intra-African migrants and the Buff-spotted Flufftail (Table 3.1). Summer and winter altitudinal plots are presented for two Palearctic migrants, the White Stork and the Barn Swallow, for which overwintering birds were recorded in more than 15 pentads The Buff-spotted Flufftail is included because there are records for 79 pentads in summer, when it produces its remarkable breeding season call (Taylor 1997). There were winter records from fewer than 15 pentads.

Table 3.1. Altitudinal migration in KwaZulu-Natal. Each row contains the data for one of the 304 species considered. The table is sorted by the Sum of Absolute Differences between the summer and winter altitudinal preference curves for the species (see text). There are three columns for summer and three for winter; they give the number of pentads in which the species was recorded in each season, the maximum value of the Jacobs Index in each season, and the height class of that index. The final column gives the difference between the summer and winter maximum height classes. Apart from sampling variation, this difference provides a first estimate of the number of height classes involved in the altitudinal migration. Positive values indicate downwards altitudinal migration in winter, and negative values apparent upwards migration. The bottom of the table includes results for 18 migrants which were only present in summer, except as occasional winter vagrants. Buff-spotted Flufftail, a resident species, is also included (see text)

Species	SAD	Pentads in summer	Jacobs Index Summer maximum	Position Summer maximum	Pentads in winter	Jacobs Index winter maximum	Position Winter maximum	Difference in position of maxima
Peregrine Falcon	14.12	39	0.9254	21	24	0.793	11	10
Verreaux's Eagle	13.40	31	0.4852	20	19	0.976	21	-1
Black-crowned Night-Heron	13.11	23	0.6911	17	16	0.9727	21	-4
African Reed-Warbler	12.65	138	0.5794	11	36	0.8193	3	8
White Stork	12.46	152	0.4585	21	30	0.4891	7	14
Spotted Thick-knee	12.20	24	0.6578	7	20	0.8469	3	4
Wing-snapping Cisticola	12.14	178	0.3945	16	39	0.6197	5	11
Barratt's Warbler	11.66	69	0.8118	21	53	0.608	15	6
White-rumped Swift	11.55	235	0.4042	21	31	0.4612	3	18
White-backed Duck	10.63	53	0.7476	21	28	0.801	11	10
Alpine Swift	10.09	128	0.6938	21	37	0.6686	14	7
African Dusky Flycatcher	9.78	190	0.2817	9	147	0.581	4	5
Little Rush-Warbler	9.53	211	0.3512	10	126	0.6086	3	7
Fiery-necked Nightjar	9.25	35	0.7588	1	43	0.6906	15	-14
African Paradise-Flycatcher	9.20	255	0.3516	5	114	0.6847	4	1

Species	SAD	Pentads in summer	Jacobs Index Summer maximum	Position Summer maximum	Pentads in winter	Jacobs Index winter maximum	Position Winter maximum	Difference in position of maxima
African Black Swift	9.14	208	0.6006	21	85	0.553	3	18
Green-backed Heron	8.86	31	0.8009	1	20	0.8525	3	-2
Red-capped Lark	8.85	52	0.8745	21	53	0.731	21	0
Plain-backed Pipit	8.81	69	0.3637	3	88	0.4573	16	-13
Blue-mantled Crested-Flycatcher	8.79	47	0.3611	14	50	0.6206	6	8
Olive Thrush	8.48	206	0.2775	11	154	0.3131	21	-10
Little Sparrowhawk	8.44	35	0.4016	8	39	0.6533	13	-5
Shelley's Francolin	8.20	52	0.5557	12	45	0.6769	9	3
Southern Masked-Weaver	8.09	98	0.5183	21	57	0.4323	15	6
Dark-capped Yellow Warbler	8.09	170	0.5914	11	93	0.352	10	1
Common Starling	8.07	70	0.3935	17	52	0.844	21	-4
Malachite Kingfisher	8.04	146	0.3863	21	109	0.4376	5	16
Squacco Heron	7.92	33	0.8438	1	19	0.626	1	0
White-starred Robin	7.85	20	0.5826	13	22	0.4042	13	0
Klaas's Cuckoo	7.81	171	0.447	3	40	0.5999	6	-3
Yellow-throated Petronia	7.72	100	0.4099	6	73	0.6688	5	1
Groundscraper Thrush	7.66	48	0.6882	15	41	0.5925	19	-4
Black Saw-wing	7.64	255	0.406	4	153	0.5667	5	-1
Cape Rock-Thrush	7.54	93	0.7587	21	108	0.6439	20	1
Croaking Cisticola	7.52	152	0.4378	6	54	0.7971	5	1
Rock Kestrel	7.47	41	0.9666	21	90	0.7814	21	0

Species	SAD	Pentads in summer	Jacobs Index Summer maximum	Position Summer maximum	Pentads in winter	Jacobs Index winter maximum	Position Winter maximum	Difference in position of maxima
Long-billed Pipit	7.29	43	0.5905	14	39	0.7301	18	-4
Lesser Striped Swallow	7.26	202	0.6113	3	96	0.5743	5	-2
Violet-backed Starling	7.22	134	0.4153	4	17	0.6565	4	0
African Wattled Lapwing	7.21	49	0.3911	12	29	0.5856	14	-2
White-throated Swallow	7.16	231	0.3625	16	81	0.5707	15	1
Long-billed Crombec	7.12	65	0.5842	5	46	0.7955	3	2
Purple Heron	7.04	89	0.5854	1	67	0.6699	3	-2
Golden-breasted Bunting	7.01	158	0.4356	11	122	0.3729	16	-5
Martial Eagle	6.95	34	0.3895	8	40	0.1701	13	-5
Olive Bush-Shrike	6.89	132	0.5423	6	74	0.4697	12	-6
African Black Duck	6.83	123	0.3676	15	96	0.4255	4	11
Bush Blackcap	6.77	52	0.8029	21	32	0.6405	16	5
Half-collared Kingfisher	6.76	40	0.6433	16	16	0.7385	15	1
Ashy Flycatcher	6.75	53	0.6094	6	56	0.8409	2	4
Forest Canary	6.73	115	0.2889	14	89	0.5119	13	1
African Marsh-Harrier	6.71	91	0.6791	11	70	0.5905	21	-10
Three-banded Plover	6.69	111	0.4755	17	96	0.5561	1	16
White-winged Widowbird	6.55	61	0.5537	14	19	0.3778	13	1
African Crowned Eagle	6.50	78	0.4723	6	63	0.5198	5	1
Yellow-throated Woodland-Warbler	6.44	65	0.6308	21	43	0.659	12	9
Rock Dove	6.41	75	0.737	1	75	0.562	1	0
Red-fronted Tinkerbird	6.41	109	0.5464	3	68	0.4792	1	2

Species	SAD	Pentads in summer	Jacobs Index Summer maximum	Position Summer maximum	Pentads in winter	Jacobs Index winter maximum	Position Winter maximum	Difference in position of maxima
Cape Canary	6.30	219	0.4557	21	221	0.3536	10	11
Grey Cuckooshrike	6.27	43	0.4687	12	60	0.5177	13	-1
Rock Martin	6.16	166	0.816	21	174	0.3356	4	17
Crowned Lapwing	6.10	45	0.6958	7	52	0.6945	11	-4
Common Scimitarbill	6.10	38	0.6799	12	30	0.4837	14	-2
Black-shouldered Kite	6.09	143	0.3341	21	124	0.4668	16	5
African Purple Swamphen	6.07	41	0.8138	1	38	0.739	1	0
Brown-throated Martin	6.04	205	0.416	21	188	0.2777	15	6
Greater Striped Swallow	5.93	254	0.3427	14	70	0.6965	15	-1
Zitting Cisticola	5.91	249	0.2719	14	133	0.4923	5	9
Cattle Egret	5.90	200	0.3231	14	169	0.3599	2	12
Spotted Eagle-Owl	5.85	65	0.4526	16	57	0.6912	16	0
African Snipe	5.85	34	0.489	18	27	0.7455	17	1
African Quailfinch	5.85	78	0.6307	16	62	0.6392	16	0
Orange-breasted Waxbill	5.85	47	0.3694	16	38	0.5402	2	14
Mocking Cliff-Chat	5.79	63	0.5936	12	54	0.6448	4	8
Little Egret	5.79	57	0.811	1	44	0.5613	1	0
African Palm-Swift	5.78	116	0.581	3	83	0.7992	1	2
Lesser Honeyguide	5.76	121	0.5868	4	69	0.7358	2	2
African Pied Wagtail	5.72	88	0.6226	1	77	0.6492	5	-4
Cape Vulture	5.71	79	0.8119	21	74	0.7711	21	0
Southern Double-collared Sunbird	5.63	80	0.4426	14	92	0.5549	13	1

Species	SAD	Pentads in summer	Jacobs Index Summer maximum	Position Summer maximum	Pentads in winter	Jacobs Index winter maximum	Position Winter maximum	Difference in position of maxima
Lesser Swamp-Warbler	5.62	152	0.6965	10	115	0.4557	21	-11
Crested Barbet	5.58	157	0.5196	5	155	0.342	3	2
Scaly-throated Honeyguide	5.53	47	0.7376	12	46	0.3567	11	1
Denham's Bustard	5.53	40	0.6913	17	30	0.7199	21	-4
Red-billed Quelea	5.51	144	0.561	13	106	0.6175	17	-4
Emerald-spotted Wood-Dove	5.50	102	0.4675	2	92	0.7084	3	-1
African Hoopoe	5.48	178	0.3811	12	164	0.4336	4	8
Giant Kingfisher	5.47	154	0.5027	4	120	0.3124	3	1
Helmeted Guineafowl	5.46	178	0.3679	13	135	0.5148	16	-3
Malachite Sunbird	5.45	125	0.7252	21	70	0.4895	19	2
Lanner Falcon	5.45	170	0.3985	21	150	0.3607	21	0
Black-winged Stilt	5.39	37	0.8316	7	24	0.7979	7	0
White-breasted Cormorant	5.36	154	0.4872	1	119	0.5055	1	0
Swainson's Spurfowl	5.36	35	0.6859	14	20	0.7799	15	-1
Green Wood-Hoopoe	5.32	125	0.4212	12	115	0.5546	5	7
Blacksmith Lapwing	5.30	163	0.4356	17	163	0.2563	14	3
Greater Double-collared Sunbird	5.30	152	0.6491	21	168	0.3462	20	1
African Rail	5.26	65	0.7058	11	53	0.6403	16	-5
Crowned Hornbill	5.26	51	0.7325	5	70	0.6183	4	1
White-faced Duck	5.25	107	0.4723	7	74	0.5373	11	-4
Rufous-naped Lark	5.22	199	0.4182	5	121	0.557	5	0

Species	SAD	Pentads in summer	Jacobs Index Summer maximum	Position Summer maximum	Pentads in winter	Jacobs Index winter maximum	Position Winter maximum	Difference in position of maxima
Southern Pochard	5.21	40	0.6358	16	22	0.5505	16	0
Black-winged Lapwing	5.15	68	0.6384	17	71	0.5612	14	3
Brown-backed Honeybird	5.12	76	0.4095	6	57	0.6408	5	1
Yellow-billed Kite	5.11	267	0.322	4	117	0.6104	5	-1
African Spoonbill	5.06	103	0.6539	16	92	0.5937	17	-1
Southern Ground-Hornbill	5.04	22	0.6991	13	16	0.5187	9	4
Fiscal Flycatcher	5.02	48	0.7056	12	88	0.5544	12	0
Yellow-billed Egret	5.01	58	0.6507	16	26	0.7244	16	0
Rufous-chested Sparrowhawk	5.01	25	0.6323	16	18	0.5547	14	2
African Harrier-Hawk	4.99	163	0.4025	13	117	0.4232	18	-5
African Goshawk	4.99	93	0.3879	2	84	0.5157	3	-1
Goliath Heron	4.99	44	0.9082	1	35	0.7508	1	0
Woolly-necked Stork	4.98	65	0.876	1	49	0.7704	1	0
Black Sparrowhawk	4.88	94	0.4232	1	104	0.4852	15	-14
Scarlet-chested Sunbird	4.86	40	0.6705	5	27	0.8397	1	4
Kittlitz's Plover	4.85	22	0.7045	1	18	0.7925	7	-6
Secretarybird	4.81	57	0.8544	20	56	0.6948	18	2
African Darter	4.79	145	0.4898	10	138	0.4893	10	0
Mountain Wheatear	4.79	35	0.9119	21	23	0.6559	21	0
African Fish-Eagle	4.78	162	0.391	13	139	0.4275	1	12
Barn Owl	4.74	31	0.5604	14	29	0.7904	15	-1
Red-billed Teal	4.70	91	0.579	17	66	0.5469	7	10
Olive Woodpecker	4.65	90	0.3884	14	76	0.4228	19	-5
Pied Kingfisher	4.64	138	0.4969	17	129	0.4582	3	14

Species	SAD	Pentads in summer	Jacobs Index Summer maximum	Position Summer maximum	Pentads in winter	Jacobs Index winter maximum	Position Winter maximum	Difference in position of maxima
Grey Heron	4.52	167	0.5393	21	119	0.3439	3	18
African Wood-Owl	4.46	21	0.4415	19	21	0.454	19	0
Little Swift	4.43	185	0.4564	4	88	0.7316	1	3
Lazy Cisticola	4.42	173	0.512	6	158	0.4479	5	1
Greater Honeyguide	4.41	85	0.3186	20	39	0.4672	1	19
Black Cuckooshrike	4.37	83	0.4991	6	81	0.5909	4	2
Orange-breasted Bush-Shrike	4.37	138	0.5234	6	78	0.6485	5	1
Sentinel Rock-Thrush	4.30	22	0.9896	21	49	0.9573	21	0
Spur-winged Goose	4.25	198	0.3581	16	147	0.402	11	5
Laughing Dove	4.25	181	0.3081	2	145	0.3368	2	0
Kurrichane Thrush	4.25	164	0.5797	4	118	0.4319	5	-1
Water Thick-knee	4.23	31	0.8724	1	26	0.8247	3	-2
Red-winged Francolin	4.21	66	0.8138	21	41	0.6365	17	4
Black Crake	4.20	125	0.5248	11	107	0.4756	11	0
Golden Weaver	4.18	35	0.557	10	18	0.6504	7	3
Cardinal Woodpecker	4.17	170	0.5697	6	140	0.4068	2	4
Trumpeter Hornbill	4.15	65	0.5097	11	61	0.5989	4	7
Mountain Wagtail	4.13	47	0.6255	3	37	0.4403	4	-1
White-necked Raven	4.13	209	0.4699	6	217	0.4491	21	-15
Streaky-headed Seedeater	4.08	208	0.4559	4	170	0.538	5	-1
Narina Trogon	4.05	82	0.3716	6	30	0.4813	3	3
Fan-tailed Widowbird	3.98	255	0.317	10	186	0.5135	10	0
Little Grebe	3.95	178	0.5622	16	175	0.4211	16	0
Burchell's Coucal	3.94	166	0.5904	3	122	0.5	3	0

Species	SAD	Pentads in summer	Jacobs Index Summer maximum	Position Summer maximum	Pentads in winter	Jacobs Index winter maximum	Position Winter maximum	Difference in position of maxima
Long-crested Eagle	3.91	195	0.3519	16	178	0.3394	11	5
Brubru	3.91	84	0.5457	13	55	0.5115	15	-2
Red-throated Wryneck	3.89	177	0.3039	13	146	0.2758	14	-1
Red-chested Flufftail	3.87	66	0.4109	14	29	0.7077	16	-2
Familiar Chat	3.84	164	0.383	6	180	0.3397	6	0
Pin-tailed Whydah	3.84	270	0.2678	10	145	0.375	5	5
Yellow Bishop	3.83	77	0.7463	21	59	0.5352	18	3
African Stonechat	3.80	264	0.2183	16	260	0.1868	10	6
Chinspot Batis	3.78	135	0.3977	7	128	0.5586	5	2
African Olive-Pigeon	3.78	128	0.4452	11	122	0.5189	13	-2
Anteating Chat	3.74	53	0.648	17	38	0.6201	16	1
Green Twinspot	3.73	37	0.4652	6	30	0.6778	1	5
South African Shelduck	3.68	77	0.5568	16	96	0.6616	17	-1
Reed Cormorant	3.65	193	0.5874	16	195	0.3563	16	0
Red-faced Mousebird	3.60	79	0.4999	6	80	0.5348	5	1
Natal Spurfowl	3.60	185	0.3926	11	161	0.4157	3	8
African Green-Pigeon	3.59	32	0.8054	1	33	0.7573	1	0
African Pipit	3.55	237	0.292	14	201	0.303	9	5
Golden-tailed Woodpecker	3.55	139	0.5383	6	127	0.5854	3	3
Knysna Turaco Turaco	3.54	70	0.5084	13	49	0.4939	12	1
Tambourine Dove	3.48	152	0.6398	4	116	0.6545	2	2
Cape Weaver	3.47	207	0.4013	16	160	0.471	16	0
Cape Batis	3.47	178	0.3668	6	173	0.2835	12	-6
Lemon Dove	3.44	35	0.3839	20	27	0.4989	20	0
Swee Waxbill	3.40	98	0.358	17	70	0.5148	9	8
African Sacred Ibis	3.40	169	0.4979	15	144	0.3917	17	-2
Common Moorhen	3.39	169	0.2993	11	144	0.3791	10	1
Hamerkop	3.31	173	0.533	3	132	0.4915	2	1

Species	SAD	Pentads in summer	Jacobs Index Summer maximum	Position Summer maximum	Pentads in winter	Jacobs Index winter maximum	Position Winter maximum	Difference in position of maxima
Red-collared Widowbird	3.28	261	0.1642	11	180	0.3915	11	0
Southern Bald Ibis	3.25	87	0.7903	21	87	0.5382	21	0
Red-necked Spurfowl	3.24	97	0.4668	14	75	0.5436	19	-5
White-fronted Bee-eater	3.21	20	0.9476	1	20	0.9536	1	0
Black-crowned Tchagra	3.15	163	0.5376	3	123	0.6719	5	-2
Southern Tchagra	3.14	97	0.5883	6	76	0.6802	4	2
Yellow-billed Duck	3.12	208	0.4445	16	167	0.4892	16	0
Terrestrial Brownbul	3.09	124	0.4303	7	122	0.4502	6	1
Thick-billed Weaver	3.00	157	0.4644	2	108	0.5719	1	1
Dusky Indigobird	3.00	152	0.6213	5	20	0.6318	3	2
Bar-throated Apalis	2.99	215	0.4432	6	176	0.4643	5	1
Bearded Vulture	2.98	33	0.9769	21	32	0.924	21	0
Blue Crane	2.98	73	0.5603	14	37	0.5467	16	-2
Neddicky Neddicky	2.92	264	0.3588	5	197	0.501	6	-1
Red-backed Mannikin	2.90	60	0.5008	2	51	0.6469	4	-2
Pied Starling	2.87	101	0.5622	16	72	0.6785	16	0
Acacia Pied Barbet	2.86	19	0.7386	13	19	0.6873	13	0
Amethyst Sunbird	2.84	269	0.3983	10	230	0.3832	6	4
Hottentot Teal	2.81	34	0.7657	1	24	0.6853	7	-6
Ground Woodpecker	2.81	50	0.9349	21	35	0.8665	21	0
Great Egret	2.79	90	0.5244	16	51	0.4752	16	0
Cape Crow	2.75	206	0.4399	17	203	0.4426	16	1
Cape Grassbird	2.72	241	0.3307	10	187	0.2254	20	-10
Rufous-winged Cisticola	2.69	33	0.9032	1	19	0.9655	1	0

Species	SAD	Pentads in summer	Jacobs Index Summer maximum	Position Summer maximum	Pentads in winter	Jacobs Index winter maximum	Position Winter maximum	Difference in position of maxima
Southern Red Bishop	2.67	251	0.2765	16	210	0.3469	10	6
Chorister Robin-Chat	2.64	67	0.5254	20	44	0.5497	20	0
Hadeda Ibis	2.59	279	0.1697	16	262	0.1917	10	6
Speckled Mousebird	2.55	272	0.36	5	245	0.2881	3	2
Brimstone Canary	2.53	175	0.5176	5	161	0.5631	5	0
Yellow-breasted Apalis	2.52	66	0.8199	1	71	0.742	1	0
Wattled Crane	2.51	42	0.6299	18	36	0.5653	18	0
Cape Sparrow	2.50	177	0.4336	16	153	0.5155	15	1
Purple-banded Sunbird	2.44	23	0.9189	1	24	0.9133	1	0
Grey-headed Bush-Shrike	2.42	95	0.6636	4	72	0.6088	4	0
Common Waxbill	2.39	270	0.326	10	249	0.2754	10	0
Jackal Buzzard	2.37	229	0.4047	21	231	0.38	16	5
Buff-streaked Chat	2.36	92	0.5652	17	93	0.4878	20	-3
Grey Crowned Crane	2.34	129	0.5602	16	93	0.5191	17	-1
Levaillant's Cisticola	2.34	248	0.2474	16	215	0.308	10	6
Cape Robin-Chat	2.31	249	0.2372	14	246	0.2687	10	4
House Sparrow	2.31	248	0.441	3	215	0.3195	2	1
Egyptian Goose	2.30	227	0.3134	16	227	0.2624	15	1
Southern Black Flycatcher	2.30	165	0.6156	2	173	0.5844	3	-1
Rattling Cisticola	2.29	122	0.7306	3	95	0.6389	3	0
Barn Swallow	2.28	289	0.2446	4	23	0.5239	1	3
Yellow-throated Longclaw	2.26	142	0.6022	4	125	0.5727	6	-2
African Jacana	2.25	73	0.7576	1	67	0.7096	1	0

Species	SAD	Pentads in summer	Jacobs Index Summer maximum	Position Summer maximum	Pentads in winter	Jacobs Index winter maximum	Position Winter maximum	Difference in position of maxima
Gurney's Sugarbird	2.24	21	0.8163	20	22	0.8212	20	0
Pied Crow	2.21	227	0.3411	3	234	0.2829	5	-2
Southern Grey-headed Sparrow	2.17	271	0.2648	5	236	0.154	5	0
Red-knobbed Coot	2.16	168	0.4216	16	152	0.4143	16	0
Tawny-flanked Prinia	2.15	216	0.5057	3	200	0.4865	3	0
Cape Shoveler	2.14	40	0.755	17	28	0.739	17	0
Southern Black Tit	2.11	206	0.4957	4	194	0.43	5	-1
Red-winged Starling	2.08	251	0.4103	21	245	0.3709	21	0
Cape Wagtail	2.05	279	0.1548	10	264	0.1964	10	0
Yellow Weaver	2.02	91	0.8099	1	55	0.862	1	0
Brown-hooded Kingfisher	2.02	169	0.5041	5	150	0.5915	5	0
Wailing Cisticola	2.00	142	0.8087	21	86	0.7329	21	0
Drakensberg Prinia	1.98	177	0.3826	16	158	0.4073	14	2
Bronze Mannikin	1.98	176	0.6493	3	172	0.5286	2	1
Sombre Greenbul	1.97	222	0.4661	3	200	0.4135	5	-2
Olive Sunbird	1.96	118	0.6786	4	134	0.5512	5	-1
Purple-crested Turaco	1.91	132	0.6641	4	114	0.7129	3	1
Dark-backed Weaver	1.90	87	0.5945	1	69	0.4612	1	0
Speckled Pigeon	1.85	211	0.5406	21	202	0.4873	21	0
Common Myna	1.83	154	0.5054	3	137	0.5614	2	1
Cape Turtle-Dove	1.81	263	0.3069	15	247	0.2637	15	0
Black-headed Heron	1.77	239	0.3871	16	221	0.3011	15	1
Blue Waxbill	1.75	98	0.6537	4	96	0.616	5	-1
Red-capped Robin-Chat	1.74	129	0.6755	4	105	0.6813	1	3

Species	SAD	Pentads in summer	Jacobs Index Summer maximum	Position Summer maximum	Pentads in winter	Jacobs Index winter maximum	Position Winter maximum	Difference in position of maxima
Black-throated Wattle-eye	1.73	18	0.9867	1	21	0.9778	1	0
Long-tailed Widowbird	1.71	139	0.5349	16	93	0.5231	15	1
Red-eyed Dove	1.71	274	0.2644	3	270	0.1473	3	0
Black-backed Puffback	1.71	186	0.5503	4	162	0.4421	4	0
Yellow-rumped Tinkerbird	1.68	88	0.7257	2	68	0.679	5	-3
Grey Sunbird	1.67	97	0.6075	4	80	0.711	2	2
Cape Longclaw	1.64	189	0.4699	14	167	0.4653	18	-4
Little Bee-eater	1.62	78	0.6842	2	70	0.7171	3	-1
Black-collared Barbet	1.62	187	0.5713	4	179	0.4952	5	-1
Wire-tailed Swallow	1.57	39	0.7508	1	51	0.7754	3	-2
Black-headed Oriole	1.53	258	0.3178	10	230	0.341	4	6
Forest Buzzard	1.53	62	0.4692	11	43	0.5219	12	-1
Yellow-fronted Canary	1.51	248	0.4213	3	213	0.4728	3	0
Cape White-eye	1.51	283	0.2056	4	255	0.2758	5	-1
Fork-tailed Drongo	1.47	277	0.2107	11	270	0.1567	4	7
Cape Glossy Starling	1.46	208	0.5065	4	187	0.4183	3	1
Square-tailed Drongo	1.46	46	0.8025	4	38	0.8307	1	3
Bokmakierie	1.37	145	0.6042	18	128	0.5785	18	0
African Firefinch	1.36	205	0.4984	5	193	0.4612	5	0
Gorgeous Bush-Shrike	1.28	89	0.7528	4	47	0.6826	5	-1
Common Fiscal	1.26	284	0.1447	16	275	0.1287	16	0
Green-backed Camaroptera	1.25	195	0.561	4	155	0.5224	3	1
White-bellied Sunbird	1.25	165	0.5941	3	148	0.5817	5	-2

Species	SAD	Pentads in summer	Jacobs Index Summer maximum	Position Summer maximum	Pentads in winter	Jacobs Index winter maximum	Position Winter maximum	Difference in position of maxima
Southern Boubou	1.21	272	0.3099	5	250	0.3021	6	-1
Grey-headed Gull	1.13	20	0.9825	1	20	0.9892	1	0
Village Weaver	1.10	238	0.3993	3	221	0.3519	3	0
Spectacled Weaver	1.10	194	0.5702	3	187	0.4906	3	0
Red-faced Cisticola	1.07	75	0.7797	3	51	0.7798	3	0
Yellow-bellied Greenbul	1.05	40	0.9182	1	38	0.9168	1	0
Black-bellied Starling	1.02	86	0.7695	2	73	0.7526	1	1
Dark-capped Bulbul	0.95	288	0.1554	3	274	0.1662	10	-7
White-browed Scrub-Robin	0.93	145	0.6082	5	140	0.5697	5	0
Collared Sunbird	0.88	157	0.6139	4	156	0.5304	4	0
White-eared Barbet	0.81	49	0.8827	1	52	0.7905	1	0
Grey Waxbill	0.49	17	0.8599	1	20	0.7837	2	-1
Kelp Gull	0.43	17	0.9814	1	18	0.9832	1	0
Swift Tern	0.40	16	0.9818	1	19	0.9915	1	0
Amur Falcon	*	140	0.4224	14	*	*	*	*
Black Kite	*	23	0.6603	7	*	*	*	*
Wahlberg's Eagle	*	105	0.5328	12	*	*	*	*
Steppe Buzzard	*	258	0.2852	11	*	*	*	*
Common Quail	*	144	0.4735	16	*	*	*	*
Red-chested Cuckoo	*	253	0.2473	5	*	*	*	*
Black Cuckoo	*	182	0.4399	4	*	*	*	*
Jacobin Cuckoo	*	41	0.4683	12	*	*	*	*
African Emerald Cuckoo	*	124	0.5192	6	*	*	*	*
Diderick Cuckoo	*	252	0.253	6	*	*	*	*
Horus Swift	*	111	0.5492	21	*	*	*	*

Species	SAD	Pentads in summer	Jacobs Index Summer maximum	Position Summer maximum	Pentads in winter	Jacobs Index winter maximum	Position Winter maximum	Difference in position of maxima
African Pygmy-Kingfisher	*	60	0.5778	6	*	*	*	*
Common House-Martin	*	100	0.5975	17	*	*	*	*
Banded Martin	*	102	0.5645	16	*	*	*	*
Willow Warbler	*	167	0.4263	5	*	*	*	*
Marsh Warbler	*	118	0.4412	9	*	*	*	*
Spotted Flycatcher	*	94	0.6443	21	*	*	*	*
Red-backed Shrike	*	77	0.6636	5	*	*	*	*
Buff-spotted Flufftail	*	79	0.4943	6	*	*	*	*

Results for individual species

The results presented here commence with 10 species selected from the 285 species of Table 3.1 which had both summer and winter altitude preference curves. They were chosen to illustrate the diversity of patterns that were observed. Given that the data analysis used here is exploratory, this seems the appropriate first step to introduce the methods. For each of the selected species, the summer and winter altitudinal preference curve are supplemented by the SABAP2 distribution maps (Underhill and Brooks 2016b). These distribution maps are confined to the study transect, degree cells 2929, 2930 and 2931, and also display the rows of pentads immediately to the north and south of the study area. These distribution maps show the distributions in summer (October to March) and winter (April to September), which is the same division as used for the altitudinal preference curves. These distribution maps supplement the summer-winter altitudinal preference curves, and help with their interpretation. After the examples, there is an overview summary of the results.

For each of the selected species, the text aims to interpret the curve, and to do this in the light of summer and winter distribution maps for the study area. The text also aims to discuss the results in relation to previous hypotheses about the altitudinal status of the species. In other words, these species texts contain elements of discussion for that species, rather than only presenting the results of the analyses. Other presentation strategies would result in duplication. The text for the earlier species presented tends to contain more detail and explanation than for later species. As in Chapter 2, the layout of this section posed challenges. In the end, it was decided to start the text for each species on a new page, even though this meant large gaps on the previous page.

African Paradise Flycatcher, *Terpsiphone viridis*

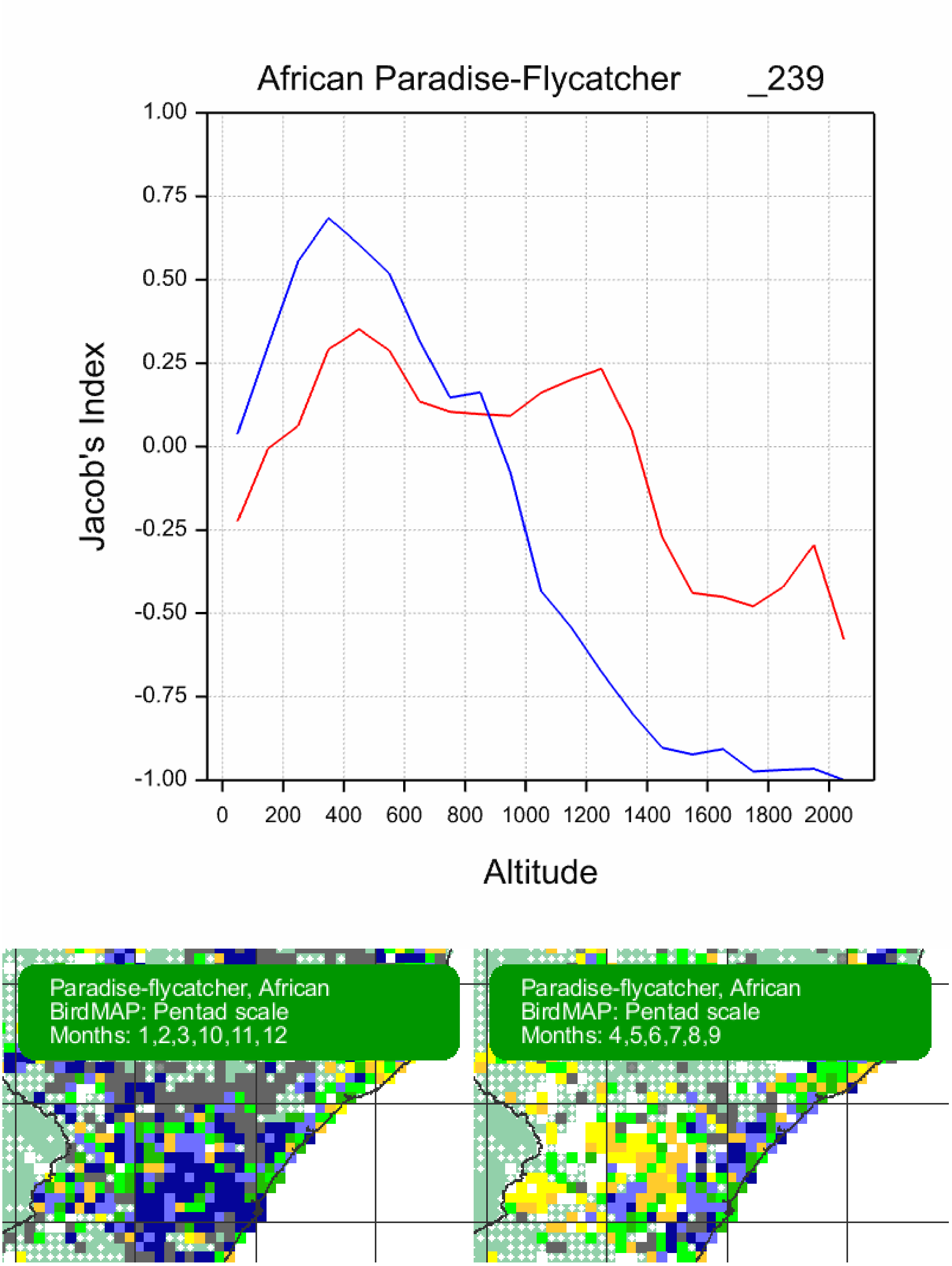


Figure 3.1. The altitudinal preference curves for summer and for winter for the African Paradise Flycatcher, and the summer and winter distribution maps for study transect in KwaZulu-Natal.

In summer there are more African Paradise Flycatchers at altitudes between 100 m and 1400 m than one would expect given the amount of land available at these altitudes (Figure 3.1). There is not total avoidance of altitudes above 1400 m; some African Paradise Flycatchers do utilise these high altitude areas in summer.

In winter there is almost total avoidance of high altitudes above 1400 m. Some African Paradise Flycatchers do occur at altitudes between 1000 m and 1300 m but there are fewer than one would expect given the amount of area available at these altitudes. African Paradise Flycatchers are preferentially choosing 100 m to 900 m with main altitude preference at 300–400 m in winter.

The African Paradise Flycatcher is a woodland species and undertakes both coastal migration and altitudinal migration in KwaZulu-Natal. African Paradise Flycatcher migrates northwards along the coast and predominantly winters on the coastal plain in northern KwaZulu-Natal, Swaziland and Mozambique (Berruti et al. 1994, Cyrus and Robson 1980). Birds residing in woodlands at higher altitudes in KwaZulu-Natal during summer migrate to lower altitudes in winter (Berruti et al. 1994). Using SABAP1 data, they noted that above 300 m there was a substantial winter decrease in reporting rate. This is confirmed by the present analysis.

Black-bellied Starling, *Lamprotornis corruscus*

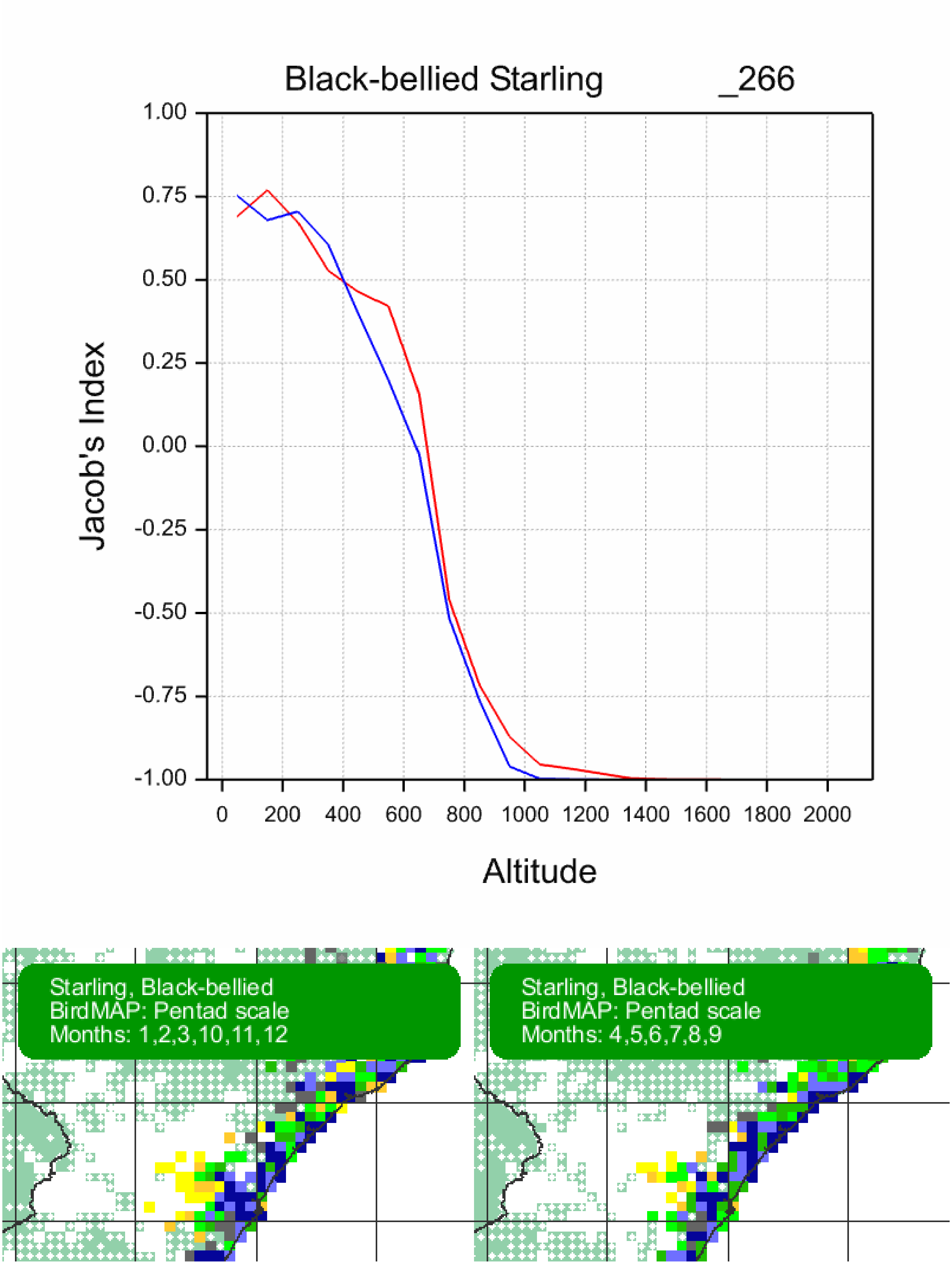


Figure 3.2. The altitudinal preference curves for summer and for winter for the Black-bellied Starling, and the summer and winter distribution maps for study transect in KwaZulu-Natal.

In summer Black-bellied Starlings are preferentially choosing altitudes below 700 m. Main altitude preference is 0–200 m (Figure 3.2). Above 700 m there are fewer birds than one would predict given the area available with complete avoidance above 1400 m.

In winter there are more Black-bellied Starlings below 600 m than one would expected given the area. Main preference is at the coastal level. There are fewer birds than one would expect above 600 m and there is total avoidance of altitudes above 1100 m in winter.

Black-bellied Starling occurs along the KwaZulu-Natal coastal belt and lower midlands (Cyrus and Robson 1980). It is found in coastal forest and riverine woodland and ranges marginally into inland evergreen forests (Cyrus and Robson 1980). It is a summer breeder (Cyrus and Robson 1980).

There appears to be no evidence for seasonal altitudinal movement. Craig (1997a) stated that movement of this species appeared to be in relation to the availability of fruit and flocks do not remain in one area for extended periods. Seasonality of rainfall along the coast changes with latitude and the birds may move along the coast in response to this (Craig 1997a).

Bokmakierie, *Telophorus zeylonus*

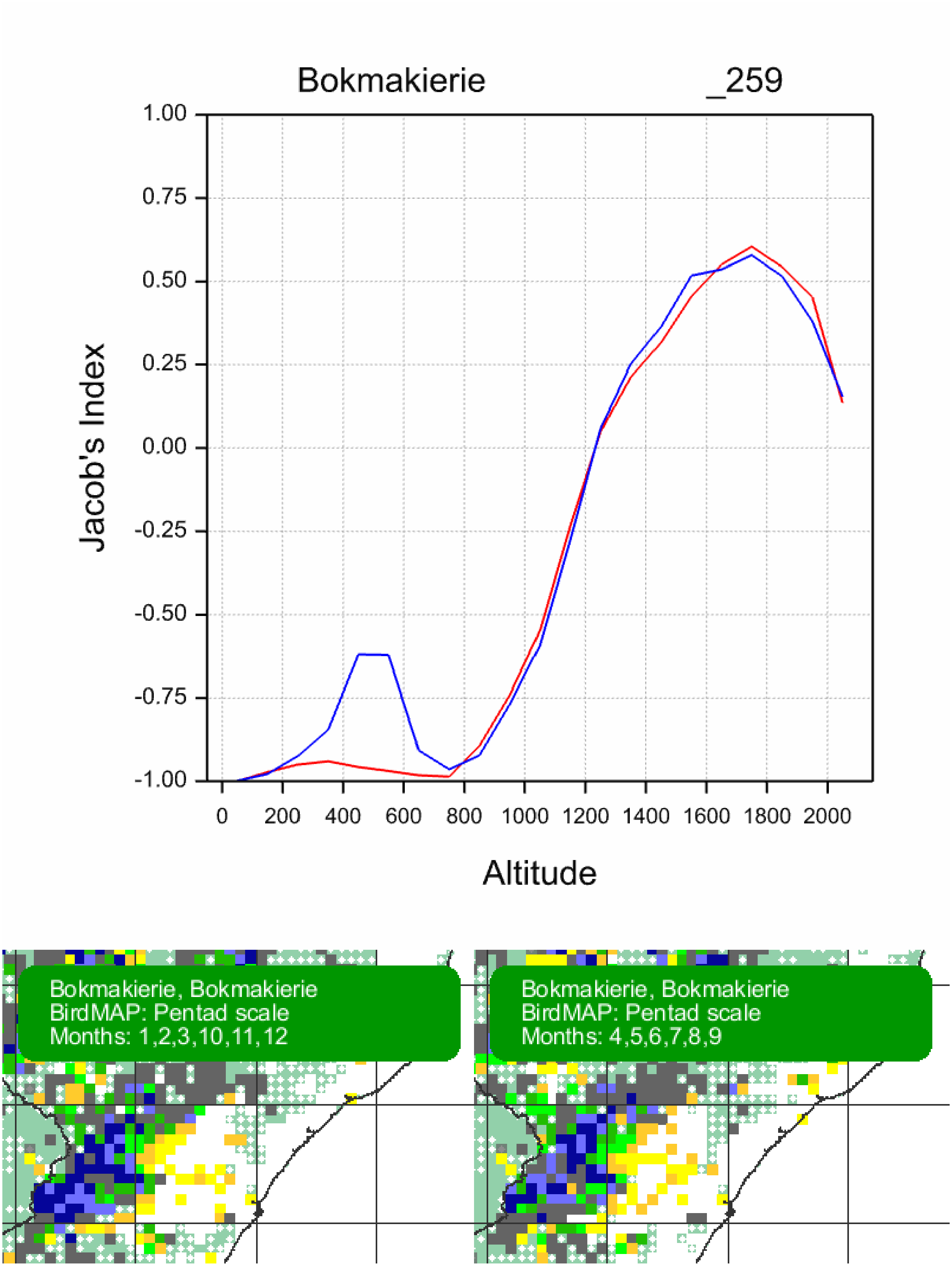


Figure 3.3. The altitudinal preference curves for summer and for winter for the Bokmakierie, and the summer and winter distribution maps for study transect in KwaZulu-Natal.

There is almost complete avoidance by Bokmakierie of altitudes below 800 m in summer (Figure 3.3). Some birds do occur below 800 m in winter but there are far fewer than one would predict given the area. In summer and winter the numbers of birds increases above 800 m to be in proportion to the area available at around 1300 m. Above 1300 m there are disproportionately more birds than land available. Main altitude preference throughout the year is 1700–1800 m. Altitude preference decreases above 1800 m but there is still a preference at 2000+ m.

Bokmakierie is a high-altitude species (Little and Bainbridge 1992). It is found on the slopes of the Drakensberg inhabiting scrubby habitats on rocky hillsides. Bokmakierie can also be found around farmsteads and gardens (Cyrus and Robson 1980). Bokmakierie is common up to roughly 2600 m in the Sani Pass, which is situated in grid cell 2929 in the study transect, but is also present at even higher altitudes, although less common (Little and Bainbridge 1992).

Oatley (2017) writes: “A very widespread bird in South Africa and one which is found (and presumably breeds) in the highest peaks of Lesotho in summer. It is not clear where these birds go in winter, but it can only be downwards, and they presumably join populations resident at lower altitudes.”

Cape Robin-Chat, *Cossypha caffra*

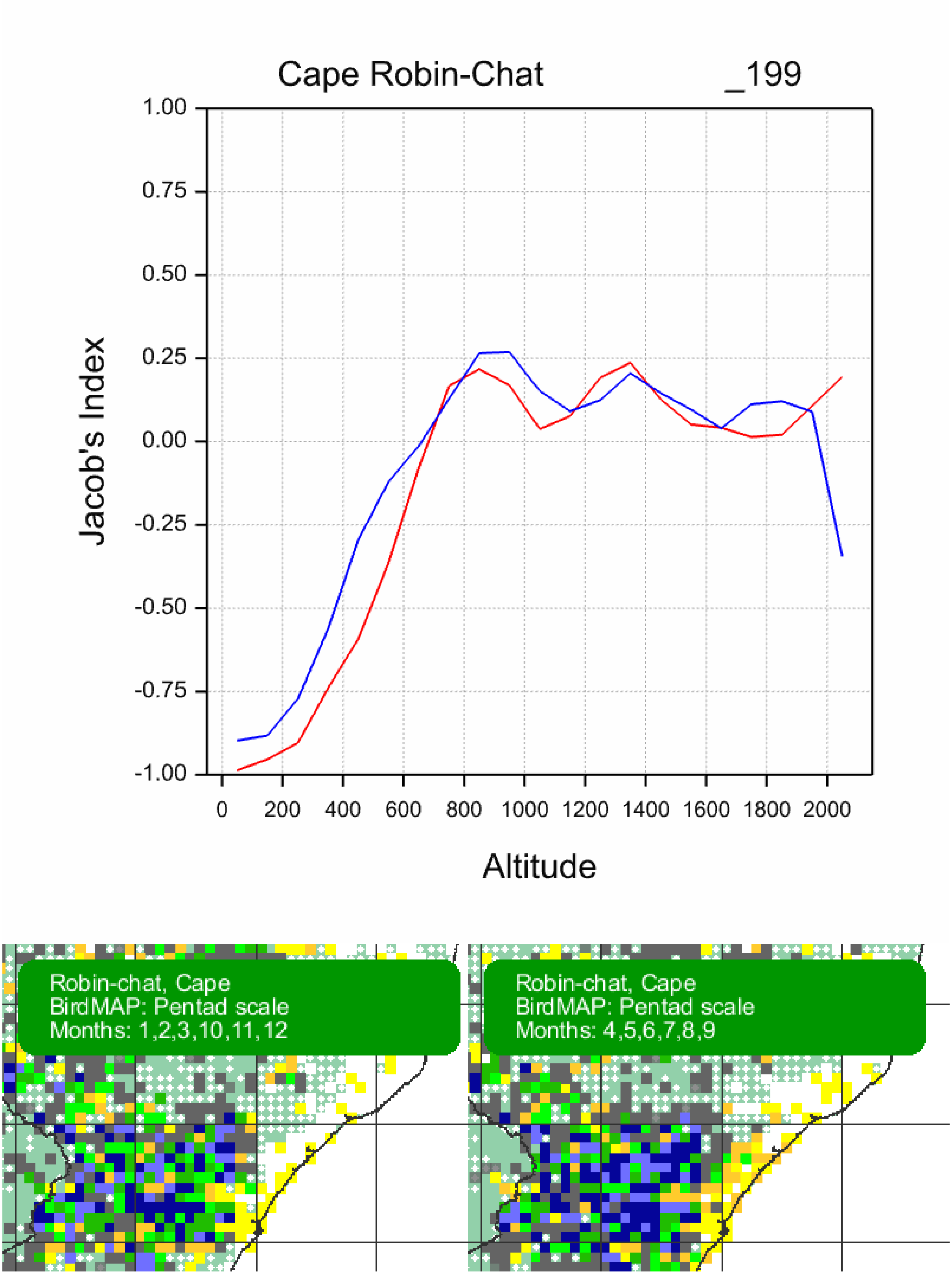


Figure 3.4. The altitudinal preference curves for summer and for winter for the Cape Robin-chat, and the summer and winter distribution maps for study transect in KwaZulu-Natal

Cape Robin-chat is virtually absent from the KwaZulu-Natal coast throughout the year, although there are clearly more birds present in this zone in winter than in summer (Figure 3.4). The number of birds increases to be in proportion to the area of land available at about 600–700 m. Between 700 m and approximately 1900 m there are slightly more Cape Robin-chats than one would expect given the area. At 2000 m and above, the number of Cape Robin-chats increases relative to area available in summer, whereas in winter, the number of birds decreases relative to the area resulting in fewer birds than expected. Although there is no large difference between the summer and winter altitudinal preference curves, the winter preference curve in blue is slightly to the left of the summer curve in red. This is indicative of a small altitudinal shift to lower altitudes in winter, suggesting that the Cape Robin-chat is a short-distance altitudinal migrant.

Cape Robin-chat is a characteristic Afromontane forest-fringe bird. It is a cover-loving species and thrives in a wide variety of habitats from evergreen forest, plantations and woodland to thickets, scrub vegetation and gardens (Oatley 1997f, Cyrus and Robson 1980). Cape Robin-Chat is common in the midlands mistbelt forest region in summer (Oatley and Arnott 1998) and absent from most of the KwaZulu-Natal coastal plain (Oatley 1997f, Cyrus and Robson 1980). During winter it is present in KwaZulu-Natal valley bushveld and coastal forest. Coastal forest is over 90 km away from the midlands mistbelt forest (Oatley and Arnott 1998). The river valleys provide passageways for some altitudinal migrants moving towards the coast and wintering areas for others (Oatley and Arnott 1998). This coastward migration is a partial migration because part of the Cape Robin-Chat population remains behind and is present even in their high altitude breeding grounds throughout the year; the extent of the movements in any given year are likely to be weather-dependent (Brown and Barnes 1984, Osborne and Tigar 1990, Oatley and Arnott 1998). But in the highest areas of Lesotho, the summer and winter reporting rates were 39% and 4%, respectively, and it can be inferred that Osborne and Tigar (1990) believed that the movement out of Lesotho was mostly westwards, towards the Free State.

Dark-capped Bulbul, *Pycnonotus barbatus*

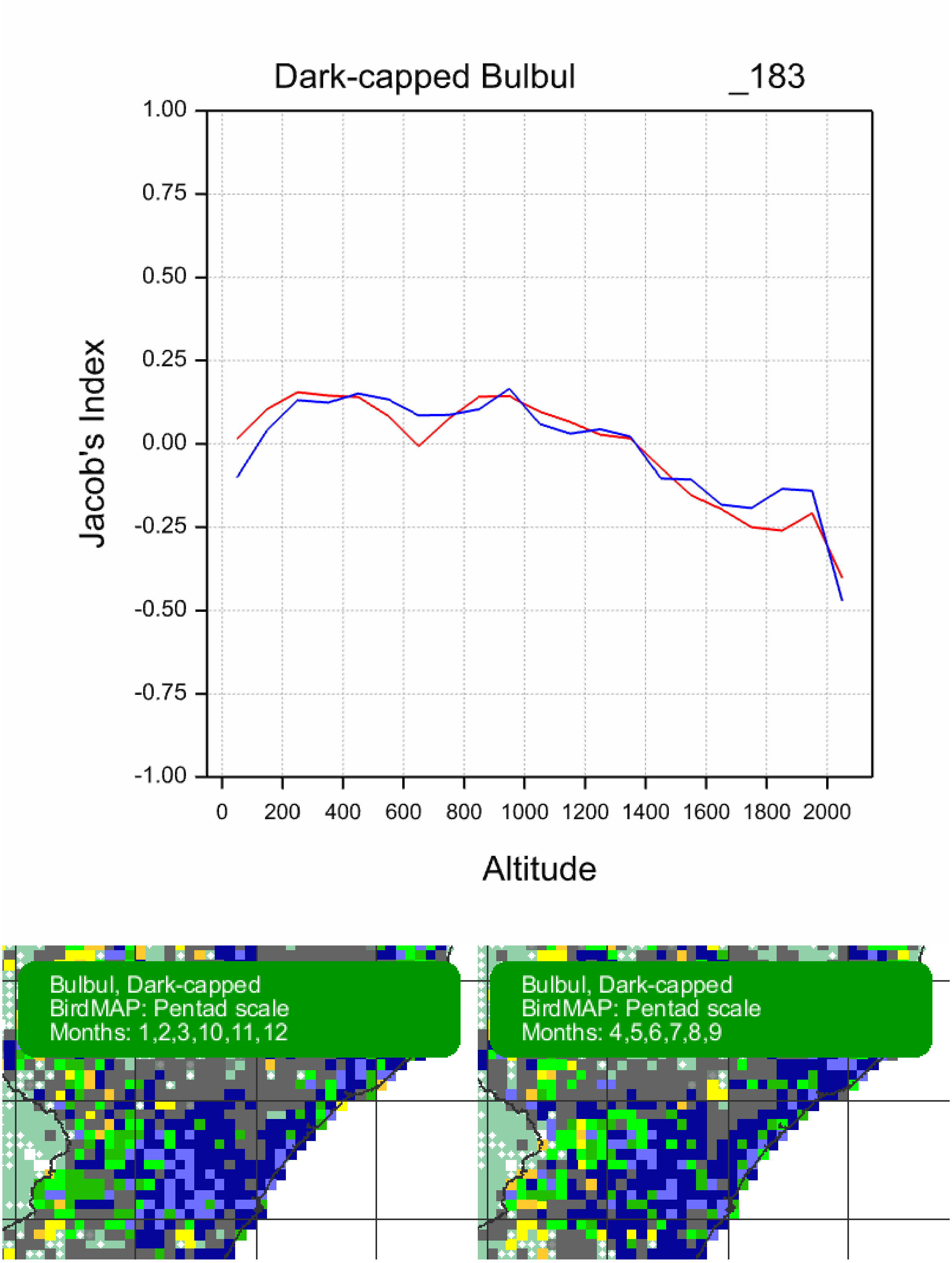


Figure 3.5. The altitudinal preference curves for summer and for winter for the Dark-capped Bulbul, and the summer and winter distribution maps for study transect in KwaZulu-Natal.

The distribution of Dark-capped Bulbul in summer and in winter is more or less in proportion to the amount of land available from sea-level up to 1400 m (Figure 3.5). Land availability and amount of land use by Dark-capped Bulbul approximately match up. Above 1400 m there are marginally fewer Dark-capped Bulbuls than one would expect given the amount of area available.

Dark-capped Bulbul is a resident species occurring up to about 2000 m (Little and Bainbridge 1992). It is found in all habitats in KwaZulu-Natal wherever trees or bushes occur (Cyrus and Robson 1980). Dark-capped Bulbul is not found in open grassland but rather along wooded watercourses, in patches of bush and in gardens in grassland habitats (Hart 1997). The species is also a resident in Lesotho, where its range has expanded eastwards into the uplands (Osborne and Tigar 1990).

Green Woodhoopoe, *Phoeniculus purpureus*

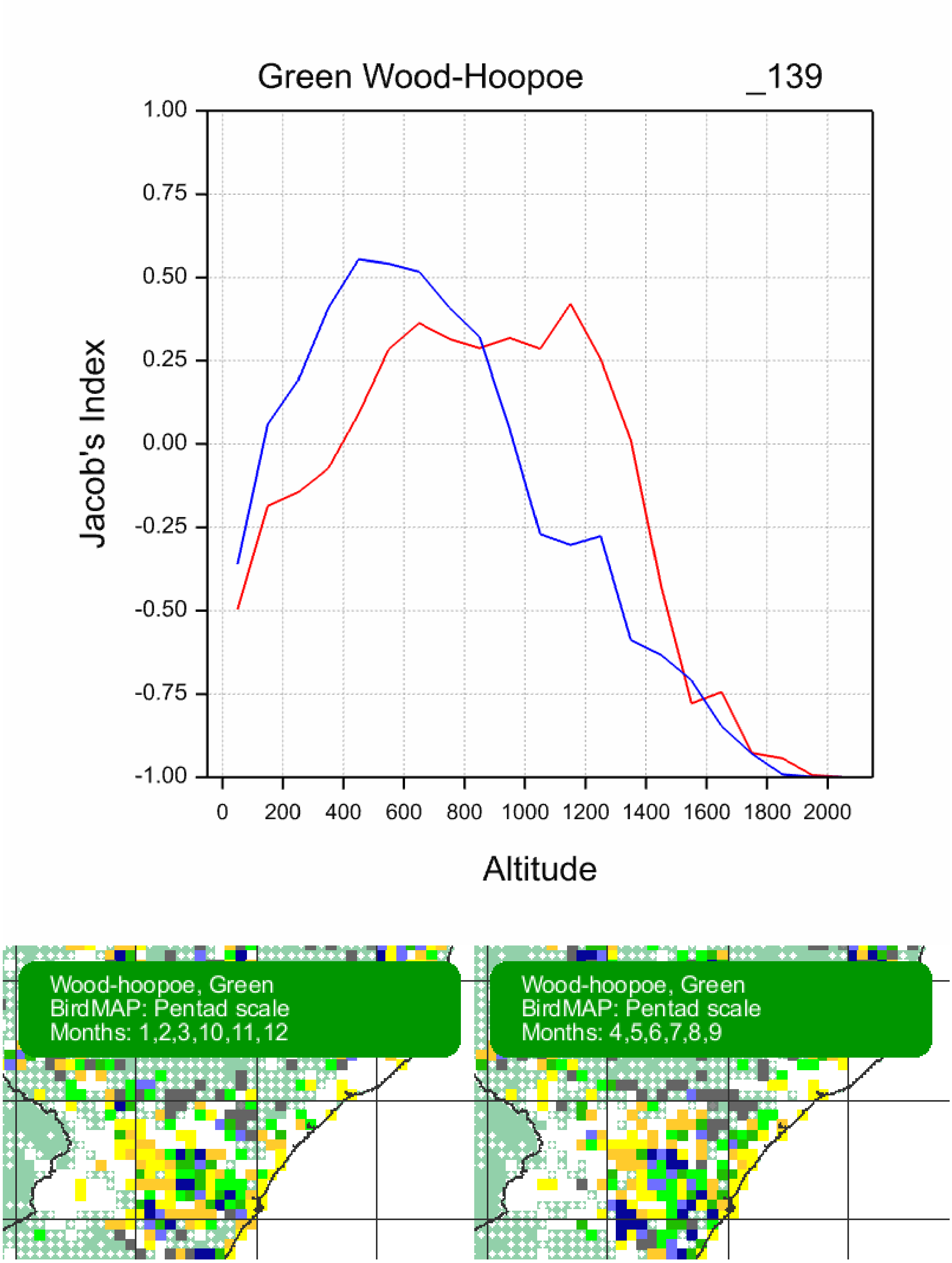


Figure 3.6. The altitudinal preference curves for summer and for winter for the Green Woodhoopoe, and the summer and winter distribution maps for study transect in KwaZulu-Natal.

In summer there are more Green Woodhoopoes between 400 m and 1300 m than one would expect given the area of land at these altitudes (Figure 3.6). There is a relatively wide altitude range for main summer preference of 600–1200 m. There is almost total avoidance of altitudes above 1800 m with no Green Woodhoopoes occurring above 2000 m.

In winter Green Woodhoopoes are preferentially selecting altitudes of 100–900 m with a main preference of 400–600 m. There is virtually total avoidance of altitudes above 1800 m with no birds present above 1900 m.

Green Woodhoopoe is almost entirely arboreal and occurs in mixed woodland and thornveld with tall trees. It also occurs in evergreen forest edges, alien plantations and gardens (Cyrus and Robson 1980). Green Woodhoopoe is an uncommon, infrequent visitor to altitudes above 1800 m (Little and Bainbridge 1992). It is thought to probably visit these higher altitude areas on short foraging trips from adjacent thornveld savanna (Little and Bainbridge 1992).

Malachite Sunbird, *Nectarinia famosa*

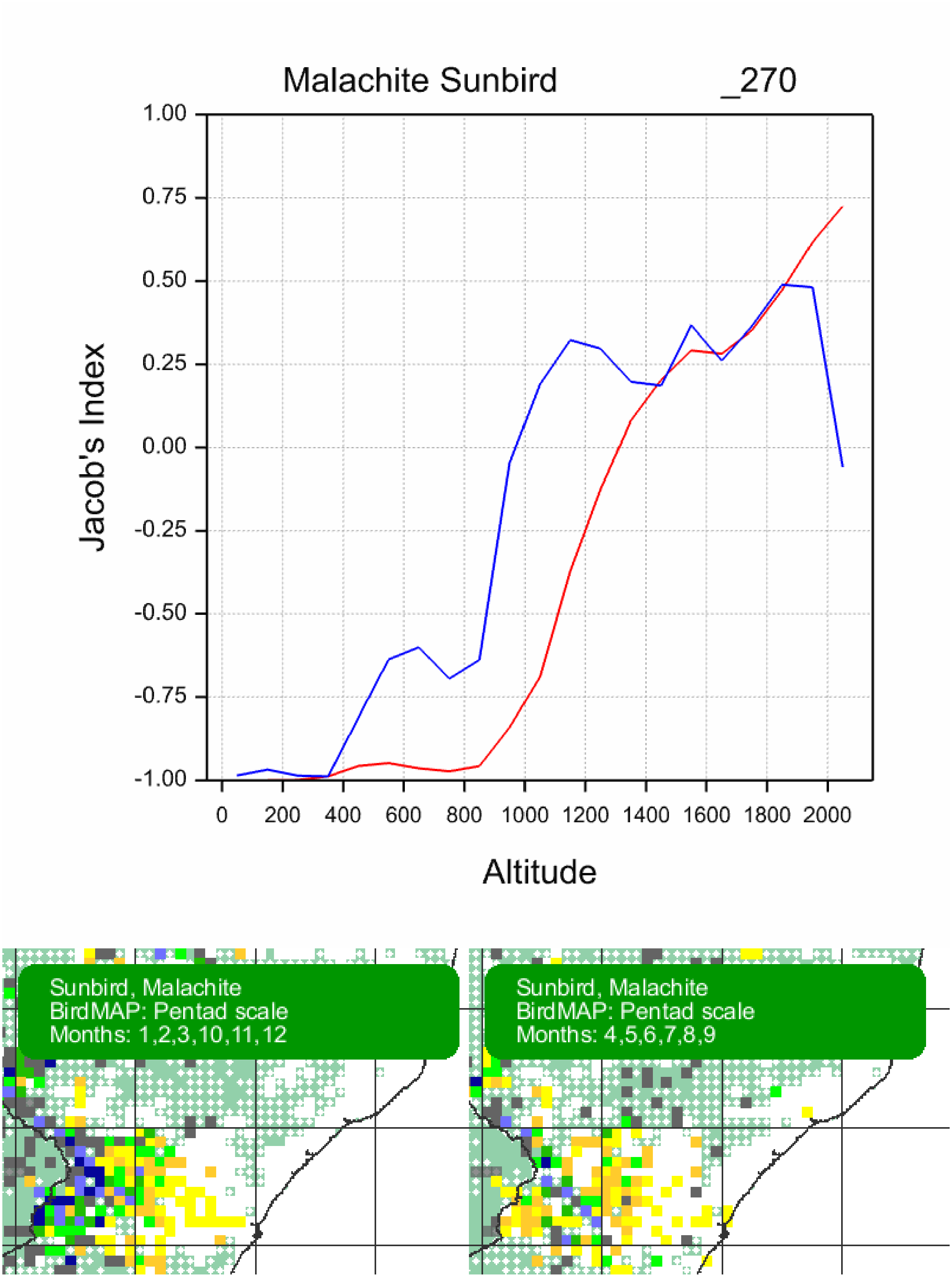


Figure 3.7. The altitudinal preference curves for summer and for winter for the Malachite Sunbird, and the summer and winter distribution maps for study transect in KwaZulu-Natal.

In summer, the Malachite Kingfisher displays complete avoidance of altitudes below 200 m (Figure 3.7). There are a few scattered records from 200 m to 800 m, indicating almost complete avoidance of this altitude range. The number of sunbirds increases above 800 m to be in proportion to the area of land available at 1300 m. Altitude preference continues to increase with increasing altitude with there being more birds present than one would expect given the area. Altitude preference peaks at 2000+ m and may continue to increase to higher altitudes as shown in the distribution map.

There is almost total avoidance of areas from sea-level to 300 m by Malachite Sunbirds in winter. The number of birds increases above 300 m to be in proportion to the area available at 900–1000 m. From 1000 m to 2000 m there are more birds than one would expect given the area. Main altitude preference is at approximately 1900 m in winter. Altitude preference appears to decline above 2000 m, with significantly fewer birds at very high altitudes than in summer.

Malachite Sunbirds are found in higher altitude areas. It is often associated with hillsides with scrub vegetation, proteas and aloes (Cyrus and Robson 1980, Fraser 1997). Malachite Sunbirds are primarily nectivorous and gather in large numbers at flowering Proteaceae (Fraser 1997). Altitudinal seasonal movements are considered to be characteristic of this species (Johnson and Maclean 1994). These movements are thought to be in response to the flowering of food plants (Fraser 1997). Skead (1967) dealt comprehensively with the movements of Malachite Sunbirds. Populations that spend the summer months in the highlands of Lesotho and KwaZulu-Natal, at altitudes in excess of 3000 m, leave these areas and move to lower altitudes in KwaZulu-Natal in winter. Brown and Barnes (1984) support these statements as they recorded Malachite Sunbirds above 2865 m from November to February with breeding records in this region for November and December. Osborne and Tigar (1990) found that most Malachite Sunbirds migrate from upland areas of Lesotho in winter.

Male Malachite Sunbirds in breeding plumage are striking and unmistakable, but are far less conspicuous in eclipse plumage. The female resembles other female sunbirds, but is relatively large in size (Fraser 1997). However, varying conspicuousness from summer to winter is unlikely to influence the analysis and it can be considered an accurate reflection of these birds' distributions and movements.

Olive Thrush, *Turdus olivaceus*

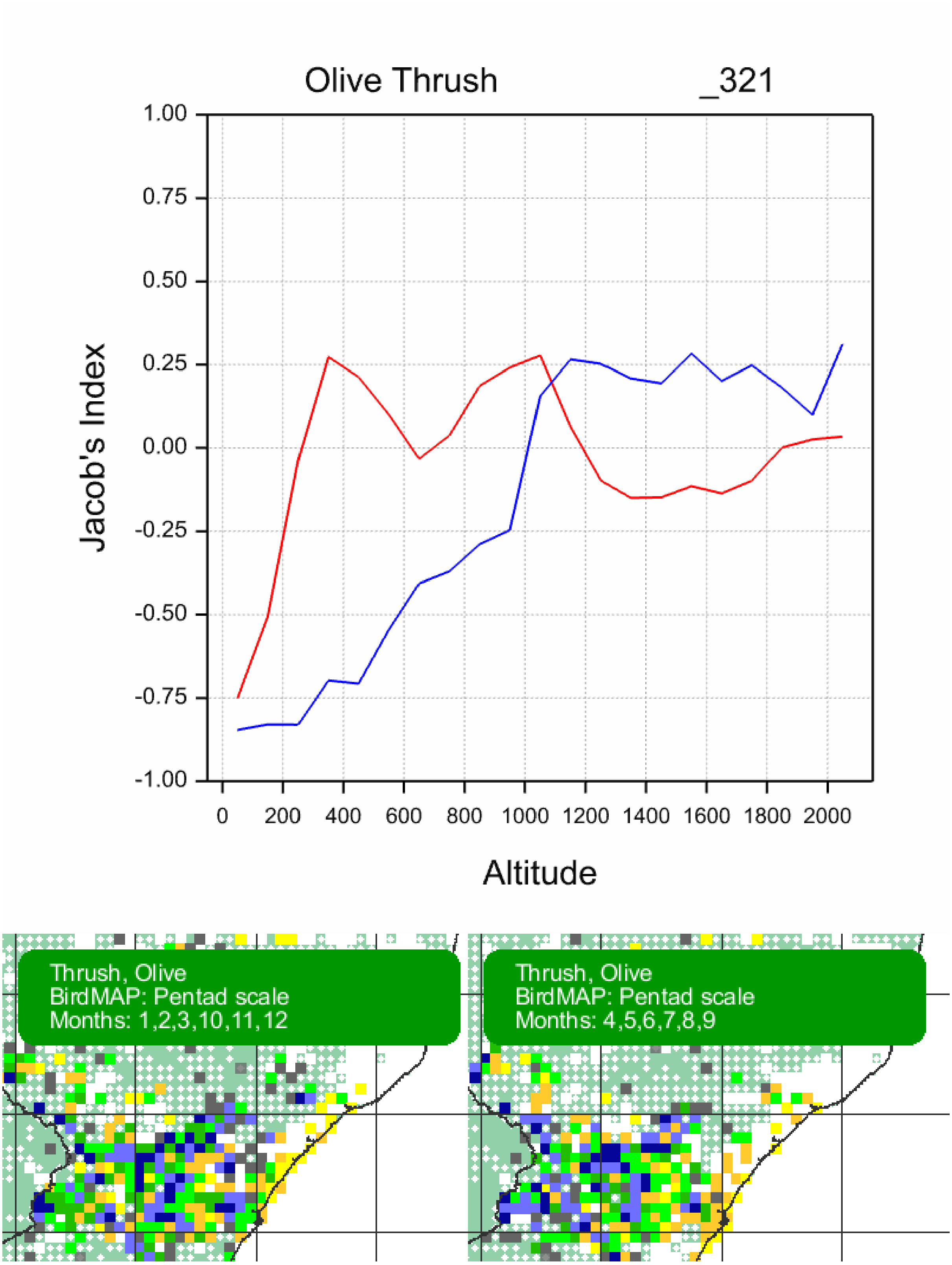


Figure 3.8. The altitudinal preference curves for summer and for winter for the Olive Thrush, and the summer and winter distribution maps for study transect in KwaZulu-Natal.

The Olive Thrush is remarkable in that both the seasonal distribution maps and altitudinal preference curves suggest that it is a "reverse altitudinal migrant" in that it moves to higher altitudes in winter. The reporting rates of Olive Thrushes along the coast in summer are relatively small, apart from the southeastern corner of the study transect (Figure 3.8). The numbers increase to there being more Olive Thrushes than what would be expected given the area of land at 300–1200 m. The number of birds is roughly in proportion to the area available at 1200–2000+ m.

At the coast in winter, reporting rates of thrushes remain low, and show a decrease in the southeastern corner compared with summer. The number of birds increases to be in proportion to the area available at 1000 m. Between 1000 m and 2000+ m there are more birds in winter than one would expect given the area.

Olive Thrush is primarily a species of evergreen forests with a preference for riverine bush and montane forest up to 2000 m (Little and Bainbridge 1992, Vernon and Herremans 1997). Olive Thrush is also found in alien plantations and gardens (Oatley 2017, Cyrus and Robson 1980, Vernon and Herremans 1997). Olive Thrush is a shy species, but is more conspicuous during the breeding season when it sings (Vernon and Merremans 1997). Altitudinal migration is suspected in KwaZulu-Natal (Johnson and Maclean 1994). Oatley (2017) states that there is some evidence of altitudinal migration in KwaZulu-Natal but it is only partial and tends to be clouded by the presence of resident populations at many altitude levels throughout the year. It is possible that there is an influx of birds into these high altitude areas from elsewhere in the range. It is for example, feasible that these birds come from populations which occur in summer in the forests along the Escarpment between KwaZulu-Natal and the Free State. This surprizing and counter-intuitive result requires further investigation. The Olive Thrush was the only species considered to be an altitudinal migrant in Ethiopia (Ash and Atkins 2009)

Sentinel Rock Thrush, *Monticola explorator*

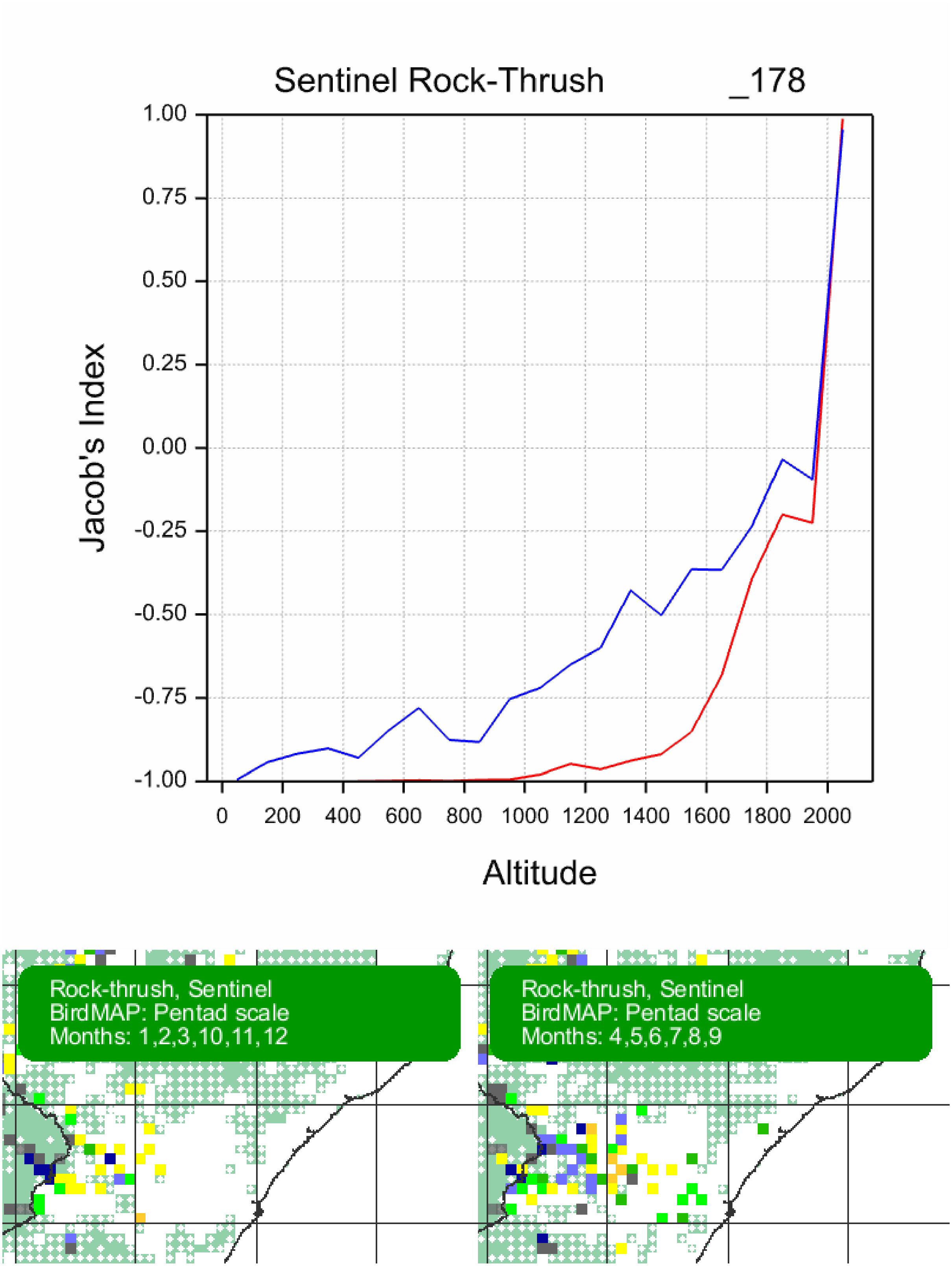


Figure 3.9. The altitudinal preference curves for summer and for winter for the Sentinel Rock Thrush, and the summer and winter distribution maps for study transect in KwaZulu-Natal.

Sentinel Rock Thrush has a strong preference for altitudes above 2000 m in summer and in winter (Figure 3.9). Sentinel Rock Thrush is virtually completely absent below 1000 m in summer. However, in winter there is a scattering of records at altitudes below 1000 m and almost to the coast. At altitudes between 1000 m and 1900 m, there are more Sentinel Rock Thrushes in winter than in summer.

Sentinel Rock Thrush resides in the highlands of Lesotho and KwaZulu-Natal above 2000m during the summer breeding season (Osborne and Tigar 1990, Little and Bainbridge 1992). It undertakes altitudinal migrations between high-altitude grasslands in summer and lower-altitude grasslands in winter (to about 1800 m) (Little and Bainbridge 1992). This is only a partial migration and probably only involves those birds forced to leave areas covered in heavy snow (Tarboton et al. 1987, Osborne and Tigar 1990). Birds depart the lower-altitude wintering grounds to return to higher levels in August (Tim Wood pers. comm.).

Oatley (2017) writes about Sentinel Rock Thrush: “A regular non-forest altitudinal migrant which can be found breeding in summer across the Drakensberg foothills and over the whole of the high mountain ranges in Lesotho. In the winter months it may be encountered at much lower altitudes. A pair of birds appeared in the Queen Elizabeth Park at an altitude of 900 m near Pietermaritzburg for two successive winters, frequenting the office parking lot. Individuals have also been recorded in Durban and at Cowies Hill near Pinetown, only some 14 km inland. However, on a brief visit to Lesotho in July 1971, I found these Rock Thrushes to be fairly common on rocky ridges at an altitude of about 2900 m. The noon temperature here was relatively mild compared with that on a nearby mountain range where at 3300 m there were widespread areas of snow and ice. It is possible that these birds had only moved a short distance down from higher levels; certainly their presence seemed to indicate that they do not totally evacuate the alpine zone in winter.”

Brown and Barnes (1984) recorded Sentinel Rock Thrushes above 2865 m throughout the year, with records of breeding in November and December. Their summer and winter bird counts were identical suggesting that no movement from these very high altitudes took place during the study period (November 1980 to

December 1982). The years in which the counts were made were particularly warm and dry. Snowfalls were light and melted in a few days. They acknowledge that these mild conditions may have resulted in atypical patterns of bird movements.

Southern Tchagra, *Tchagra tchagra*

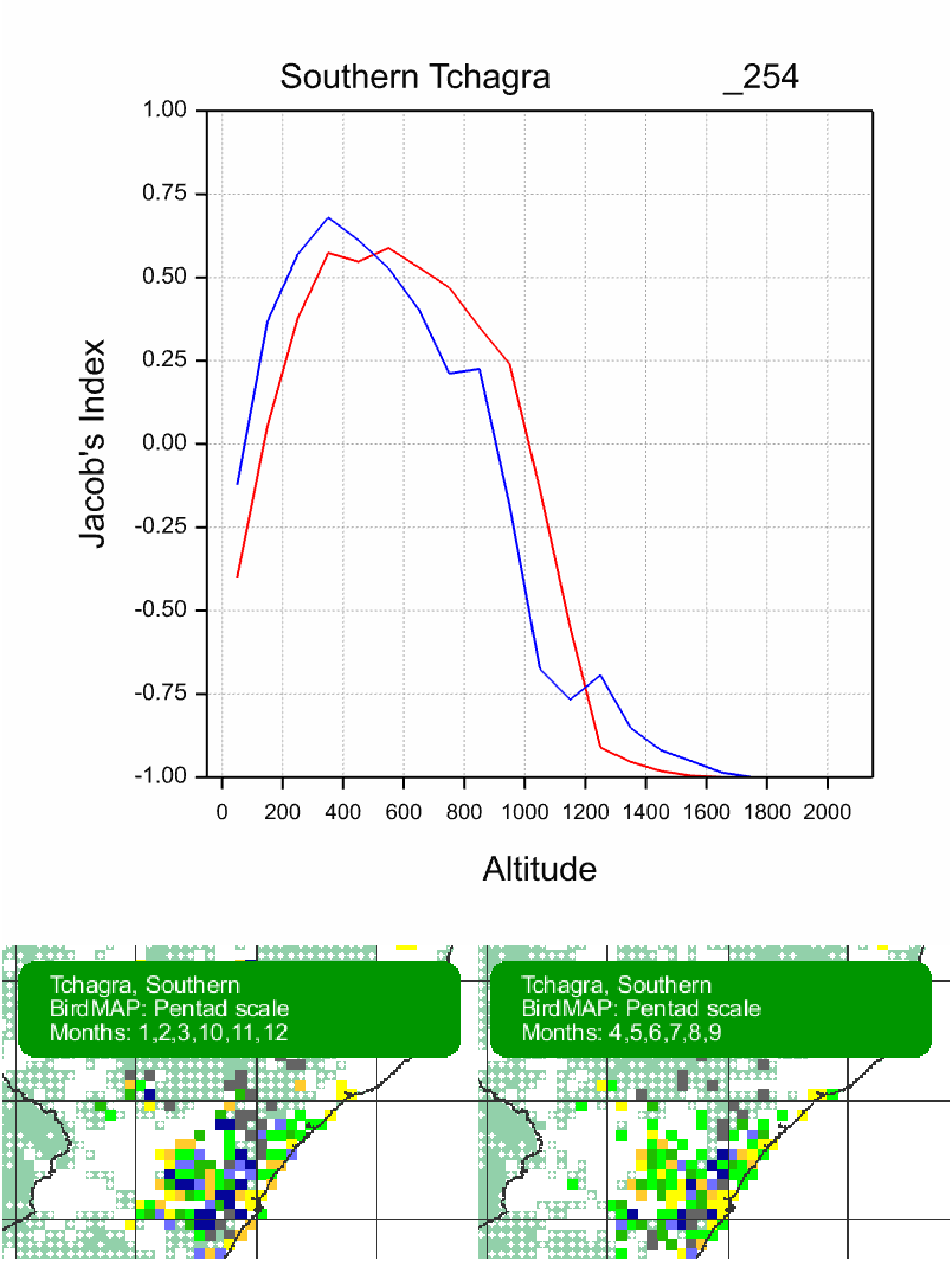


Figure 3.10. The altitudinal preference curves for summer and for winter for the Southern Tchagra, and the summer and winter distribution maps for study transect in KwaZulu-Natal.

In summer Southern Tchagras are preferentially choosing altitudes approximately 200–1000 m with main preference at 500–600 m (Figure 3.10). There is not total avoidance of coastal areas but there are fewer birds than one would expect given the area. Above 1000 m there are again fewer birds than expected. Numbers decrease to almost complete avoidance of altitudes 1200–1600 m. There is total avoidance of areas above 1600 m by Southern Tchagras in summer.

In winter the distribution of Southern Tchagras follows a similar pattern to the summer distribution and altitude preference. In winter tchagras have an altitude preference of roughly 100–900 m, with main preference 300–400 m. Above 900 m there are fewer birds than predicted given the amount of area. Bird numbers decrease to there being only handfuls at 1100–1300 m, almost total avoidance at 1300–1700 m and complete avoidance above 1700 m.

Southern Tchagra inhabits a broad band along the KwaZulu-Natal coast. It occurs in dense coastal bush and thickly wooded valleys (Cyrus and Robson 1980; Johnson 1997c).

There is no evidence for seasonal altitudinal movements.

Overview of results

The species presented in Table 3.1 can be categorised into six groups: migrants (Palearctic or intra-African migrants, i.e. non-altitudinal migrants), definite residents, definite altitudinal migrants, possible residents, possible altitudinal migrants, and species that show no clear preference.

There is a group of 18 migrant species which are present in the study transect in summer, but are almost completely absent in winter. The vast majority of individuals of these species migrate northwards out of the study transect in winter and only very few birds remain in southern Africa. They are Palearctic or intra-African migrants. Migrants which had been recorded in at least 50 pentads in summer were included in the analysis. There are eight Palearctic migrants: Amur Falcon, Black Kite, Steppe Buzzard, Common House Martin, Willow Warbler, Marsh Warbler, Spotted Flycatcher and Red-backed Shrike; and 10 intra-African migrants: Wahlberg's Eagle, Common Quail, Red-chested Cuckoo, Black Cuckoo, Jacobin Cuckoo, African Emerald Cuckoo, Diderick Cuckoo, Horus Swift, African Pygmy Kingfisher and Banded Martin. None of these are altitudinal migrants.

There is a group of 77 species which are classified as residents. They are defined as the species with a SAD less than or equal to 2.50 (Table 3.1). The species at this cut-point is Cape Sparrow (SAD=2.50). The majority of species in this group are low or mid-to-low altitude residents. There is a small group of species that reside at high and mid-to-high altitudes. These species are somehow able to endure difficult conditions during cold winters to be able to remain at these higher elevations. The high-altitude residents are: Bokmakierie, Cape Longclaw, Long-tailed Widowbird, Cape Turtle-Dove, Speckled Pigeon, Drakensberg Prinia, Wailing Cisticola, Cape Shoveler, Gurney's Sugarbird, Levaillant's Cisticola, Grey Crowned Crane, Buff-streaked Chat, Jackal Buzzard and Cape Sparrow. Species that fall into this high-altitude-resident category but have an SAD greater than 2.50 but less than 3.00 are Wattled Crane, Chorister Robin-Chat, Cape Crow, Ground Woodpecker, Blue Crane and Bearded Vulture. Anteating Chat should be included in this group of high-altitude residents even though it has a SAD of 3.74.

Forty-four definite altitudinal migrants were identified. These are defined as the species with a SAD greater than 7.00 (Table 3.1). The species at this cut-point is Golden-breasted Bunting (SAD=7.01). The common movement trend of species in this group is to move from higher altitudes in summer to lower altitudes in winter. There are nine species in the group of 44 definite altitudinal migrants that are either Palearctic or intra-African migrants. The one Palearctic migrant is White Stork. The eight intra-African migrants are: African Reed Warbler, White-rumped Swift, African Black Swift, Klaas's Cuckoo, Black Saw-wing Swallow, Lesser Striped Swallow, Violet-backed Starling and White-throated Swallow. These species have small populations which remain at lower altitudes during winter.

There are three southern African species that appear to show the reverse movement pattern, migrating to higher altitudes in winter. These species are Verreaux's Eagle, Plain-backed Pipit and Olive Thrush (Table 3.1).

Then there is the remaining 164 species, of which three are intra-African migrants: Greater Striped Swallow, Yellow-billed Kite and Little Swift. This remaining group of species can be divided into three groups: species which are possible residents ($2.5<SAD<4.0$), species which do not display a clear preference ($4.0<SAD<5.5$), and species which are possible altitudinal migrants ($5.5<SAD<7.0$) (Table 3.1).

In search of explanations

For the five habitat types, the chi-square test of association, indicates that the migration strategy is independent of habitat type (Table 3.2). For eight of the 11 diet types, the chi-square test of association suggests a significant relationship (Table 3.3). But in seven of the eight cases, the significance is attributable to a large expected value for the indeterminate movement strategy. There were 44 frugivores among the 285 species considered in the analysis, and fruit was the only diet type for which the significance appears to be related to altitudinal migration strategy, but it is inversely related ($p=0.010$). Fruit was found to be a predicator of residence among birds in the study transect in KwaZulu-Natal. More resident birds than expected had fruit as their food source (observed value of 45.5% versus expected value of 18.5%). In addition, fewer frugivores than expected were found to be altitudinal migrants (observed value of 9.1% vs expected value of 20.4%) and possible altitudinal migrants (observed value of 9.1% vs expected value of 16.7%).

Of the 44 species which were classified as having fruit as the main diet or as a major component of their diet, four each were classified as altitudinal migrants, possible altitudinal migrants, and no clear preference. However, 19 were classified as residents, and 12 as possible residents. Of the 30 residents and possible residents (68% of 44 species), 11 had their peak altitudinal preference class above 1000 m. For example, Red-winged Starling had peak preference at the highest altitude class (above 2000 m) in both summer and winter, and the Chorister Robin-Chat had peak preference in the 1900–2000 m class (Table 3.1).

Mass was available in Hockey et al. (2005) for 283 of the 285 species. The association between mass class and altitudinal migration category was significant (chi-square test of association, 12 degrees of freedom = 25.35, P=0.013) (Table 3.4). However, a comparison between the observed and expected values of Table 3.4 reveals that the largest differences were in the species which showed no clear preferences whether they were altitudinal migrants or not, in the middle column of Table 3.4. Interesting results, in relation to altitudinal migration, would have been obtained if the large differences were in the corners of the contingency table.

Table 3.2. Results of the chi-square tests for Habitat variables in relation to altitudinal migration category as determined by the SAD for 285 species in KwaZulu-Natal. Each row contains the observed values transformed to percentages. The set of expected values, also transformed to percentage is in the bottom row of the table, and is the same for all Habitat variables. The P-values from the standard chi-squared test are given (when appropriate, i.e. one or more of the expected values is less than 5, the P-value for non-parametric alternative to the chi-square test, described by Roff and Bentzen (1989) is also calculated).

Habitat	n	Resident	Possible Resident	No Clear Preference	Possible Migrant	Altitudinal Migrant	P-value	Perm P-value
Cliff	16	12.5	12.5	18.8	18.8	37.5	0.109	0.099
Forest	67	32.8	23.9	16.4	16.4	10.4	0.440	
Woodland	100	33.0	23.0	20.0	12.0	12.0	0.380	
Grassland	54	18.5	29.6	14.8	20.4	16.7	0.170	
Savanna	75	25.3	17.3	28.0	13.3	16.0	0.476	
Wetland	95	21.1	23.2	24.2	15.8	15.8	0.592	
Expected values		18.5	29.6	14.8	20.4	16.7		

Table 3.3. Results of the chi-square tests for Diet variables in relation to altitudinal migration category as determined by the SAD for 285 species in KwaZulu-Natal. Each row contains the observed values transformed to percentages. The set of expected values, also transformed to percentage is in the bottom row of the table, and is the same for all Diet variables.

Food	n	Resident	Possible Resident	No Clear Preference	Possible Migrant	Altitudinal Migrant	P-value	Perm P-value
Carrion	5	40.0	20.0	20.0	20.0	0.0	0.882	0.935
Mammal	13	7.7	7.7	38.5	30.8	15.4	0.114	0.109
Bird	20	10.0	10.0	50.0	10.0	20.0	0.012	0.015
Reptile	17	17.6	11.8	52.9	5.9	11.8	0.024	0.020
Fish	22	13.6	13.6	45.5	9.1	18.2	0.046	0.051
Aquatic Invertebrates	17	0.0	35.3	35.3	5.9	23.5	0.043	0.039
Terrestrial Invertebrates	208	30.8	20.2	18.3	13.5	17.3	0.040	
Freshwater Invertebrates	27	11.1	14.8	48.1	14.8	11.1	0.007	0.005
Fruit	44	45.5	27.3	9.1	9.1	9.1	0.010	
Seeds	67	25.4	31.3	16.4	14.9	11.9	0.250	
Nectar	13	61.5	7.7	23.1	7.7	0.0	0.044	0.032
Expected values		18.5	29.6	14.8	20.4	16.7		

Table 3.4. Results of the chi-square tests for Mass classes in relation to altitudinal migration category as determined by the SAD for 283 species in KwaZulu-Natal. The observed and expected numbers in each category, with the expected values given in brackets.

Mass (g)	Resident	Possible Resident	No Clear Preference	Possible Migrant	Altitudinal Migrant	Total
<19 g	24 (19.0)	15 (14.8)	7 (14.8)	14 (10.4)	10 (10.9)	70
19 g–46 g	23 (19.3)	14 (15.1)	9 (15.1)	10 (10.5)	15 (11.0)	71
46 g–285 g	18 (19.0)	16 (14.8)	17 (14.8)	8 (10.4)	11 (10.9)	70
>285 g	12 (19.6)	15 (15.3)	27 (15.3)	10 (10.7)	8 (11.2)	72
Total	77	60	60	42	44	283

Discussion

It is relatively easy to pick out the clear-cut altitudinal migrants, such as African Dusky Flycatcher, and the resident species which have essentially identical altitudinal distributions in summer and winter, such as Black-bellied Starling. Many species have been proposed as altitudinal migrants in KwaZulu-Natal. These claims are evaluated against the results obtained in this dissertation. For some species, the suggestion that they are altitudinal migrants is clearly incorrect, and for other species the hypothesis is supported by the bird atlas data.

The species that appear in this analysis are those species for which there is sufficient data to produce reliable altitudinal preference curves and distribution maps that are an accurate depiction of species' movement and distribution patterns. There are species, such as the Drakensberg Siskin *Crithagra symonsi,* which only appear at lower altitudes after extraordinarily heavy snowfalls (Oatley 2017). Examples of such infrequent movement in response to extreme conditions are widespread in animals as mobile as birds (Oatley 2017). Such species have not been included in this analysis due to insufficient data records of their seasonal movement.

The species selected for the Results are a representative collection of all the different patterns observed. Particularly striking are the species which show almost identical altitude choice in summer and winter. These are clearly residents. Black-bellied Starling has the same preference for relatively low altitudes in both summer and winter (Figure 3.2), Bokmakierie has the same preference for relatively high altitudes throughout the year (Figure 3.3) and Dark-capped Bulbul has a fairly uniform distribution across the altitude classes year-round. There are similar examples in Appendix D: Long-tailed Widowbird (Figure D.16), Red-faced Cisticola (Figure D.21) and White-bellied Sunbird (Figure D.27).

There are 77 of these species (Table 3.1), which all had a SAD score less than or equal to 2.50. These resident species have almost identical summer-winter altitude preferences at all altitudes. Examples of residents which occur at coastal-to-low-altitude levels are: African Firefinch, Black-backed Puffback, Black-bellied Starling, Bronze Mannikin, Brown-hooded Kingfisher, Collared Sunbird, Gorgeous Bush-Shrike, Green-backed Camaroptera, Little Bee-eater, Red-faced Cisticola, Spectacled Weaver, Village Weaver, White-bellied Sunbird, White-browed Scrub-Robin, White-eared Barbet, Wire-tailed Swallow and Yellow-bellied Greenbul. Southern Boubou and Forest Buzzard are examples of low and high mid-altitude level resident species respectively. Speckled Pigeon is an example of a mid-to-high-altitude resident. Examples of high-altitude non-migrant species are Bokmakierie, Buff-streaked Chat, Cape Longclaw, Drakensberg Prinia, Long-tailed Widowbird and Wailing Cisticola (Table 3.1).

Dark-capped Bulbul, Common Fiscal, Fork-tailed Drongo, Cape White-eye and Red-eyed Dove are all generally ubiquitous with no strong altitude preferences or avoidances.

A number of species are altitudinal migrants, which all have a SAD score of 7.0 or greater. They can be roughly divided into three broad categories: High-to-mid altitude migrants, high-to-low altitude migrants and mid-to-low altitude migrants. Examples of high-to-mid altitude migrants are Alpine Swift, Barratt's Warbler and White Stork. Examples of high-to-low altitude migrant species include African Dusky Flycatcher, African Paradise Flycatcher, Black Saw-wing Swallow and Wing-snapping Cisticola. Examples of mid-to-low altitude migrants are African Reed Warbler, Croaking Cisticola, Little Rush Warbler and Yellow-throated Petronia.

Some of the species classified as high-altitude resident species could possibly be very-high-altitude migratory species, such as Bokmakierie and Ground Woodpecker. SABAP2 has good coverage up to 2000 m. Above this altitude the data coverage is poor because many of the high-altitude areas are often inaccessible or difficult for citizen scientists to access. Consequently there is little SABAP2 information on the distribution of species at altitudes above 2000 m. The data from Osborne and Tigar (1990) would potentially be helpful but this was collected on a 15-minute grid, as opposed to the 5-minute grid of SABAP2. The 15-minute grid generated 62 QDGCs for Lesotho, whereas the 5-minute grid generates 421 pentads. The altitudinal variation within a QDGC in Lesotho is large (compare Figure 2 of Osborne and Tigar 1990 with Appendix B), and probably not amenable to the analyses performed here.

The study area is a narrow transect of southern Africa. It is therefore important to consider when interpreting the result that the birds that create the winter pattern might not be the same birds that created the summer pattern. Birds from other parts of southern Africa may be entering the KwaZulu-Natal study transect in winter and birds in the transect may be leaving and migrating elsewhere in the country.

Results presented here in relation to earlier proposals about species which are altitudinal migrants

Johnson and Maclean (1994) proposed 75 species as altitudinal migrants in KwaZulu-Natal. For many of those species, the evidence for altitudinal migration was largely anecdotal and frequently based on a single observation. Of the 75 species, this study showed that 29 are in fact altitudinal migrants (Table 3.1). In addition to these 29 species, Cape Crow is only a marginal altitudinal migrant. Familiar Chat may be an altitudinal migrant or a partial altitudinal migrant. Altitudinal movement only occurs in populations at higher altitudes. There is no altitudinal movement at lower altitudes. Plain-backed Pipit shows a reverse altitudinal movement, moving to higher altitudes in winter.

Twenty-four of the species listed by Johnson and Maclean (1994) were not considered in this analysis to be altitudinal migrants: Red-chested Flufftail, Fiery-necked Nightjar, Speckled Mousebird, Red-faced Mousebird, Crowned Hornbill, Olive Woodpecker, Buff-streaked Chat, Chorister Robin-Chat, White-browed Scrub-Robin, Tawny-flanked Prinia, Drakensberg Prinia, Cape Wagtail, Bokmakierie, Red-winged Starling, Cape White-eye, Thick-billed Weaver, Cape Weaver, Fan-tailed Widowbird, Long-tailed Widowbird, Common Waxbill, Bronze Mannikin, Red-backed Mannikin, Yellow-fronted Canary and Brimstone Canary. In addition to these 24 species, Lesser Swamp Warbler and Wailing Cisticola do not appear to be altitudinal migrants. The results however, for Lesser Swamp Warbler might not be definitive because most of the records are based on sound rather than sight, with birds being more vocal in summer (Barnes and Herremans 1997). Like Lesser Swamp Warbler, the data for Wailing Cisticola should be treated with caution because many of the records are based on call. During the breeding season males of this species are more conspicuous owing to their vocalisations (Berruti 1997c). However, increased conspicuousness should not affect this analysis.

There are 17 of the 75 species listed for which there is insufficient SABAP2 atlas data to be able to comment on seasonal altitudinal movements: Black Harrier, Buff-spotted Flufftail, Striped Flufftail, Black-winged Plover, Horus Swift, Thick-billed Lark, Orange-breasted Rockjumper, Sickle-wing Chat, Layard’s Titbabbler, Yellow

Warbler, Broad-tailed Warbler, Fairy Flycatcher, Mountain Pipit, Yellow-breasted Pipit, Drakensberg Siskin, Yellow Canary and Kurrichane Thrush.

Berruti et al. (1994) made use of data from the First Southern African Bird Atlas Project (SABAP1) and the reporting rate as an index of relative abundance. The study focused both on coastal migration, dividing the coastal region of the Western Cape, Eastern Cape and KwaZulu-Natal into six sections, and on altitudinal migration in KwaZulu-Natal, dividing the province into only three altitudinal bands (0–300 m, 300–900 m and 900–1500 m a.s.l.). They considered only a small subset of forest species.

Berruti et al. (1994) proposed that Cape Turtle Dove, Fiscal Shrike and House Sparrow are resident species because they showed no marked seasonal variations in reporting rates. This present study confirms that these three species are in fact resident species and do not undertake migrations.

Pygmy Kingfisher is proposed by Berruti et al. (1994) as a summer coastal migrant from the eastern tropics, from Mozambique northwards, to South Africa. It is a summer visitor to KwaZulu-Natal occurring from the coast up to about 900 m in a wide variety of wooded habitats (Cyrus and Robson 1980). The claim of Pygmy Kingfisher being a summer coastal migrant to KwaZulu-Natal is supported by the data in this current study.

Mangrove Kingfisher is also thought to be a coastal migrant from the Transkei to KwaZulu-Natal (Berruti et al. 1994). This study has insufficient SABAP2 data on Mangrove Kingfisher to either support or refute this claim. Black Saw-wing Swallow is regarded by Berruti et al. (1994) as a coastal migrant in the southern part of its range with birds arriving from the Western Cape in KwaZulu-Natal and the Transkei. They however also state that in KwaZulu-Natal the species shows an altitudinal shift in distribution with few birds occurring above 900 m during the winter months. This altitudinal movement is supported by the altitudinal preference curve for this species. According to Berruti et al. (1994) it is not known whether the birds that occur at higher altitudes in KwaZulu-Natal move eastwards to the coast or northwards to Mozambique. Therefore the birds wintering on the KwaZulu-Natal coast could either be the Black Saw-wing Swallows migrating from the Western Cape, or they could be the birds that spend the summer months at higher altitudes in KwaZulu-Natal, or it could be a combination of the two. Berruti et al. (1994) proposed that Spotted Thrush is a winter coastal migrant to KwaZulu-Natal from the Transkei. This analysis has insufficient data on Spotted Thrush to either support or refute this claim. African Paradise Flycatcher is thought to be a coastal migrant from the Western Cape to KwaZulu-Natal, where the birds overwinter on the coast (Berruti et al. 1994). This study shows that during winter in KwaZulu-Natal, African Paradise Flycatchers undertake altitudinal migrations from higher altitudes to the coast. Based on the current study and that by Berruti et al. (1994), it is unclear whether the birds that occur at higher altitudes in KwaZulu-Natal move to the coast or elsewhere in the country during winter. Similar to the Black Saw-wing Swallow scenario, the African Paradise Flycatchers wintering on the KwaZulu-Natal coast could either be birds migrating from the Western Cape, or they could be the birds that spend the summer months at higher altitudes in KwaZulu-Natal, or it could be a combination of the two.

Berruti et al. 1994 found that Buff-spotted Flufftail and Narina Trogon show a summer or spring peak in reporting rates. These two species are however usually detected by their calls. The seasonality of reporting rates could reflect seasonal changes in vocalisations or seasonal migrations (Berruti et al. 1994). Berruti et al. (1994) concluded that Buff-spotted Flufftail does not undertake altitudinal movements, but possibly movement along the coast. There is only sufficient summer SABAP2 data for Buff-spotted Flufftail which is probably a consequence of seasonality of calling, but could possibly indicate that it is a summer visitor in KwaZulu-Natal and overwinters elsewhere. Berruti et al. (1994) proposed Narina Trogon as an altitudinal and coastal migrant further north to Mozambique in winter. This study gives Narina Trogon a SAD score of 4.05. The altitude curve shows that this species is largely resident with a slight altitudinal shift to lower altitudes in winter.

Berruti et al. (1994) stated that their analysis gave no evidence of altitudinal or coastal migrations in Grey Cuckooshrikes. This analysis gives Grey Cuckooshrike a SAD score of 6.274 indicating that is it very possibly an altitudinal migrant. The altitudinal curve also suggests a seasonal altitudinal movement to lower altitudes in winter.

Berruti et al. (1994) found Red-capped Robin-Chat to be present throughout the year above 900 m, although as a comparatively rare resident. They state that if altitudinal migration occurs then it is confined to a small proportion of the population. Berruti et al. (1994) suggests that Red-capped Robin-Chat is essentially resident in KwaZulu-Natal. This finding is in agreement with the current study.

The Ashy Flycatcher is not considered an altitudinal or coastal migrant by Berruti et al. (1994). The altitudinal curve produced for this species suggests that there is an altitudinal movement from low-to-mid altitudes towards the coast in winter.

Berruti et al. (1994) found no evidence to support coastal migration but some evidence to support limited altitudinal migration in Blue-mantled Crested Flycatcher. The analysis of altitudinal migration in this study supports the notion of altitudinal migration in this species.

Berruti et al (1994) found evidence to indicate altitudinal movements in White-starred Robin and African Dusky Flycatcher. They found there to be a winter increase in reporting rates below 300 m in White-starred Robin. They concluded that White-starred Robin is a partial altitudinal migrant because there are still numerous birds wintering at higher altitudes. This finding is in agreement with the current study. White-starred Robin has an SAD score of 7.85. The seasonal altitudinal preference curves show a very definite partial altitudinal movement to lower altitudes in winter with many birds still remaining at higher altitudes. Berruti et al. (1994) found a definitive altitudinal seasonality in African Dusky Flycatcher in KwaZulu-Natal, with numbers decreasing substantially above 900 m in winter and a converse increase coast-wards. This finding is in agreement with the finding in the current study. African Dusky Flycatcher has an SAD score of 9.78 and the altitudinal preference curves show a clear seasonal altitudinal movement towards the coast in winter, returning to higher altitudes in summer.

Explanations of altitudinal migration

Boyle (2017) pointed out that altitudinal migrants are found across many foraging guilds and environments so that neither diet nor habitat is a predictor of being an altitudinal migrant. Boyle (2017) noted that the body size of altitudinal migrants ranged “from under a few grams to several kilograms”. The overall conclusions of Boyle’s (2017) review were that generalisations with respect to causes were, at this stage, not possible, that there was a large diversity of patterns, and that, unlike long-distance migration which can be studied on a species level, altitudinal migration would need to be studied on the level of the individual bird. This lack of simple common factors related to altitudinal migration was also a finding of this study (Tables 3.2 and 3.3).

The one pattern that did emerge was that the overwhelming majority of frugivores were residents or possible residents. Resident frugivores were spread across all the height classes, with individual species having preferences in all the classes. This suggests that fruit must be continuously available in the study area in KwaZulu-Natal throughout the year, with birds switching between plant species as their fruit becomes available. An all-year study of the diet of the Red-winged Starling and the Chorister Robin-Chat, especially at high altitudes would help improve understanding.

CHAPTER 4

Conclusion

This dissertation has devised a quantitative method to objectively examine altitudinal preferences of bird species and illustrated this using the KwaZulu-Natal study area. These altitudinal preferences were then examined seasonally, in summer and winter. In this way, I explored the altitudinal movements of birds using this novel approach to deduce the extent of altitudinal migration. Because no birds were actually observed moving, it can be concluded that the bird atlas data from SABAP2 were “strong enough” to provide strong hypotheses on which species are involved in altitudinal migration and also the extent and locality of the migration.

I explored possible explanations for the observed movement patterns. In particular, I attempted to answer the question: “Why are some species residing at higher elevations in the Drakensberg Mountains altitudinal migrants and other species are not?” No meaningful relationships were found between the extent of altitudinal migration and a set of life history characteristics, including diet, mass, habitat etc. Knowledge about what drives these altitudinal movements is still unknown.

Altitudinal migration is a phenomenon that occurs in many bird species from many different taxonomic lineages.

An important and applied outcome of this dissertation is that the graphical outputs generated should be considered by the authors of bird field guides and monographs as illustrations for their species texts. These graphics summarise information that is hard to describe in words.

The use of bird atlas data in this way highlights an additional value of citizen science. It demonstrates that the accumulation of large numbers of bird atlas checklists throughout the year can provide robust quantitative data for analyses beyond the simple description of species distributions, which is regarded as the primary role of atlas projects.

Recommendations for future studies

Within KwaZulu-Natal, future studies could investigate whether the observed correlation between residency and frugivory is merely a statistical artefact or whether it is a real relationship. This could start with a desktop study of the seasonality of fruiting in KwaZulu-Natal and whether there are plant species providing fruit throughout the year. This study lies at the interface between botany and ornithology, and practical fieldwork would need to consider particular frugivorous bird species, and ask how and when they switch between species of fruiting plants to enable them to meet foraging needs throughout the year without moving. This is probably a project that would need to have individually marked birds that could be monitored throughout the year.

The main take-home message from Boyle (2017) was that developing an understanding of altitudinal migration would be a complex process. Thus it is not surprising that the essentially univariate analyses performed here only delivered one statistically interesting result. The opportunity however remains open to use the bird atlas data to conduct more sophisticated multifactorial analyses, with several explanatory variables in the models. However, Boyle (2017) warns of contrasts between the study of obligate long-distance migrants, in which all individuals of the species are genetically programmed to migrate, and the study of altitudinal migration, in which intraspecific variation appears to play a major role. This produces a partial migration in which each bird takes the decision to migrate or not depending on its own cost-benefit analysis of endogenous and exogenous factors. In the study area of KwaZulu-Natal and adjacent Lesotho, both Brown and Barnes (1984) and Osborne and Tigar (1990) noted that the extent of emigration from high altitude areas varied between years, and that this was attributable to local weather conditions such as snowfall. Their comments are echoed by Boyle (2017). The value of statistical modelling might be limited, and that the big advances in the study of altitudinal migration will be achieved by long term fieldwork studies.

Besides KwaZulu-Natal, there are opportunities for the study of altitudinal migration elsewhere in Africa. Burgess and Mlingwa (2000) cast doubts on the existence of altitudinal migration in the Eastern Arc Mountains of East Africa; but their analysis is unlikely to be the last word on this topic. In addition, there must be opportunities to study altitudinal migration in the enormous block of mountains in Ethiopia. Although altitudinal migration was mentioned explicitly only for the Olive Thrush in Ash and Atkins (2009), it is clear from their discussion of migration that they knew that altitudinal migration was a widespread phenomenon among the bird species of the region; it is probable that they shied away from discussing it because, in the word of Boyle (2017), it is “messy”.

Given the likelihood that there is inter-year variability in altitudinal migration, it would be a valuable sub-project within SABAP2 to encourage citizen scientists to obtain as much data for as many pentads as possible on a seasonal basis (summer and winter) within the transect of this study area in KwaZulu-Natal. It would also be extremely valuable to increase the coverage of the highest-altitude pentads (those above 2000 m) in both summer and winter, and to improve the coverage of adjacent Lesotho, once again both in summer and in winter. These proposals for atlas fieldwork implement the recommendation contained in the final sentence of Boyle (2017): “Explicitly designing studies to allow detection and documentation of the patterns and prevalence of altitudinal migration at community or population levels should be a priority in future ornithological studies.”

Implications for conservation

It is self-evident that more than a single site needs to be considered for the conservation of a migrant bird species; both sites occupied in summer and those occupied in winter are needed. The approach developed in this dissertation can be used to select the appropriate altitude bands for species in summer and winter; the atlas distribution maps can then be used to select candidate pentads for both periods, and corridors between them. Local knowledge would be needed to choose appropriate sites within the pentad, and this would need to be followed up by detailed fieldwork. It would also be important to establish, probably through a project involving ringing, whether the selected sites for summer and winter are connected and whether birds actually move between them seasonally.

Even for the resident species with a clear preference for a fairly narrow range of altitudes, this approach is useful, because it provides guidance on the preferred altitudinal choice of the species. Selection of pentads with highest reporting rates would need to be ground-truthed by fieldwork.

Montane bird species are thought to be at particularly at risk from climate change (Dirnböck 2011). Chamberlain et al. (2016) developed a set of 10 threats related to Alpine bird species using expert opinion. Most of these appear to apply equally well, to a greater or lesser extent, to the high altitude parts of the study area considered here, and adjacent Lesotho (Osborne and Tigar 1994): urbanisation, afforestation, grazing, abandonment, climate change, fire, hunting, leisure, mining and energy. For the species demonstrated by this study to have preferences for the highest altitudes (Table 3.1), a workshop to discuss each of these species in relation to the 10 threats proposed by Chamberlain et al. (2016) would make a substantial contribution to the conservation of the montane species of the Drakensberg Mountains.

References

Ash, C. 2009. The historical quest for birds in Ethiopia and Eritrea. In: Birds of Ethiopia and Eritrea. Ash, J. and Atkins, J (eds). pp. 13–21. Christopher Helm, London.

Ash, J. and Atkins, J. 2009. Birds of Ethiopia and Eritrea. Christopher Helm, London.

Ainsley, J. and Underhill, L.G. 2017. Gamification (persuasive design) in the Second Southern African Bird Atlas Project. Vogelwelt 137: 19–22.

Allan, D.G., Harrison, J.A., Herremans, M., Navarro, R.A. and Underhill, L.G. 1997. Southern African geography. In: The Atlas of Southern African Birds. Volume 1: Non-passerines. Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V. and Brown, C.J. (eds). pp. lxv–ci. BirdLife South Africa, Johannesburg.

Altwegg, R., Broms, K., Erni, B., Barnard, P., Midgley, G.F. and Underhill, L.G. 2012. Novel methods reveal shifts in migration phenology of Barn Swallows in South Africa. Proceedings of the Royal Society of London B 279: 1485–1490.

Anderson, M.D. 1997. Hadeda Ibis *Bostrychia hagedash.* In: The Atlas of Southern African Birds. Volume 1: Non-passerines. Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V. and Brown, C.J. (eds). pp. 108–109. BirdLife South Africa, Johannesburg.

Barnes, K.N. and Herremans, M. 1997. Cape Reed Warbler *Acrocephalus gracilirostris.* In: The Atlas of Southern African Birds. Volume 2: Passerines. Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V. and Brown, C.J. (eds). pp. 238–239. BirdLife South Africa, Johannesburg.

Berruti, A. 1997a. Barratt's Warbler *Bradypterus barratti*. In: The Atlas of Southern African Birds. Volume 2: Passerines. Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V. and Brown, C.J. (eds). pp. 248–249. BirdLife South Africa, Johannesburg.

Berruti, A. 1997b. Yellowthroated Warbler *Phylloscopus ruficapillus.* In: The Atlas of Southern African Birds. Volume 2: Passerines. Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V. and Brown, C.J. (eds). pp. 256–257. BirdLife South Africa, Johannesburg.

Berruti, A. 1997c. Wailing Cisticola *Cisticola lais.* In: The Atlas of Southern African Birds. Volume 2: Passerines. Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V. and Brown, C.J. (eds). pp. 298–299. BirdLife South Africa, Johannesburg.

Berruti, A. 1997d. Redfaced Cisticola *Cisticola erythrops.* In: The Atlas of Southern African Birds. Volume 2: Passerines. Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V. and Brown, C.J. (eds). pp. 306–307. BirdLife South Africa, Johannesburg.

Berruti, A. 1997e. Lazy Cisticola *Cisticola aberrans.* In: The Atlas of Southern African Birds. Volume 2: Passerines. Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V. and Brown, C.J. (eds). pp. 314–315. BirdLife South Africa, Johannesburg.

Berruti, A., Harrison, J.A. and Navarro, R.A. 1994. Seasonal migration of terrestrial birds along the southern and eastern coasts of Southern Africa. Ostrich 65: 54–65.

Boyle, A.W. 2017. Altitudinal bird migration in North America. The Auk: Ornithological Advances 134: 443–465.

Brooke, R.K. 1997. Alpine swift *Apus melba.* In: The Atlas of Southern African Birds. Volume 1: Non-passerines. Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V. and Brown, C.J. (eds). pp. 623–625. BirdLife South Africa, Johannesburg.

Brown, C.J. 1997. Bearded Vulture *Gypaetus barbatus.* In: The Atlas of Southern African Birds. Volume 1: Non-passerines. Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V. and Brown, C.J. (eds). pp. 154–155. BirdLife South Africa, Johannesburg.

Brown, C.J. and Barnes, P.R. 1984. Birds of the Natal Alpine Belt. Lammergeyer 33: 1–13.

Brown, M. 2006. Annual and seasonal trends in avifaunal species richness in a coastal lowlands forest reserve in South Africa. Ostrich 77: 58–66.

Burgess, N.D. and Mlingwa, C.O.F. 2000. Evidence for altitudinal migration of forest birds between montane Eastern Arc and lowland forests in East Africa. Ostrich 71: 184–190.

Bussière, E.M.S., Underhill, L.G. and Altwegg, R. 2015. Patterns of bird migration phenology in South Africa suggest northern hemisphere climate as the most consistent driver of change. Global Change Biology 21: 2179–2190.

Chamberlain, D. E., Pedrini, P., Brambilla, M., Rolando, A. and Girardello, M. 2016. Identifying key conservation threats to Alpine birds through expert knowledge. PeerJ 4: e1723. http://doi.org/10.7717/peerj.1723

Clancey, P.A. 1964. The Birds of Natal and Zululand. Oliver & Boyd, Edinburgh and London.

Clancey, P.A. 1997. Malachite Kingfisher *Alcedo cristata.* In: The Atlas of Southern African Birds. Volume 1: Non-passerines. Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V. and Brown, C.J. (eds). pp. 646–647. BirdLife South Africa, Johannesburg.

Cooper, J., Crawford, R.J.M., Suter, W. and Williams, A.J. 1990. Distribution, population size and conservation of the Swift Tern *Sterna bergii* in southern Africa. Ostrich 61: 56–65.

Craig, A.J.F.K. 1997a. Blackbellied Starling *Lamprotornis corruscus.* In: The Atlas of Southern African Birds. Volume 2: Passerines. Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V. and Brown, C.J. (eds). pp. 474–475. BirdLife South Africa, Johannesburg.

Craig, A.J.F.K. 1997b. Longtailed Widow *Euplectes progne.* In: The Atlas of Southern African Birds. Volume 2: Passerines. Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V. and Brown, C.J. (eds). pp. 590–591. BirdLife South Africa, Johannesburg.

Crawford, R.J.M. 1997. Swift Tern *Sterna bergii.* In: The Atlas of Southern African Birds. Volume 2: Non-passerines. Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V. and Brown, C.J. (eds). pp. 470–471. BirdLife South Africa, Johannesburg.

Cyrus, D.P. and Robson, N.F. 1980. Bird Atlas of Natal. University of Natal Press, Pietermaritzburg.

Davies, R.A.G. and Allan, D.G. 1997. Black Eagle *Aquila verreauxii.* In: The Atlas of Southern African Birds. Volume 1: Non-passerines. Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V. and Brown, C.J. (eds). pp. 175–177. BirdLife South Africa, Johannesburg.

De Swardt, D.H. 1991. The seasonal movements of Gurney's Sugarbird *Promerops gurneyi* in the Lydenburg area, Transvaal. Ostrich 62: 40–44.

Dunn, A.M. and Weston, M.A. 2008. A review of terrestrial bird atlases of the world and their application. Emu 108: 42–67.

Dirnböck, T., Essl, F. and Babitsch, W. 2011. Disproportional risk for habitat loss of high-altitude endemic species under climate change. Global Change Biology 17: 990–996.

Dybbro, T. 1976. De Danske Ynglefugles Udbredelse. Häftad Dansk Ornithologisk Forening, Copenhagen.

Earlé, R. and Grobler, N. 1987. First atlas of bird distribution in the Orange Free State. National Museum, Bloemfontein.

Earlé, R.A. 1997. Rock Martin *Hirundo fuligula.* In: The Atlas of Southern African Birds. Volume 2: Passerines. Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V. and Brown, C.J. (eds). pp. 70–71. BirdLife South Africa, Johannesburg.

Ethiopian Wildlife and Natural History Society. 1996. Important bird areas of Ethiopia: a first inventory. Ethiopian Wildlife and Natural History Society, Addis Ababa.

Fraser, M.W. 1997. Malachite Sunbird *Nectarinia famosa.* In: The Atlas of Southern African Birds. Volume 2: Passerines. Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V. and Brown, C.J. (eds). pp. 488–490. BirdLife South Africa, Johannesburg.

Genstat Seventeenth Edition 2014. GenStat Reference Manual (Release 17). VSN International, Hemel Hempstead, Hertfordshire, UK.

Gibbons, D.W., Reid, J.B. and Chapman, R.A. 1993. The New Atlas of Breeding Birds in Britain and Ireland: 1988–1991. T & AD Poyser, London.

Gibbons, D.W., Donald, P.F. Bauer, H., Fornasari, L. and Dawson, I.K. 2007. Mapping avian distributions: the evolution of bird atlases. Bird Study 54: 324–334.

Greenwood, J.J.D. 2017. The History of the EBCC Atlas of European Breeding Birds. Vogelwelt 137: 3–18.

Griffioen, P. 2001. Temporal changes in the distributions of bird species in eastern Australia. Unpubl. PhD thesis, La Trobe University, Australia.

Hagemeijer, E.J.M. and Blair, M.J. (eds). 1997. The EBCC Atlas of European Breeding Birds: Their Distribution and Abundance. T. and A.D. Poyser, London.

Harebottle, D.M., Smith, N., Underhill, L.G. and Brooks, M. 2007. Southern African Bird Atlas Project 2 – Instruction Manual. Animal Demography Unit, University of Cape Town, Cape Town.

Harrison, J.A. 1997. Stonechat *Saxicola torquata.* In: The Atlas of Southern African Birds. Volume 2: Passerines. Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V. and Brown, C.J. (eds). pp. 190–192. BirdLife South Africa, Johannesburg.

Harrison, J. A. and Navarro, R.A. 1994. Modelled reporting rates as indices of changes in relative abundance with altitude and season. In: Bird Numbers 1992. Distribution Monitoring and Ecological Aspects. Hagemeijer, E.J.M. and Verstrael, T.J. pp. 607–618. Statistics Netherlands, Coorburg/Heelen.

Harrison, J.A. and Underhill, L.G. 1997. Introduction and methods. In: The Atlas of Southern African Birds. Volume 1: Non-passerines. Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V. and Brown, C.J. (eds). pp. xliii–lxiv. BirdLife South Africa, Johannesburg.

Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V. and Brown, C.J. (eds). 1997. The Atlas of Southern African Birds. BirdLife South Africa, Johannesburg.

Harrison, J.A., Underhill, L.G. and Barnard, P. 2008. The seminal legacy of the Southern African Bird Atlas Project. South African Journal of Science 104: 82–84.

Hart, A.P.L. 1997. Blackeyed Bulbul *Pycnonotus barbatus.* In: The Atlas of Southern African Birds. Volume 2: Passerines. Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V. and Brown, C.J. (eds). pp. 138–139. BirdLife South Africa, Johannesburg.

Herrando, S., Keller, V., Voříšek, P., Kipson, M., Franch, M., Anton, M., Pla, M., Villero, D., Sierdsema, H., Kampichler, C., Telenský, T., Gillings, S., Johnston, A., Gottschallk, T., Guélat, J., Sattlet, T., Brotons, L., Titeux, N., Jiguet, F., Kéry, M. and Milanesi, P. 2017. High resolution maps for the second European Breeding Bird Atlas: a first provision of standardised data and pilot modelled maps. Vogelwelt 137: 33–41.

Hiestermann, J. and Rivers-Moore, N. 2015. Predictive modelling of wetland occurrence in KwaZulu-Natal, South Africa. South African Journal of Science: 111(7/8), Art. #2014-0179, 10 pages.

Hockey, P., Underhill, L., Neatherway, M. and Ryan, P. 1989. Altas of the birds of the southwestern Cape. Cape Bird Club, Cape Town.

Hockey, P.A.R., Dean, W.R.J. and Ryan, P.G. (eds). 2005. Roberts' Birds of Southern Africa. 7th edition. The Trustees of John Voeckler Bird Book Fund, Cape Town.

Jacobs, J. 1974. Quantitative measurement of food selection – a modification of the forage ratio and Ivlev's electivity index. Oecologia 14: 413–417.

Jarvis, A., Reuter, H.I., Nelson, A. and Guevara, E. 2008. Hole-filled SRTM for the globe Version 4. Available online at http://www.cgiar-csi.org/data/srtm-90m-digital-elevation-database-v4-1

Jenkins, A.R. and Underhill, L.G. 1997. Pied Crow *Corvus albus.* In: The Atlas of Southern African Birds. Volume 2: Passerines. Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V. and Brown, C.J. (eds). pp. 104–105. BirdLife South Africa, Johannesburg.

Johnson, D.N. 1997a. Dusky Flycatcher *Muscicapa adusta*. In: The Atlas of Southern African Birds. Volume 2: Passerines. Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V. and Brown, C.J. (eds). pp. 334–336. BirdLife South Africa, Johannesburg.

Johnson, D.N. 1997b. Bluegrey Flycatcher *Muscicapa caerulescens*. In: The Atlas of Southern African Birds. Volume 2: Passerines. Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V. and Brown, C.J. (eds). pp. 338–339. BirdLife South Africa, Johannesburg.

Johnson, D.N. 1997c. Southern Tchagra *Tchagra tchagra.* In: The Atlas of Southern African Birds. Volume 2: Passerines. Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V. and Brown, C.J. (eds). pp. 422–423. BirdLife South Africa, Johannesburg.

Johnson, D.N. and Maclean, G.L. 1994. Altitudinal migration in Natal. Ostrich 65: 86 –94.

La Sorte, F.A. and Jetz, W. 2010. Projected range contractions of montane biodiversity under global warming. Proceedings of the Royal Society B: Biological Sciences 277: 3401–3410.

Lechowicz, M.J. 1982. The sampling characteristics of electivity indices. Oecologia 52: 22–30.

Little, R.M. 1997a. Greywing Francolin *Francolinus africanus.* In: The Atlas of Southern African Birds. Volume 1: Non-passerines. Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V. and Brown, C.J. (eds). pp. 280–281. BirdLife South Africa, Johannesburg.

Little, R.M. 1997b. Shelley's Francolin *Francolinus shelleyi.* In: The Atlas of Southern African Birds. Volume 1: Non-passerines. Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V. and Brown, C.J. (eds). pp. 282–283. BirdLife South Africa, Johannesburg.

Little, R.M. 1997c. Natal Francolin *Francolinus natalensis.* In: The Atlas of Southern African Birds. Volume 1: Non-passerines. Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V. and Brown, C.J. (eds). pp. 292–293. BirdLife South Africa, Johannesburg.

Little, R.M. 1997d. Rednecked Francolin *Francolinus afer.* In: The Atlas of Southern African Birds. Volume 1: Non-passerines. Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V. and Brown, C.J. (eds). pp. 294–295. BirdLife South Africa, Johannesburg.

Little, R.M. 1997e. Swainson's Francolin *Francolinus swainsonii.* In: The Atlas of Southern African Birds. Volume 1: Non-passerines. Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V. and Brown, C.J. (eds). pp. 296–297. BirdLife South Africa, Johannesburg.

Little, R.M. and Allan, D.G. 1997. Redwing Francolin *Francolinus levaillantii.* In: The Atlas of Southern African Birds. Volume 1: Non-passerines. Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V. and Brown, C.J. (eds). pp. 284–285. BirdLife South Africa, Johannesburg.

Little, R.M. and Bainbridge, W.R. 1992. Birds of the Natal Drakensberg Park. Natal branch of the Wildlife Society of Southern Africa, South Africa.

Little, R.M. and Crowe, T. 2000. Gamebirds of Southern Africa. Struik Publishers, Cape Town.

Loftie-Eaton, M. 2014. Geographic range dynamics of South Africa's bird species. MSc dissertation, University of Cape Town, Cape Town.

Lord, J. and Munns, D.J. (eds). 1970. Atlas of breeding birds of the West Midlands. Collins, London.

McCullagh, P. 2003. John Wilder Tukey. 16 June 1915 – 26 July 2000. Biographical Memoirs of the Fellows of the Royal Society 49: 537–555.

Mucina, L and Rutherford, M.C. (eds) 2010. (CD set). The Vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19. South African National Biodiversity Institute, Pretoria.

Mundy, P.J. and Herremans, M. 1997. Redbilled Quelea *Quelea quelea.* In: The Atlas of Southern African Birds. Volume 2: Passerines. Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V. and Brown, C.J. (eds). pp. 573–575. BirdLife South Africa, Johannesburg.

Nachman, G. 1984. A mathematical model of the functional relationship between density and the spatial distribution of a population. Journal of Animal Ecology 50: 453–460.

Norries, C.A. 1960. The breeding distribution of thirty bird species in 1952. Bird Study 7: 129–184.

Oatley, T.B. 1982. The Starred Robin in Natal, part 2: annual cycles and feeding ecology. Ostrich 53: 193–205.

Oatley, T.B. 1997a. Ground Woodpecker *Geocolaptes olivaceus.* In: The Atlas of Southern African Birds. Volume 1: Non-passerines. Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V. and Brown, C.J. (eds). pp. 736–737. BirdLife South Africa, Johannesburg.

Oatley, T.B. 1997b. Grey Cuckooshrike *Coracina caesia.* In: The Atlas of Southern African Birds. Volume 2: Passerines. Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V. and Brown, C.J. (eds). pp. 88–89. BirdLife South Africa, Johannesburg.

Oatley, T.B. 1997c. Bush Blackcap *Lioptilus nigricapillus.* In: The Atlas of Southern African Birds. Volume 2: Passerines. Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V. and Brown, C.J. (eds). pp. 132–133. BirdLife South Africa, Johannesburg.

Oatley, T.B. 1997d. Sombre Bulbul *Andropadus importunus.* In: The Atlas of Southern African Birds. Volume 2: Passerines. Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V. and Brown, C.J. (eds). pp. 144–145. BirdLife South Africa, Johannesburg.

Oatley, T.B. 1997e. Natal Robin *Cossypha natalensis.* In: The Atlas of Southern African Birds. Volume 2: Passerines. Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V. and Brown, C.J. (eds). pp. 198–199. BirdLife South Africa, Johannesburg.

Oatley, T.B. 1997f. Cape Robin *Cossypha caffra.* In: The Atlas of Southern African Birds. Volume 2: Passerines. Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V. and Brown, C.J. (eds). pp. 200–201. BirdLife South Africa, Johannesburg.

Oatley, T.B. 1997g. Starred Robin *Pogonocichla stellata.* In: The Atlas of Southern African Birds. Volume 2: Passerines. Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V. and Brown, C.J. (eds). pp. 206–207. BirdLife South Africa, Johannesburg.

Oatley, T. and Arnott, G. 1998. Robins of Africa. Acorn Books and Russel Friedman Books, Halfway House, Johannesburg, South Africa.

Oatley, T.B. 2017. Altitudinal migration in south-east Africa. Biodiversity Observations 8.49: 1–22.

Okes N.C., Hockey P.A.R. and Cumming, G.C. 2008. Habitat use and life history as predictors of bird responses to habitat change. Conservation Biology 22: 151−162.

Osborne, P.E. and Tigar, B.J. 1990. The status and distribution of birds in Lesotho. Unpublished report, Nature Conservation Bureau Ltd, Newburgh, Berkshire, U.K.

Osborne, P.E. and Tigar, B.J. 1992. Priorities for bird conservation in Lesotho, southern Africa. Biological Conservation 61: 159–169.

Perring, F. and Walters, S. 1962. Atlas of British Flora. Nelson, London.

Piper, S.E. 1997. Cape Wagtail *Motacilla capensis.* In: The Atlas of Southern African Birds. Volume 2: Passerines. Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V. and Brown, C.J. (eds). pp. 378–379. BirdLife South Africa, Johannesburg.

Rebelo, A.G. 2007. *Protea roupelliae* subsp*. roupelliae* Meisn. Silver Sugarbush Silwerblaarsuikerbos. Downloaded from: http://www.proteaatlas.org.za/PROTEA_ATLAS_Protea1.pdf on 8 December 2016.

Reuter H.I, Nelson, A. and Jarvis, A. 2007. An evaluation of void filling interpolation methods for SRTM data, International Journal of Geographic Information Science, 21: 983–1008.

Rodewald, P.E. 2015. Birds of North America. Cornell Laboratory of Ornithology, Ithaca, New York, United States of America. http://birdsna.org

Roff, D.A. and Bentzen, P. 1989. The statistical analysis of mitochondrial DNA polymorphisms: χ^2 and the problem of small samples. Molecular Biology and Evolution 6: 539–545.

Sharrock, J.T.R. 1976. The Atlas of Breeding Birds in Britain and Ireland. British Trust for Ornithology, Tring, United Kingdom.

Skead, C.J. 1967. Sunbirds of Southern Africa. Also Sugarbirds, White-eyes and the Spotted Creeper. A.A. Balkema, Cape Town.

Tarboton, W., Kemp, M. and Kemp, A. 1987. Birds of the Transvaal. Transvaal Museum, Pretoria.

Taylor, P.B. 1997. Buffspotted Flufftail *Sarothrura elegans*. In: The Atlas of Southern African Birds. Volume 1: Non-passerines. Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V. and Brown, C.J. (eds). pp. 330–331. BirdLife South Africa, Johannesburg.

Tjørve, K.M.C., Geertsema, G.H. and Underhill, L.G. 2005. Do sugarbirds feed on arthropods inside or outside *Protea* inflorescences? Emu 105: 293–297.

Tree, A.J. 1997. Whitebellied Sunbird *Nectarinia talatala.* In: The Atlas of Southern African Birds. Volume 2: Passerines. Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V. and Brown, C.J. (eds). pp. 508–509. BirdLife South Africa, Johannesburg.

Tukey, J.W. 1977. Exploratory Data Analysis. Addison-Wesley, New York.

Underhill, L.G. 1999. Avian demography: statistics and ornithology. Ostrich 70: 61–70.

Underhill, L.G. 2016. The fundamentals of the SABAP2 protocol. Biodiversity Observations 7.42: 1–12.

Underhill, L.G. and Brooks, M. 2016a. SABAP2 after nine years, mid 2007–mid 2016: coverage progress and priorities for the Second Southern African Bird Atlas Project. Biodiversity Observations 7.37: 1–17.

Underhill, L.G. and Brooks, M. 2016b. Pentad-scale distribution maps for bird atlas data. Biodiversity Observations 7.52: 1–8.

Underhill, L.G. and Brooks, M. 2016c. Displaying changes in bird distributions between SABAP1 and SABAP2. Biodiversity Observations 7.62: 1–13.

Underhill, L.G., Brooks, M. and Loftie-Eaton, M. 2017. The Second Southern African Bird Atlas Project: protocol, process, product. Vogelwelt 137: 64–70.

Van Zyl, A.J. 1997. Rock Kestrel *Falco tinnunculus.* In: The Atlas of Southern African Birds. Volume 1: Non-passerines. Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V. and Brown, C.J. (eds). pp. 264–265. BirdLife South Africa, Johannesburg.

Vernon, C.J. and Herremans, M. 1997. Olive Thrush *Turdus olivaceus.* In: The Atlas of Southern African Birds. Volume 2: Passerines. Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V. and Brown, C.J. (eds). pp. 154–155. BirdLife South Africa, Johannesburg.

Woodward, R. and Woodward, J. 1899. Natal Birds. Davis, Pietermaritzburg.

Yeatman, L. 1976. Altas des Oiseaux nicheurs de France de 1970 a 1975. Societe Ornithologique de France, Paris.

Appendix A

Scientific names of species mentioned in the text

Table A.1 The common and scientific names for all species mentioned in this dissertation. The list is sort by the English common names. The taxonomy is that used by the Second Southern African Bird Atlas Project (SABAP2) (Underhill 2016).

Common name	**Scientific name**
Acacia Pied Barbet	*Tricholaema leucomelas*
African Black Duck	*Anas sparsa*
African Black Swift	*Apus barbatus*
African Crowned Eagle	*Stephanoaetus coronatus*
African Darter	*Anhinga rufa*
African Dusky Flycatcher	*Muscicapa adusta*
African Emerald Cuckoo	*Chrysococcyx cupreus*
African Firefinch	*Lagonosticta rubricata*
African Fish-Eagle	*Haliaeetus vocifer*
African Goshawk	*Accipiter tachiro*
African Green-Pigeon	*Treron calvus*
African Harrier-Hawk	*Polyboroides typus*
African Hoopoe	*Upupa africana*
African Jacana	*Actophilornis africanus*
African Marsh-Harrier	*Circus ranivorus*
African Olive-Pigeon	*Columba arquatrix*
African Palm-Swift	*Cypsiurus parvus*
African Paradise-Flycatcher	*Terpsiphone viridis*
African Pied Wagtail	*Motacilla aguimp*
African Pipit	*Anthus cinnamomeus*
African Purple Swamphen	*Porphyrio madagascariensis*
African Pygmy-Kingfisher	*Ispidina picta*
African Quailfinch	*Ortygospiza atricollis*
African Rail	*Rallus caerulescens*
African Reed-Warbler	*Acrocephalus baeticatus*
African Sacred Ibis	*Threskiornis aethiopicus*
African Snipe	*Gallinago nigripennis*
African Spoonbill	*Platalea alba*
African Stonechat	*Saxicola torquatus*
African Wattled Lapwing	*Vanellus senegallus*
African Wood-Owl	*Strix woodfordii*
Alpine Swift	*Tachymarptis melba*
Amethyst Sunbird	*Chalcomitra amethystina*
Amur Falcon	*Falco amurensis*
Anteating Chat	*Myrmecocichla formicivora*

Common name	**Scientific name**
Ashy Flycatcher	*Muscicapa caerulescens*
Banded Martin	*Riparia cincta*
Barn Owl	*Tyto alba*
Barn Swallow	*Hirundo rustica*
Barratt's Warbler	*Bradypterus barratti*
Bar-throated Apalis	*Apalis thoracica*
Bearded Vulture	*Gypaetus barbatus*
Black Crake	*Amaurornis flavirostris*
Black Cuckoo	*Cuculus clamosus*
Black Cuckooshrike	*Campephaga flava*
Black Kite	*Milvus migrans*
Black Saw-wing	*Psalidoprocne holomelaena*
Black Sparrowhawk	*Accipiter melanoleucus*
Black-backed Puffback	*Dryoscopus cubla*
Black-bellied Starling	*Lamprotornis corruscus*
Black-collared Barbet	*Lybius torquatus*
Black-crowned Night-Heron	*Nycticorax nycticorax*
Black-crowned Tchagra	*Tchagra senegalus*
Black-headed Heron	*Ardea melanocephala*
Black-headed Oriole	*Oriolus larvatus*
Black-shouldered Kite	*Elanus caeruleus*
Blacksmith Lapwing	*Vanellus armatus*
Black-throated Wattle-eye	*Platysteira peltata*
Black-winged Lapwing	*Vanellus melanopterus*
Black-winged Stilt	*Himantopus himantopus*
Blue Crane	*Anthropoides paradiseus*
Blue Waxbill	*Uraeginthus angolensis*
Blue-mantled Crested-Flycatcher	*Trochocercus cyanomelas*
Bokmakierie	*Neafrapus boehmi*
Brimstone Canary	*Crithagra sulphuratus*
Bronze Mannikin	*Spermestes cucullatus*
Brown-backed Honeybird	*Prodotiscus regulus*
Brown-hooded Kingfisher	*Halcyon albiventris*
Brown-throated Martin	*Riparia paludicola*
Brubru	*Nilaus afer*
Buff-spotted Flufftail	*Sarothrura elegans*
Buff-streaked Chat	*Oenanthe bifasciata*
Burchell's Coucal	*Centropus burchellii*
Bush Blackcap	*Lioptilus nigricapillus*
Cape Batis	*Batis capensis*
Cape Canary	*Serinus canicollis*
Cape Crow	*Corvus capensis*
Cape Glossy Starling	*Lamprotornis nitens*
Cape Grassbird	*Sphenoeacus afer*
Cape Longclaw	*Macronyx capensis*

Common name	**Scientific name**
Cape Robin-Chat	*Cossypha caffra*
Cape Rock-Thrush	*Monticola rupestris*
Cape Shoveler	*Anas smithii*
Cape Sparrow	*Passer melanurus*
Cape Turtle-Dove	*Streptopelia capicola*
Cape Vulture	*Gyps coprotheres*
Cape Wagtail	*Motacilla capensis*
Cape Weaver	*Ploceus capensis*
Cape White-eye	*Zosterops capensis*
Cardinal Woodpecker	*Dendropicos fuscescens*
Cattle Egret	*Bubulcus ibis*
Chinspot Batis	*Batis molitor*
Chorister Robin-Chat	*Cossypha dichroa*
Collared Sunbird	*Hedydipna collaris*
Common Fiscal	*Lanius collaris*
Common House-Martin	*Delichon urbicum*
Common Moorhen	*Gallinula chloropus*
Common Myna	*Acridotheres tristis*
Common Quail	*Coturnix coturnix*
Common Scimitarbill	*Rhinopomastus cyanomelas*
Common Starling	*Sturnus vulgaris*
Common Waxbill	*Estrilda astrild*
Crested Barbet	*Trachyphonus vaillantii*
Croaking Cisticola	*Cisticola natalensis*
Crowned Hornbill	*Tockus alboterminatus*
Crowned Lapwing	*Vanellus coronatus*
Dark-backed Weaver	*Ploceus bicolor*
Dark-capped Bulbul	*Pycnonotus tricolor*
Dark-capped Yellow Warbler	*Chloropeta natalensis*
Denham's Bustard	*Neotis denhami*
Diderick Cuckoo	*Chrysococcyx caprius*
Drakensberg Prinia	*Prinia hypoxantha*
Dusky Indigobird	*Vidua funerea*
Egyptian Goose	*Alopochen aegyptiaca*
Emerald-spotted Wood-Dove	*Turtur chalcospilos*
Familiar Chat	*Cercomela familiaris*
Fan-tailed Widowbird	*Euplectes axillaris*
Fiery-necked Nightjar	*Caprimulgus pectoralis*
Fiscal Flycatcher	*Sigelus silens*
Forest Buzzard	*Buteo trizonatus*
Forest Canary	*Crithagra scotops*
Fork-tailed Drongo	*Dicrurus adsimilis*
Giant Kingfisher	*Megaceryle maximus*
Golden Weaver	*Ploceus xanthops*
Golden-breasted Bunting	*Emberiza flaviventris*

Common name	**Scientific name**
Golden-tailed Woodpecker	*Campethera abingoni*
Goliath Heron	*Ardea goliath*
Gorgeous Bush-Shrike	*Telophorus viridis*
Great Egret	*Egretta alba*
Greater Double-collared Sunbird	*Cinnyris afer*
Greater Honeyguide	*Indicator indicator*
Greater Striped Swallow	*Hirundo cucullata*
Green Twinspot	*Mandingoa nitidula*
Green Wood-Hoopoe	*Phoeniculus purpureus*
Green-backed Camaroptera	*Camaroptera brachyura*
Green-backed Heron	*Butorides striata*
Grey Crowned Crane	*Balearica regulorum*
Grey Cuckooshrike	*Coracina caesia*
Grey Heron	*Ardea cinerea*
Grey Sunbird	*Cyanomitra veroxii*
Grey Waxbill	*Estrilda perreini*
Grey-headed Bush-Shrike	*Malaconotus blanchoti*
Grey-headed Gull	*Larus cirrocephalus*
Ground Woodpecker	*Geocolaptes olivaceus*
Groundscraper Thrush	*Psophocichla litsipsirupa*
Gurney's Sugarbird	*Promerops gurneyi*
Hadeda Ibis	*Bostrychia hagedash*
Half-collared Kingfisher	*Alcedo semitorquata*
Hamerkop	*Scopus umbretta*
Helmeted Guineafowl	*Numida meleagris*
Horus Swift	*Apus horus*
Hottentot Teal	*Anas hottentota*
House Sparrow	*Passer domesticus*
Jackal Buzzard	*Buteo rufofuscus*
Jacobin Cuckoo	*Lagonosticta rhodopareia*
Kelp Gull	*Larus dominicanus*
Kittlitz's Plover	*Charadrius pecuarius*
Klaas's Cuckoo	*Chrysococcyx klaas*
Knysna Turaco Turaco	*Tauraco corythaix*
Kurrichane Thrush	*Turdus libonyanus*
Lanner Falcon	*Falco biarmicus*
Laughing Dove	*Streptopelia senegalensis*
Lazy Cisticola	*Cisticola aberrans*
Lemon Dove	*Aplopelia larvata*
Lesser Honeyguide	*Indicator minor*
Lesser Striped Swallow	*Hirundo abyssinica*
Lesser Swamp-Warbler	*Acrocephalus gracilirostris*
Levaillant's Cisticola	*Cisticola tinniens*
Little Bee-eater	*Merops pusillus*
Little Egret	*Egretta garzetta*

Common name	**Scientific name**
Little Grebe	*Tachybaptus ruficollis*
Little Rush-Warbler	*Bradypterus baboecala*
Little Sparrowhawk	*Accipiter minullus*
Little Swift	*Apus affinis*
Long-billed Crombec	*Sylvietta rufescens*
Long-billed Pipit	*Anthus similis*
Long-crested Eagle	*Lophaetus occipitalis*
Long-tailed Widowbird	*Euplectes progne*
Malachite Kingfisher	*Alcedo cristata*
Malachite Sunbird	*Nectarinia famosa*
Marsh Warbler	*Acrocephalus palustris*
Martial Eagle	*Polemaetus bellicosus*
Mocking Cliff-Chat	*Thamnolaea cinnamomeiventris*
Mountain Wagtail	*Motacilla clara*
Mountain Wheatear	*Oenanthe monticola*
Narina Trogon	*Apaloderma narina*
Natal Spurfowl	*Pternistis natalensis*
Neddicky Neddicky	*Cisticola fulvicapilla*
Olive Bush-Shrike	*Telophorus olivaceus*
Olive Sunbird	*Cyanomitra olivacea*
Olive Thrush	*Turdus olivaceus*
Olive Woodpecker	*Dendropicos griseocephalus*
Orange-breasted Bush-Shrike	*Telophorus sulfureopectus*
Orange-breasted Waxbill	*Sporaeginthus subflavus*
Peregrine Falcon	*Falco peregrinus*
Pied Crow	*Corvus albus*
Pied Kingfisher	*Ceryle rudis*
Pied Starling	*Spreo bicolor*
Pin-tailed Whydah	*Vidua macroura*
Plain-backed Pipit	*Anthus leucophrys*
Purple Heron	*Ardea purpurea*
Purple-banded Sunbird	*Cinnyris bifasciatus*
Purple-crested Turaco	*Musophaga porphyreolopha*
Rattling Cisticola	*Cisticola chiniana*
Red-backed Mannikin	*Spermestes bicolor*
Red-backed Shrike	*Lanius collurio*
Red-billed Quelea	*Quelea quelea*
Red-billed Teal	*Anas erythrorhyncha*
Red-capped Lark	*Calandrella cinerea*
Red-capped Robin-Chat	*Cossypha natalensis*
Red-chested Cuckoo	*Cuculus solitarius*
Red-chested Flufftail	*Sarothrura rufa*
Red-collared Widowbird	*Euplectes ardens*
Red-eyed Dove	*Streptopelia semitorquata*
Red-faced Cisticola	*Cisticola erythrops*

Common name	**Scientific name**
Red-faced Mousebird	*Urocolius indicus*
Red-fronted Tinkerbird	*Pogoniulus pusillus*
Red-knobbed Coot	*Fulica cristata*
Red-necked Spurfowl	*Pternistis afer*
Red-throated Wryneck	*Jynx ruficollis*
Red-winged Francolin	*Scleroptila levaillantii*
Red-winged Starling	*Onychognathus morio*
Reed Cormorant	*Phalacrocorax africanus*
Rock Dove	*Columba livia*
Rock Kestrel	*Falco rupicolus*
Rock Martin	*Hirundo fuligula*
Rufous-chested Sparrowhawk	*Accipiter rufiventris*
Rufous-naped Lark	*Mirafra africana*
Rufous-winged Cisticola	*Cisticola galactotes*
Scaly-throated Honeyguide	*Indicator variegatus*
Scarlet-chested Sunbird	*Chalcomitra senegalensis*
Secretarybird	*Sagittarius serpentarius*
Sentinel Rock-Thrush	*Monticola explorator*
Shelley's Francolin	*Scleroptila shelleyi*
Sombre Greenbul	*Andropadus importunus*
South African Shelduck	*Tadorna cana*
Southern Bald Ibis	*Geronticus calvus*
Southern Black Flycatcher	*Melaenornis pammelaina*
Southern Black Tit	*Parus niger*
Southern Boubou	*Laniarius ferrugineus*
Southern Double-collared Sunbird	*Cinnyris chalybeus*
Southern Grey-headed Sparrow	*Passer diffusus*
Southern Ground-Hornbill	*Bucorvus leadbeateri*
Southern Masked-Weaver	*Ploceus velatus*
Southern Pochard	*Netta erythrophthalma*
Southern Red Bishop	*Euplectes orix*
Southern Tchagra	*Tchagra tchagra*
Speckled Mousebird	*Colius striatus*
Speckled Pigeon	*Columba guinea*
Spectacled Weaver	*Procellaria conspicillata*
Spotted Eagle-Owl	*Salpornis spilonotus*
Spotted Flycatcher	*Bubo africanus*
Spotted Thick-knee	*Burhinus capensis*
Spur-winged Goose	*Plectropterus gambensis*
Squacco Heron	*Ardeola ralloides*
Square-tailed Drongo	*Dicrurus ludwigii*
Steppe Buzzard	*Buteo vulpinus*
Streaky-headed Seedeater	*Crithagra gularis*
Swainson's Spurfowl	*Pternistis swainsonii*
Swee Waxbill	*Coccopygia melanotis*

Common name	**Scientific name**
Swift Tern	*Sterna bergii*
Tambourine Dove	*Turtur tympanistria*
Tawny-flanked Prinia	*Prinia subflava*
Terrestrial Brownbul	*Phyllastrephus terrestris*
Thick-billed Weaver	*Amblyospiza albifrons*
Three-banded Plover	*Charadrius tricollaris*
Trumpeter Hornbill	*Bycanistes bucinator*
Verreaux's Eagle	*Aquila verreauxii*
Village Weaver	*Ploceus cucullatus*
Violet-backed Starling	*Cinnyricinclus leucogaster*
Wahlberg's Eagle	*Aquila wahlbergi*
Wailing Cisticola	*Cisticola lais*
Water Thick-knee	*Burhinus vermiculatus*
Wattled Crane	*Bugeranus carunculatus*
White Stork	*Ciconia ciconia*
White-backed Duck	*Thalassornis leuconotus*
White-bellied Sunbird	*Cinnyris talatala*
White-breasted Cormorant	*Phalacrocorax lucidus*
White-browed Scrub-Robin	*Cercotrichas leucophrys*
White-eared Barbet	*Stactolaema leucotis*
White-faced Duck	*Dendrocygna viduata*
White-fronted Bee-eater	*Merops bullockoides*
White-necked Raven	*Corvus albicollis*
White-rumped Swift	*Apus caffer*
White-starred Robin	*Pogonocichla stellata*
White-throated Swallow	*Hirundo albigularis*
White-winged Widowbird	*Euplectes albonotatus*
Willow Warbler	*Phylloscopus trochilus*
Wing-snapping Cisticola	*Cisticola ayresii*
Wire-tailed Swallow	*Hirundo smithii*
Woolly-necked Stork	*Ciconia episcopus*
Yellow Bishop	*Euplectes capensis*
Yellow Weaver	*Ploceus subaureus*
Yellow-bellied Greenbul	*Chlorocichla flaviventris*
Yellow-billed Duck	*Coccopygia quartinia*
Yellow-billed Egret	*Anas undulata*
Yellow-billed Kite	*Egretta intermedia*
Yellow-breasted Apalis	*Apalis flavida*
Yellow-fronted Canary	*Crithagra mozambicus*
Yellow-rumped Tinkerbird	*Pogoniulus bilineatus*
Yellow-throated Longclaw	*Macronyx croceus*
Yellow-throated Petronia	*Petronia superciliaris*
Yellow-throated Woodland-Warbler	*Phylloscopus ruficapilla*
Zitting Cisticola	*Cisticola juncidis*

Appendix B

Height class percentages in each pentad

Table B.1. The columns headed 1 to 21 in this table contain the percentages of each pentad in the study area which is in each height class. Height class 1 is 0–100 m, … height class 20 is 1900–2000 m and height class 21 is 2000+ m. The column headed n provides the number of different height classes contained within each pentad.

Pentad	n	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
2900_2900	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100
2900_2905	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100
2900_2910	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	5	93
2900_2915	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	3	7	16	16	56
2900_2920	8	0	0	0	0	0	0	0	0	0	0	0	0	0	4	10	11	2	8	12	23	30
2900_2925	9	0	0	0	0	0	0	0	0	0	0	0	12	34	22	21	5	3	1	1	1	0
2900_2930	5	0	0	0	0	0	0	0	0	0	0	0	30	34	27	7	2	0	0	0	0	0
2900_2935	7	0	0	0	0	0	0	0	0	0	0	0	3	10	6	47	24	9	1	0	0	0
2900_2940	5	0	0	0	0	0	0	0	0	0	0	0	2	16	16	58	8	0	0	0	0	0
2900_2945	4	0	0	0	0	0	0	0	0	0	0	0	8	67	17	8	0	0	0	0	0	0
2900_2950	5	0	0	0	0	0	0	0	0	0	0	0	29	55	13	2	1	0	0	0	0	0
2900_2955	4	0	0	0	0	0	0	0	0	0	0	0	7	47	42	4	0	0	0	0	0	0
2900_3000	5	0	0	0	0	0	0	0	0	0	0	0	9	16	31	28	16	0	0	0	0	0
2900_3005	6	0	0	0	0	0	0	0	0	0	0	3	14	18	30	29	6	0	0	0	0	0
2900_3010	7	0	0	0	0	0	0	0	0	0	0	1	10	28	36	13	9	3	0	0	0	0
2900_3015	5	0	0	0	0	0	0	0	0	0	8	25	43	22	2	0	0	0	0	0	0	0
2900_3020	5	0	0	0	0	0	0	0	0	14	27	30	27	2	0	0	0	0	0	0	0	0
2900_3025	7	0	0	0	0	0	0	0	0	0	6	14	26	26	19	7	2	0	0	0	0	0
2900_3030	6	0	0	0	0	0	0	0	0	0	0	9	15	17	30	25	4	0	0	0	0	0
2900_3035	6	0	0	0	0	0	0	0	0	0	3	56	24	8	7	2	0	0	0	0	0	0
2900_3040	4	0	0	0	0	0	0	0	0	0	7	46	27	20	0	0	0	0	0	0	0	0
2900_3045	4	0	0	0	0	0	0	0	0	0	1	12	73	14	0	0	0	0	0	0	0	0
2900_3050	5	0	0	0	0	0	0	0	0	7	18	56	16	3	0	0	0	0	0	0	0	0
2900_3055	8	0	0	0	0	2	4	3	2	16	38	34	1	0	0	0	0	0	0	0	0	0
2900_3100	8	0	0	5	16	23	20	15	8	9	4	0	0	0	0	0	0	0	0	0	0	0
2900_3105	6	0	25	29	24	13	5	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2900_3110	8	1	20	24	26	12	7	8	2	0	0	0	0	0	0	0	0	0	0	0	0	0
2900_3115	6	0	1	10	12	35	41	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2900_3120	5	0	9	24	34	30	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2900_3125	5	35	29	17	11	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2900_3130	2	88	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2900_3135	2	97	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2900_3140	2	90	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2905_2900	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100

Pentad	n	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
2905_2905	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100
2905_2910	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100
2905_2915	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100
2905_2920	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	9	16	70
2905_2925	8	0	0	0	0	0	0	0	0	0	0	0	0	0	6	15	10	9	11	13	25	11
2905_2930	8	0	0	0	0	0	0	0	0	0	0	0	0	0	2	4	12	12	22	30	12	6
2905_2935	7	0	0	0	0	0	0	0	0	0	0	0	0	0	1	19	53	17	8	1	1	0
2905_2940	4	0	0	0	0	0	0	0	0	0	0	0	0	1	22	52	25	0	0	0	0	0
2905_2945	4	0	0	0	0	0	0	0	0	0	0	0	0	17	48	28	7	0	0	0	0	0
2905_2950	4	0	0	0	0	0	0	0	0	0	0	0	0	0	27	45	25	3	0	0	0	0
2905_2955	4	0	0	0	0	0	0	0	0	0	0	0	0	0	3	25	65	7	0	0	0	0
2905_3000	3	0	0	0	0	0	0	0	0	0	0	0	0	0	2	41	57	0	0	0	0	0
2905_3005	5	0	0	0	0	0	0	0	0	0	0	0	0	13	51	20	14	2	0	0	0	0
2905_3010	4	0	0	0	0	0	0	0	0	0	0	0	25	34	32	9	0	0	0	0	0	0
2905_3015	8	0	0	0	0	0	0	0	0	0	1	5	18	25	30	14	3	4	0	0	0	0
2905_3020	5	0	0	0	0	0	0	0	0	0	0	2	8	30	34	26	0	0	0	0	0	0
2905_3025	5	0	0	0	0	0	0	0	0	0	0	3	20	43	28	6	0	0	0	0	0	0
2905_3030	4	0	0	0	0	0	0	0	0	0	14	43	34	9	0	0	0	0	0	0	0	0
2905_3035	3	0	0	0	0	0	0	0	0	0	48	51	1	0	0	0	0	0	0	0	0	0
2905_3040	4	0	0	0	0	0	0	0	0	8	38	37	17	0	0	0	0	0	0	0	0	0
2905_3045	6	0	0	0	0	0	0	0	7	5	12	39	35	2	0	0	0	0	0	0	0	0
2905_3050	8	0	0	0	0	3	10	20	20	20	16	8	3	0	0	0	0	0	0	0	0	0
2905_3055	7	0	0	0	0	9	18	20	17	14	16	6	0	0	0	0	0	0	0	0	0	0
2905_3100	8	0	0	0	2	7	20	23	17	19	11	1	0	0	0	0	0	0	0	0	0	0
2905_3105	7	0	4	15	15	21	26	18	1	0	0	0	0	0	0	0	0	0	0	0	0	0
2905_3110	8	6	31	24	17	15	5	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0
2905_3115	5	20	37	28	11	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2905_3120	3	37	44	19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2905_3125	3	39	60	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2905_3130	2	88	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2905_3135	1	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2910_2900	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100
2910_2905	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100
2910_2910	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100
2910_2915	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100
2910_2920	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	97
2910_2925	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	11	26	57
2910_2930	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	14	18	40	16	6	0
2910_2935	6	0	0	0	0	0	0	0	0	0	0	0	0	0	10	43	16	15	12	4	0	0
2910_2940	5	0	0	0	0	0	0	0	0	0	0	0	0	0	1	11	69	18	0	1	0	0
2910_2945	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	76	20	0	0	0	0
2910_2950	5	0	0	0	0	0	0	0	0	0	0	0	0	0	8	31	42	17	2	0	0	0
2910_2955	2	0	0	0	0	0	0	0	0	0	0	0	0	0	20	80	0	0	0	0	0	0
2910_3000	3	0	0	0	0	0	0	0	0	0	0	0	0	0	18	66	16	0	0	0	0	0
2910_3005	5	0	0	0	0	0	0	0	0	0	0	0	0	0	21	30	25	23	1	0	0	0
2910_3010	4	0	0	0	0	0	0	0	0	0	0	0	0	0	3	15	55	27	0	0	0	0

Pentad	n	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
2910_3015	4	0	0	0	0	0	0	0	0	0	0	0	0	0	36	36	23	5	0	0	0	0
2910_3020	5	0	0	0	0	0	0	0	0	0	0	0	11	14	36	30	9	0	0	0	0	0
2910_3025	6	0	0	0	0	0	0	0	0	0	3	33	32	19	9	4	0	0	0	0	0	0
2910_3030	4	0	0	0	0	0	0	0	0	0	25	59	15	1	0	0	0	0	0	0	0	0
2910_3035	3	0	0	0	0	0	0	0	0	0	3	79	18	0	0	0	0	0	0	0	0	0
2910_3040	6	0	0	0	0	0	0	5	21	18	28	21	7	0	0	0	0	0	0	0	0	0
2910_3045	7	0	0	0	0	0	17	23	25	20	10	3	2	0	0	0	0	0	0	0	0	0
2910_3050	7	0	0	0	4	17	18	16	18	18	9	0	0	0	0	0	0	0	0	0	0	0
2910_3055	8	0	0	2	17	21	14	17	11	13	5	0	0	0	0	0	0	0	0	0	0	0
2910_3100	6	0	0	17	34	33	13	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0
2910_3105	6	0	0	1	6	13	38	38	4	0	0	0	0	0	0	0	0	0	0	0	0	0
2910_3110	5	0	0	4	31	35	28	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2910_3115	5	5	33	38	22	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2910_3120	3	39	40	21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2910_3125	2	98	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2910_3130	1	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2915_2900	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100
2915_2905	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100
2915_2910	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100
2915_2915	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100
2915_2920	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100
2915_2925	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	7	91
2915_2930	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	16	31	32	18
2915_2935	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	8	17	12	20	16	24
2915_2940	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	56	32	6	5	0	1
2915_2945	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	76	8	0	0	0	0
2915_2950	3	0	0	0	0	0	0	0	0	0	0	0	0	0	2	52	46	0	0	0	0	0
2915_2955	4	0	0	0	0	0	0	0	0	0	0	0	0	0	13	80	6	1	0	0	0	0
2915_3000	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	22	77	1	0	0	0	0
2915_3005	5	0	0	0	0	0	0	0	0	0	0	0	0	11	31	30	24	4	0	0	0	0
2915_3010	7	0	0	0	0	0	0	0	0	0	0	1	11	12	7	9	32	28	0	0	0	0
2915_3015	8	0	0	0	0	0	0	0	0	0	0	1	22	9	7	7	28	25	1	0	0	0
2915_3020	8	0	0	0	0	0	0	0	0	10	5	7	17	31	19	8	3	0	0	0	0	0
2915_3025	7	0	0	0	0	0	0	0	3	41	36	9	2	6	3	0	0	0	0	0	0	0
2915_3030	5	0	0	0	0	0	0	0	5	32	27	27	9	0	0	0	0	0	0	0	0	0
2915_3035	3	0	0	0	0	0	0	0	0	0	37	62	1	0	0	0	0	0	0	0	0	0
2915_3040	4	0	0	0	0	0	0	0	2	22	67	9	0	0	0	0	0	0	0	0	0	0
2915_3045	5	0	0	0	0	0	0	5	21	43	29	2	0	0	0	0	0	0	0	0	0	0
2915_3050	7	0	0	0	1	11	12	19	22	20	15	0	0	0	0	0	0	0	0	0	0	0
2915_3055	8	0	0	3	23	20	19	12	7	13	3	0	0	0	0	0	0	0	0	0	0	0
2915_3100	5	0	8	56	25	9	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2915_3105	6	0	30	28	17	21	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2915_3110	6	6	18	42	22	11	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2915_3115	4	22	45	32	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2915_3120	2	93	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2915_3125	1	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Pentad	n	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
2920_2900	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100
2920_2905	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100
2920_2910	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100
2920_2915	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100
2920_2920	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100
2920_2925	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	2	95
2920_2930	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	3	7	88
2920_2935	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	11	8	14	66
2920_2940	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12	45	22	7	7	7
2920_2945	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	40	43	13	3	0	1
2920_2950	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	32	42	19	7	0	0	0
2920_2955	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	69	25	4	2	0	0	0
2920_3000	4	0	0	0	0	0	0	0	0	0	0	0	0	17	31	40	12	0	0	0	0	0
2920_3005	6	0	0	0	0	0	0	0	0	0	0	1	19	20	40	19	1	0	0	0	0	0
2920_3010	5	0	0	0	0	0	0	0	0	0	0	7	37	40	14	2	0	0	0	0	0	0
2920_3015	5	0	0	0	0	0	0	0	0	1	5	46	44	4	0	0	0	0	0	0	0	0
2920_3020	6	0	0	0	0	0	0	6	40	32	16	5	1	0	0	0	0	0	0	0	0	0
2920_3025	3	0	0	0	0	0	0	10	78	12	0	0	0	0	0	0	0	0	0	0	0	0
2920_3030	4	0	0	0	0	0	0	2	45	44	9	0	0	0	0	0	0	0	0	0	0	0
2920_3035	3	0	0	0	0	0	0	0	0	24	50	26	0	0	0	0	0	0	0	0	0	0
2920_3040	3	0	0	0	0	0	0	0	0	4	60	36	0	0	0	0	0	0	0	0	0	0
2920_3045	4	0	0	0	0	0	0	0	6	42	50	2	0	0	0	0	0	0	0	0	0	0
2920_3050	5	0	0	0	0	0	0	6	25	38	27	4	0	0	0	0	0	0	0	0	0	0
2920_3055	6	0	0	0	1	18	35	30	14	2	0	0	0	0	0	0	0	0	0	0	0	0
2920_3100	6	0	0	4	13	33	28	20	2	0	0	0	0	0	0	0	0	0	0	0	0	0
2920_3105	6	0	7	29	34	17	10	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2920_3110	3	35	42	23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2920_3115	2	95	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2920_3120	1	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2925_2900	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100
2925_2905	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100
2925_2910	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100
2925_2915	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100
2925_2920	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	99
2925_2925	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	3	8	8	17	62
2925_2930	8	0	0	0	0	0	0	0	0	0	0	0	0	0	4	11	16	14	15	15	11	14
2925_2935	8	0	0	0	0	0	0	0	0	0	0	0	0	0	4	7	6	5	9	7	13	49
2925_2940	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	14	20	23	15	11	16
2925_2945	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	17	31	34	15	2
2925_2950	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	33	18	17	13	18	1	0
2925_2955	3	0	0	0	0	0	0	0	0	0	0	0	0	0	21	74	5	0	0	0	0	0
2925_3000	5	0	0	0	0	0	0	0	0	0	0	0	5	20	37	28	10	0	0	0	0	0
2925_3005	4	0	0	0	0	0	0	0	0	0	0	36	38	24	2	0	0	0	0	0	0	0
2925_3010	5	0	0	0	0	0	0	0	0	0	5	36	37	19	3	0	0	0	0	0	0	0
2925_3015	6	0	0	0	0	0	0	2	23	20	10	31	14	0	0	0	0	0	0	0	0	0
2925_3020	4	0	0	0	0	0	0	54	39	5	2	0	0	0	0	0	0	0	0	0	0	0

Pentad	n	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
2925_3025	4	0	0	0	0	0	2	79	18	1	0	0	0	0	0	0	0	0	0	0	0	0
2925_3030	4	0	0	0	0	0	0	8	18	38	36	0	0	0	0	0	0	0	0	0	0	0
2925_3035	3	0	0	0	0	0	0	0	0	24	65	11	0	0	0	0	0	0	0	0	0	0
2925_3040	7	0	0	0	0	2	3	3	4	29	57	2	0	0	0	0	0	0	0	0	0	0
2925_3045	7	0	0	0	0	1	11	19	16	21	21	11	0	0	0	0	0	0	0	0	0	0
2925_3050	6	0	0	0	0	13	27	29	15	13	3	0	0	0	0	0	0	0	0	0	0	0
2925_3055	5	0	0	0	9	30	46	14	1	0	0	0	0	0	0	0	0	0	0	0	0	0
2925_3100	6	0	3	21	43	19	12	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2925_3105	4	8	45	40	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2925_3110	3	82	17	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2925_3115	1	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2930_2900	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100
2930_2905	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100
2930_2910	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100
2930_2915	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100
2930_2920	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	8	11	20	58
2930_2925	8	0	0	0	0	0	0	0	0	0	0	0	0	0	1	12	17	17	18	12	13	10
2930_2930	8	0	0	0	0	0	0	0	0	0	0	0	0	3	15	24	28	18	6	2	4	0
2930_2935	10	0	0	0	0	0	0	0	0	0	0	0	2	21	31	16	18	3	3	3	1	2
2930_2940	10	0	0	0	0	0	0	0	0	0	0	0	2	4	7	14	11	21	21	18	1	1
2930_2945	8	0	0	0	0	0	0	0	0	0	0	0	0	1	10	11	9	6	26	36	1	0
2930_2950	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	20	56	21	0	0
2930_2955	8	0	0	0	0	0	0	0	0	0	0	0	0	1	13	31	21	18	8	7	1	0
2930_3000	6	0	0	0	0	0	0	0	0	0	0	0	21	29	28	8	10	4	0	0	0	0
2930_3005	5	0	0	0	0	0	0	0	0	0	0	32	45	19	3	1	0	0	0	0	0	0
2930_3010	4	0	0	0	0	0	0	0	0	0	0	56	37	5	2	0	0	0	0	0	0	0
2930_3015	5	0	0	0	0	0	0	0	0	4	7	48	36	5	0	0	0	0	0	0	0	0
2930_3020	6	0	0	0	0	0	0	11	37	22	16	10	4	0	0	0	0	0	0	0	0	0
2930_3025	5	0	0	0	0	0	1	9	37	52	1	0	0	0	0	0	0	0	0	0	0	0
2930_3030	7	0	0	0	0	5	11	36	19	19	9	1	0	0	0	0	0	0	0	0	0	0
2930_3035	6	0	0	0	0	18	15	14	17	28	8	0	0	0	0	0	0	0	0	0	0	0
2930_3040	7	0	0	0	9	18	13	14	14	30	2	0	0	0	0	0	0	0	0	0	0	0
2930_3045	5	0	0	0	0	14	31	40	11	4	0	0	0	0	0	0	0	0	0	0	0	0
2930_3050	5	0	0	9	34	43	12	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2930_3055	6	0	2	11	30	34	17	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2930_3100	5	4	43	42	10	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2930_3105	3	77	20	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2930_3110	2	91	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2935_2900	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100
2935_2905	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100
2935_2910	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100
2935_2915	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100
2935_2920	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	6	11	23	58
2935_2925	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	18	24	20	12	13	4	9
2935_2930	7	0	0	0	0	0	0	0	0	0	0	0	0	11	25	34	23	3	3	1	0	0
2935_2935	7	0	0	0	0	0	0	0	0	0	0	0	1	23	18	30	14	12	2	0	0	0

Pentad	n	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
2935_2940	5	0	0	0	0	0	0	0	0	0	0	0	18	35	35	11	1	0	0	0	0	0
2935_2945	8	0	0	0	0	0	0	0	0	0	0	0	11	28	27	14	6	6	5	3	0	0
2935_2950	7	0	0	0	0	0	0	0	0	0	0	0	0	2	9	21	44	16	5	3	0	0
2935_2955	7	0	0	0	0	0	0	0	0	0	0	0	0	1	19	13	24	32	10	1	0	0
2935_3000	6	0	0	0	0	0	0	0	0	0	0	0	0	7	34	18	16	19	6	0	0	0
2935_3005	5	0	0	0	0	0	0	0	0	0	0	0	4	11	43	32	10	0	0	0	0	0
2935_3010	6	0	0	0	0	0	0	0	0	0	7	22	34	19	16	2	0	0	0	0	0	0
2935_3015	9	0	0	0	0	0	0	5	22	24	14	24	7	2	1	1	0	0	0	0	0	0
2935_3020	4	0	0	0	0	0	0	58	38	3	1	0	0	0	0	0	0	0	0	0	0	0
2935_3025	3	0	0	0	0	0	15	72	13	0	0	0	0	0	0	0	0	0	0	0	0	0
2935_3030	4	0	0	0	0	18	29	38	15	0	0	0	0	0	0	0	0	0	0	0	0	0
2935_3035	7	0	0	0	29	38	15	8	5	1	4	0	0	0	0	0	0	0	0	0	0	0
2935_3040	7	0	3	18	27	23	16	11	2	0	0	0	0	0	0	0	0	0	0	0	0	0
2935_3045	8	0	9	21	20	23	14	7	3	3	0	0	0	0	0	0	0	0	0	0	0	0
2935_3050	7	0	5	23	25	24	15	7	1	0	0	0	0	0	0	0	0	0	0	0	0	0
2935_3055	5	0	17	37	26	16	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2935_3100	3	48	44	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2935_3105	2	82	18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2935_3110	1	100	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2940_2900	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100
2940_2905	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100
2940_2910	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	16	10	72
2940_2915	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	22	18	23	22	15
2940_2920	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	9	27	18	20	14	11
2940_2925	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	59	32	8	0	0	0
2940_2930	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13	75	11	1	0	0	0
2940_2935	7	0	0	0	0	0	0	0	0	0	0	0	0	0	6	8	29	15	14	14	14	0
2940_2940	9	0	0	0	0	0	0	0	0	0	0	0	2	9	12	27	10	13	8	10	9	0
2940_2945	6	0	0	0	0	0	0	0	0	0	1	27	28	30	11	3	0	0	0	0	0	0
2940_2950	7	0	0	0	0	0	0	0	0	0	17	11	10	7	23	26	6	0	0	0	0	0
2940_2955	8	0	0	0	0	0	0	0	0	0	2	10	6	11	39	22	9	1	0	0	0	0
2940_3000	6	0	0	0	0	0	0	0	0	0	0	7	9	25	40	17	2	0	0	0	0	0
2940_3005	5	0	0	0	0	0	0	0	0	0	0	0	6	19	56	15	4	0	0	0	0	0
2940_3010	6	0	0	0	0	0	0	0	0	0	0	17	27	32	14	8	2	0	0	0	0	0
2940_3015	7	0	0	0	0	0	0	0	3	21	35	22	10	8	1	0	0	0	0	0	0	0
2940_3020	5	0	0	0	0	0	0	1	22	52	24	1	0	0	0	0	0	0	0	0	0	0
2940_3025	4	0	0	0	0	0	0	16	47	35	2	0	0	0	0	0	0	0	0	0	0	0
2940_3030	5	0	0	0	0	1	29	25	44	1	0	0	0	0	0	0	0	0	0	0	0	0
2940_3035	6	0	0	0	1	13	13	28	40	5	0	0	0	0	0	0	0	0	0	0	0	0
2940_3040	6	0	0	6	21	19	26	22	6	0	0	0	0	0	0	0	0	0	0	0	0	0
2940_3045	6	0	16	15	18	11	27	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2940_3050	6	2	43	25	15	8	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2940_3055	5	19	28	36	16	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2940_3100	2	64	36	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2940_3105	2	84	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2945_2900	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100

Pentad	n	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
2945_2905	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100
2945_2910	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14	23	15	48
2945_2915	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	35	34	12	11	8
2945_2920	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	25	68	6	1	0	0
2945_2925	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	30	49	21	0	0	0	0
2945_2930	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	37	48	12	3	0	0	0
2945_2935	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	58	37	4	0	1	0	0
2945_2940	8	0	0	0	0	0	0	0	0	0	0	0	0	0	2	6	17	20	12	23	16	4
2945_2945	7	0	0	0	0	0	0	0	0	0	0	0	14	25	26	21	10	3	1	0	0	0
2945_2950	5	0	0	0	0	0	0	0	0	0	15	29	30	19	7	0	0	0	0	0	0	0
2945_2955	7	0	0	0	0	0	0	0	2	14	39	18	14	8	5	0	0	0	0	0	0	0
2945_3000	7	0	0	0	0	0	0	0	0	2	17	30	26	16	8	1	0	0	0	0	0	0
2945_3005	8	0	0	0	0	0	0	0	0	1	3	14	21	18	19	21	3	0	0	0	0	0
2945_3010	6	0	0	0	0	0	0	0	0	0	0	16	26	22	22	11	3	0	0	0	0	0
2945_3015	7	0	0	0	0	0	0	0	0	23	37	14	9	12	4	1	0	0	0	0	0	0
2945_3020	4	0	0	0	0	0	0	1	38	51	10	0	0	0	0	0	0	0	0	0	0	0
2945_3025	4	0	0	0	0	0	0	32	45	16	7	0	0	0	0	0	0	0	0	0	0	0
2945_3030	3	0	0	0	0	0	19	58	23	0	0	0	0	0	0	0	0	0	0	0	0	0
2945_3035	5	0	0	0	0	2	22	54	19	3	0	0	0	0	0	0	0	0	0	0	0	0
2945_3040	6	0	0	0	1	10	28	42	16	3	0	0	0	0	0	0	0	0	0	0	0	0
2945_3045	5	0	0	0	12	15	36	36	1	0	0	0	0	0	0	0	0	0	0	0	0	0
2945_3050	6	2	11	22	51	10	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2945_3055	3	51	36	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2945_3100	2	82	18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2950_2900	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100
2950_2905	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	98
2950_2910	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	19	25	14	40
2950_2915	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	63	27	7	1	1
2950_2920	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	25	56	19	0	0	0
2950_2925	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	27	36	30	4	0	0
2950_2930	5	0	0	0	0	0	0	0	0	0	0	0	0	0	3	44	36	11	6	0	0	0
2950_2935	5	0	0	0	0	0	0	0	0	0	0	0	0	6	10	42	36	6	0	0	0	0
2950_2940	6	0	0	0	0	0	0	0	0	0	0	0	4	10	9	20	46	11	0	0	0	0
2950_2945	5	0	0	0	0	0	0	0	0	0	0	0	0	2	9	26	59	4	0	0	0	0
2950_2950	6	0	0	0	0	0	0	0	0	0	0	2	7	25	38	21	7	0	0	0	0	0
2950_2955	9	0	0	0	0	0	0	0	2	5	2	11	21	25	19	12	3	0	0	0	0	0
2950_3000	8	0	0	0	0	0	5	11	13	27	13	19	11	1	0	0	0	0	0	0	0	0
2950_3005	10	0	0	0	0	0	1	6	7	3	12	9	26	29	6	1	0	0	0	0	0	0
2950_3010	6	0	0	0	0	0	0	0	7	12	27	28	19	7	0	0	0	0	0	0	0	0
2950_3015	5	0	0	0	0	0	0	0	4	62	24	7	3	0	0	0	0	0	0	0	0	0
2950_3020	4	0	0	0	0	0	0	0	16	47	34	3	0	0	0	0	0	0	0	0	0	0
2950_3025	3	0	0	0	0	0	0	0	28	48	24	0	0	0	0	0	0	0	0	0	0	0
2950_3030	4	0	0	0	0	0	1	30	67	2	0	0	0	0	0	0	0	0	0	0	0	0
2950_3035	5	0	0	0	5	18	29	36	12	0	0	0	0	0	0	0	0	0	0	0	0	0
2950_3040	5	0	0	3	30	29	30	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2950_3045	5	0	10	31	35	19	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

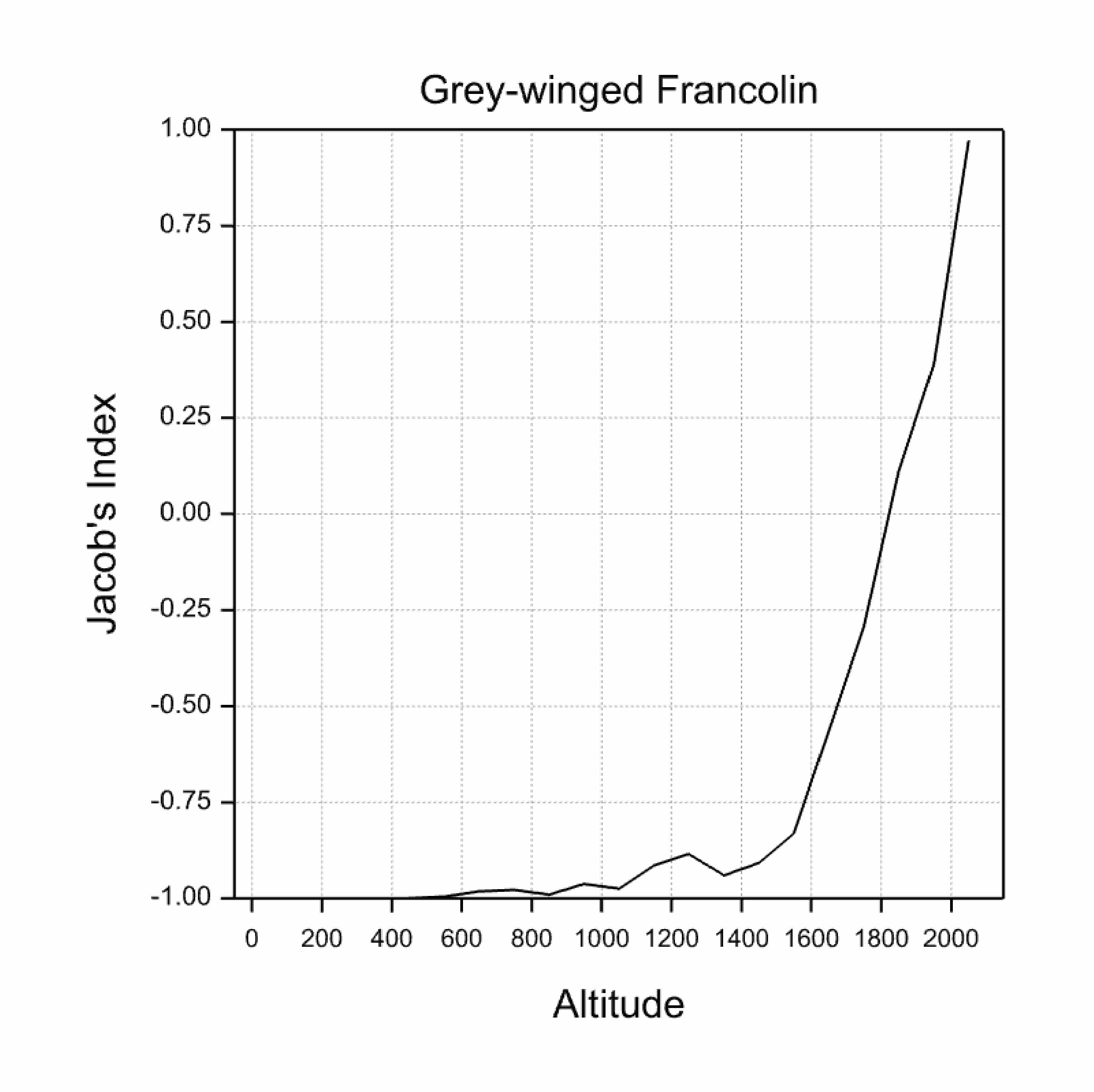
Pentad	n	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
2950_3050	3	0	29	57	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2950_3055	3	61	36	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2950_3100	2	98	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2955_2900	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	100
2955_2905	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	3	3	93
2955_2910	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	16	20	38	24
2955_2915	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	35	35	17	2	0
2955_2920	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	45	38	15	1	0	0
2955_2925	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	24	36	19	18	3	0	0
2955_2930	5	0	0	0	0	0	0	0	0	0	0	0	0	0	2	15	31	40	12	0	0	0
2955_2935	8	0	0	0	0	0	0	0	0	0	0	0	6	9	12	17	31	16	7	2	0	0
2955_2940	7	0	0	0	0	0	0	0	0	0	0	21	24	16	13	12	7	7	0	0	0	0
2955_2945	7	0	0	0	0	0	0	0	0	0	3	13	15	26	23	16	4	0	0	0	0	0
2955_2950	7	0	0	0	0	0	0	0	0	0	2	12	20	33	24	6	3	0	0	0	0	0
2955_2955	5	0	0	0	0	0	0	0	0	0	0	4	32	53	9	2	0	0	0	0	0	0
2955_3000	9	0	0	0	0	0	1	3	1	4	5	13	48	22	3	0	0	0	0	0	0	0
2955_3005	9	0	0	0	0	17	21	15	14	9	6	5	8	5	0	0	0	0	0	0	0	0
2955_3010	7	0	0	0	0	6	25	30	18	9	8	4	0	0	0	0	0	0	0	0	0	0
2955_3015	5	0	0	0	0	7	14	20	26	33	0	0	0	0	0	0	0	0	0	0	0	0
2955_3020	5	0	0	0	0	0	1	9	45	39	6	0	0	0	0	0	0	0	0	0	0	0
2955_3025	6	0	0	0	0	0	8	21	28	28	13	2	0	0	0	0	0	0	0	0	0	0
2955_3030	4	0	0	0	0	10	12	44	34	0	0	0	0	0	0	0	0	0	0	0	0	0
2955_3035	5	0	0	0	0	1	11	60	26	2	0	0	0	0	0	0	0	0	0	0	0	0
2955_3040	5	0	0	1	6	39	45	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2955_3045	4	0	10	35	48	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2955_3050	3	37	52	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2955_3055	2	91	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2955_3100	2	83	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix C

Altitude preference plots for gamebirds

In Chapter 2, the altitude preference curves for six species of spurfowl and partridges (the gamebirds) occurring in the study area in KwaZulu-Natal were presented compressed into a single figure (Figure 2.8). In this appendix, the one-page plots, as presented for the species used to illustrate the method of Chapter 2, are presented. The figures include the distribution maps for the study area.

Grey-winged Francolin, *Francolinus africanus*



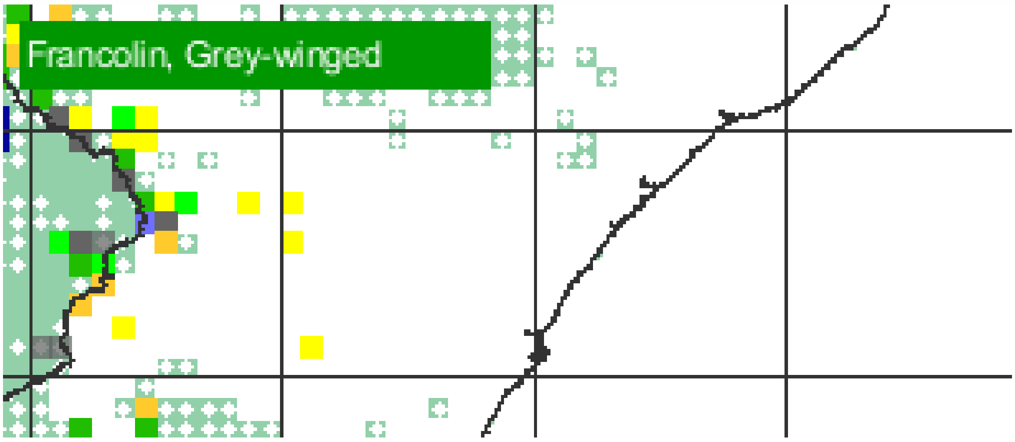
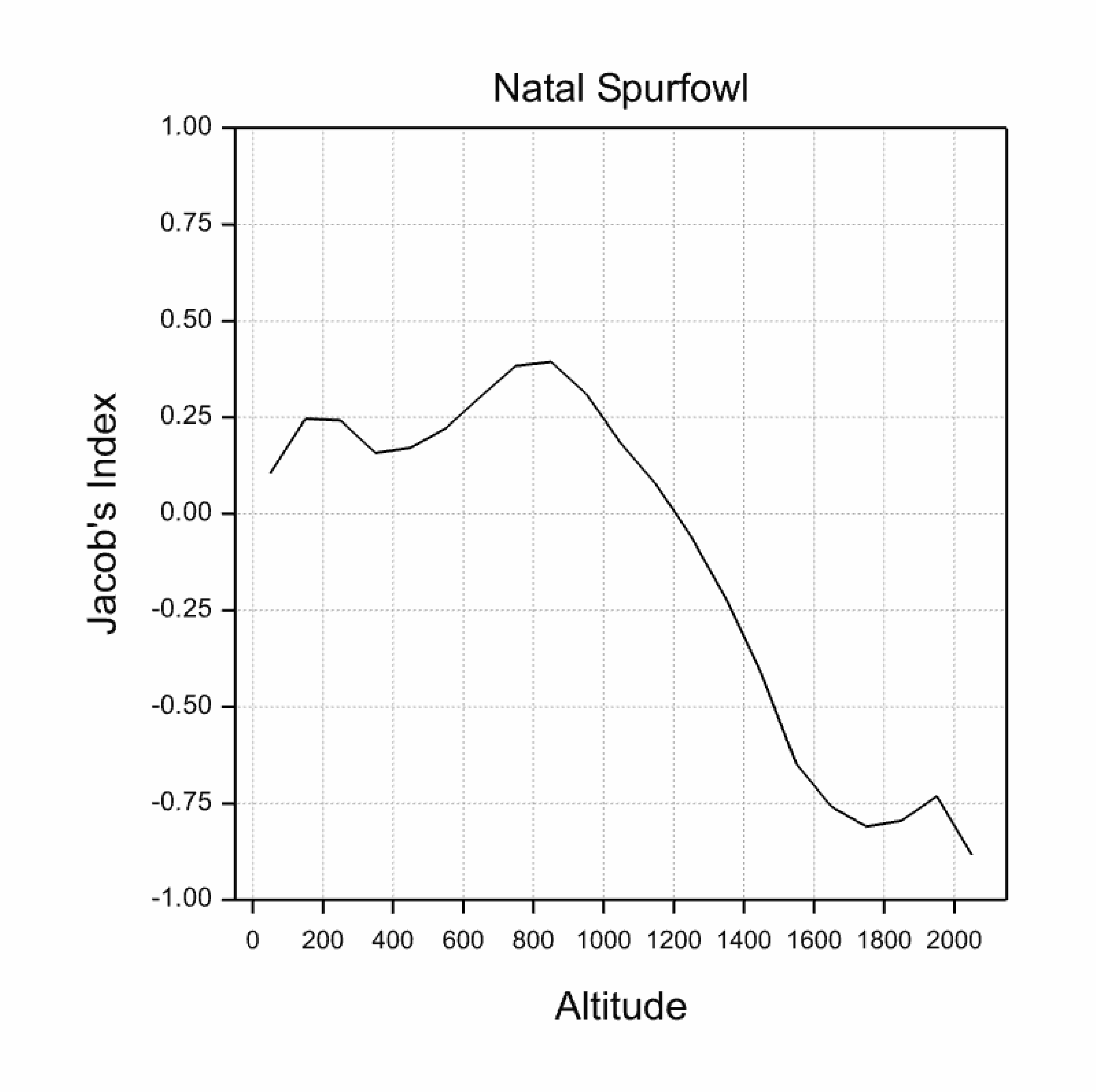


Figure C.1. The altitudinal preference curve for the Grey-winged Francolin and the distribution map for study transect in KwaZulu-Natal.

Natal Spurfowl, *Pternistis natalensis*



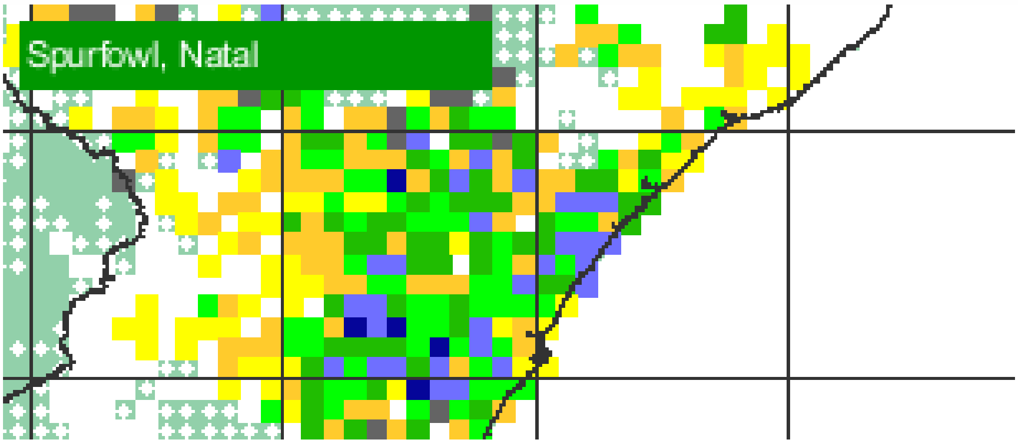
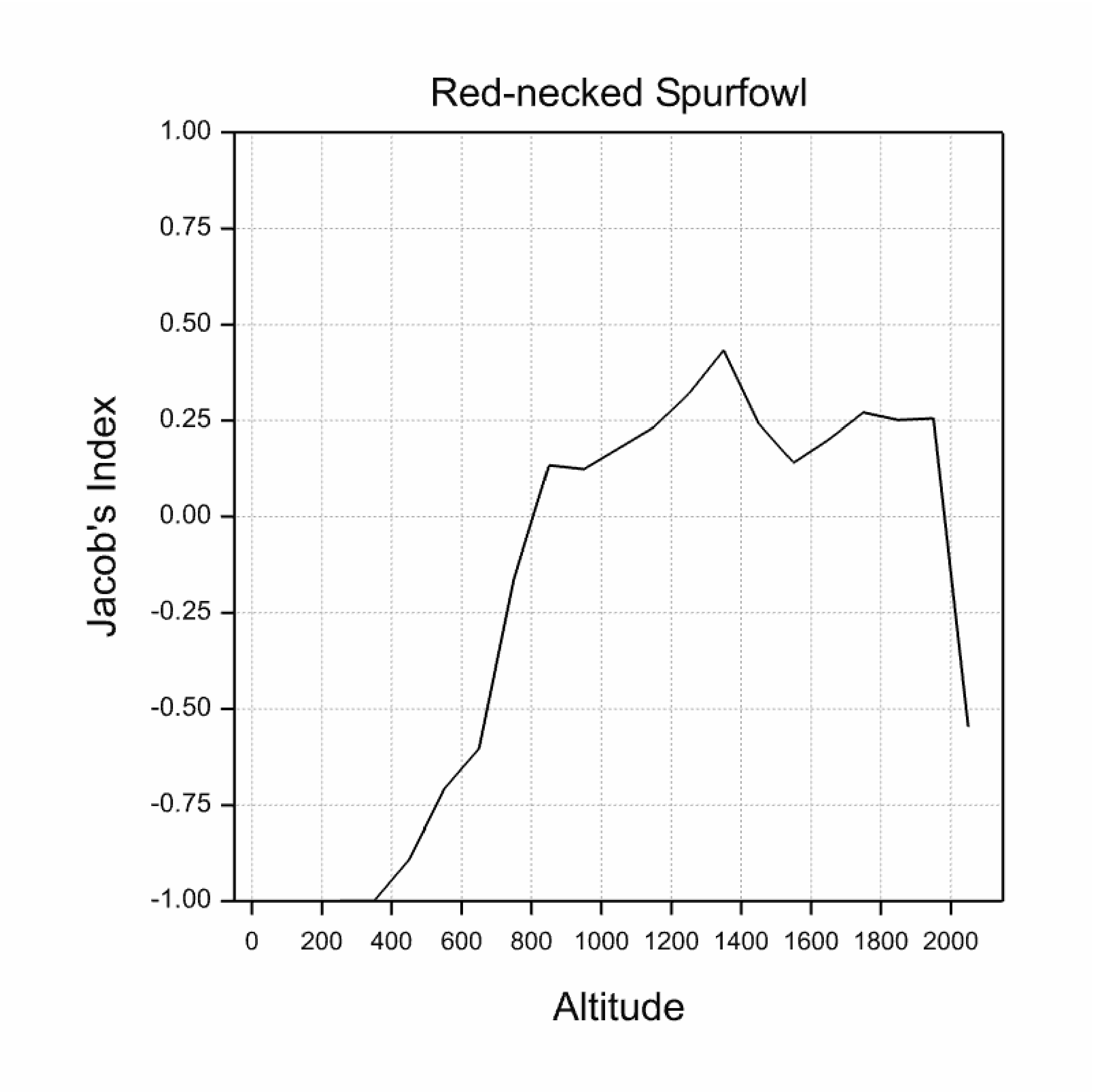


Figure C.2. The altitudinal preference curve for the Natal Spurfowl and the distribution map for study transect in KwaZulu-Natal.

Red-necked Spurfowl, *Pternistis afer*



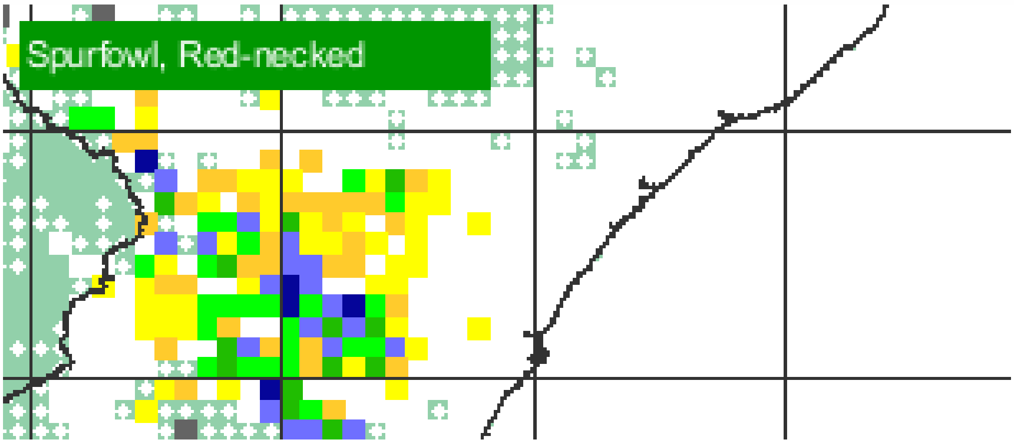
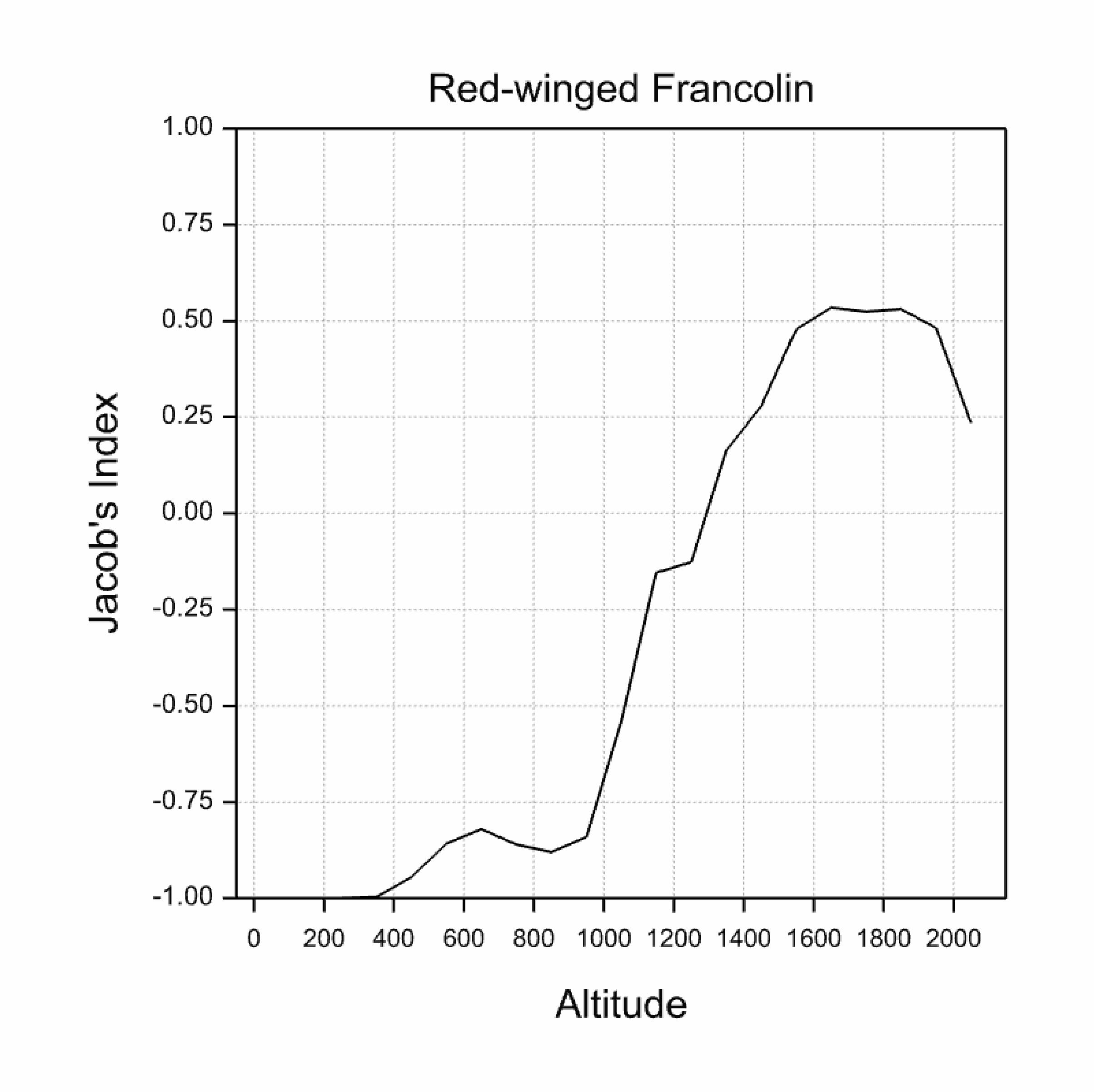


Figure C.3. The altitudinal preference curve for the Red-necked Spurfowl and the distribution map for study transect in KwaZulu-Natal.

Red-winged Francolin, *Francolinus levaillantii*



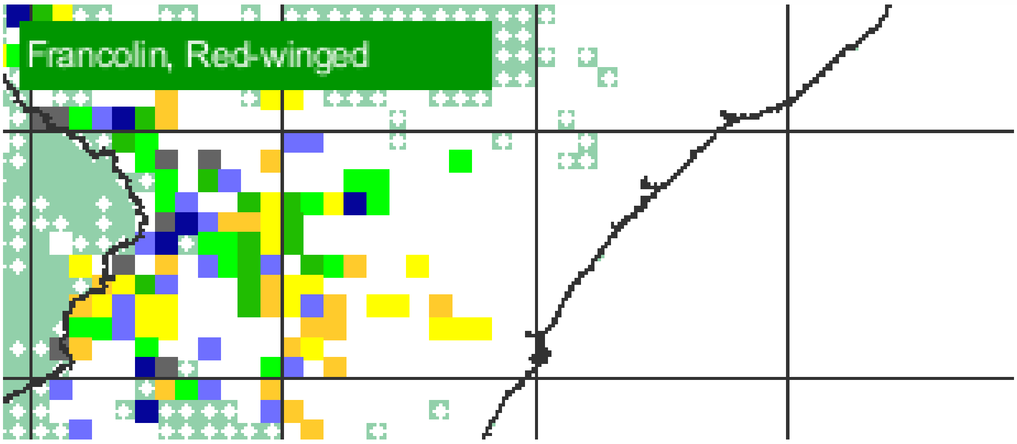
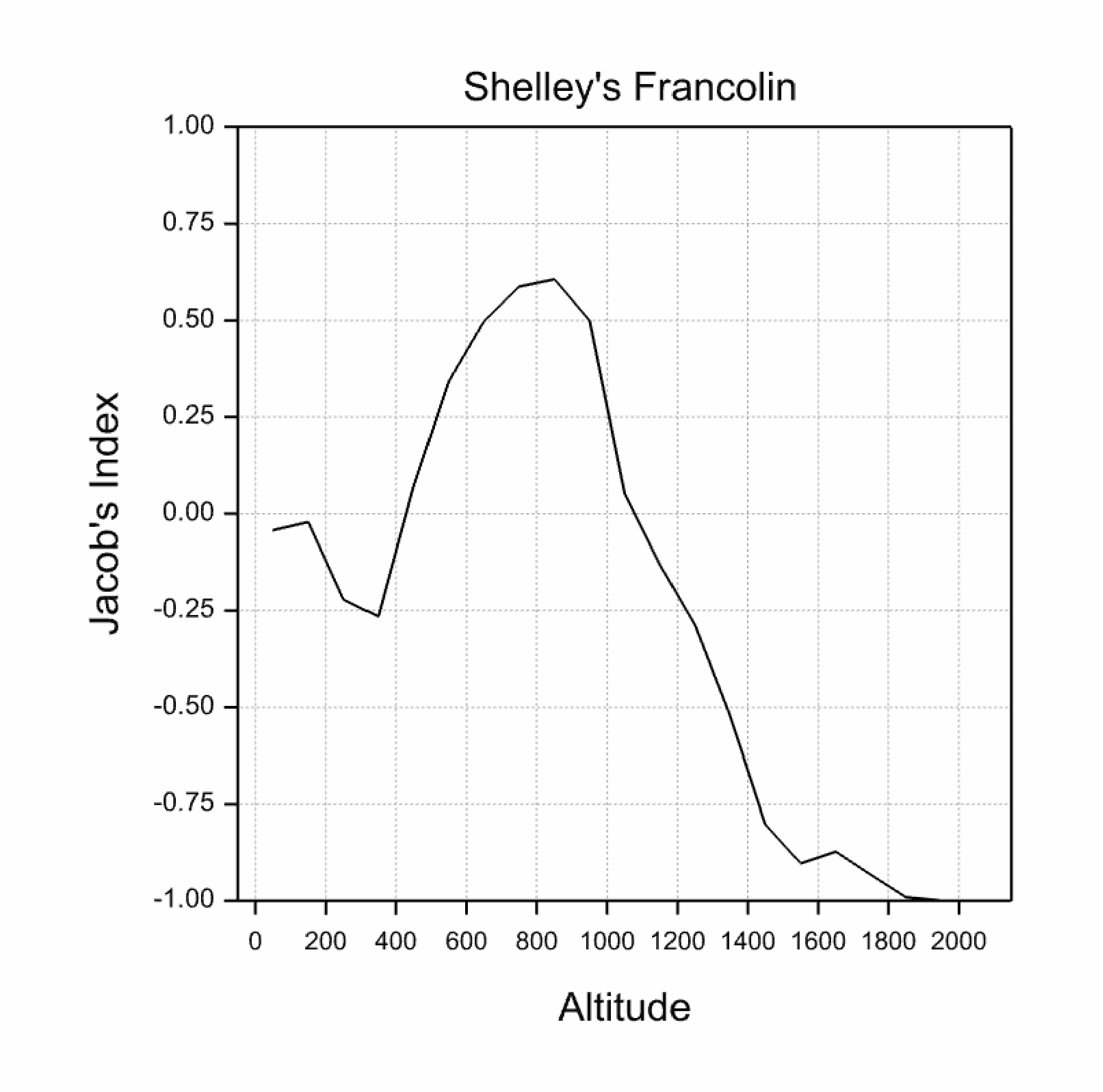


Figure C.4. The altitudinal preference curve for the Red-winged Francolin and the distribution map for study transect in KwaZulu-Natal.

Shelley’s Francolin, *Francolinus shelleyi*



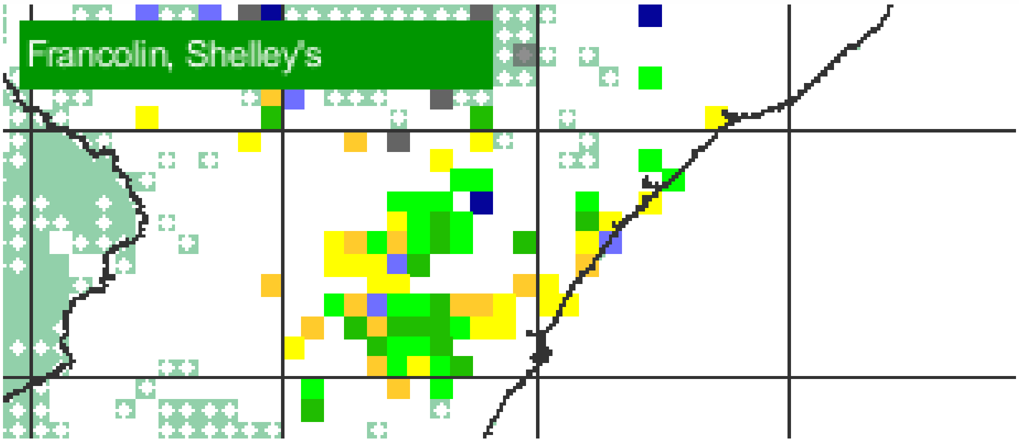
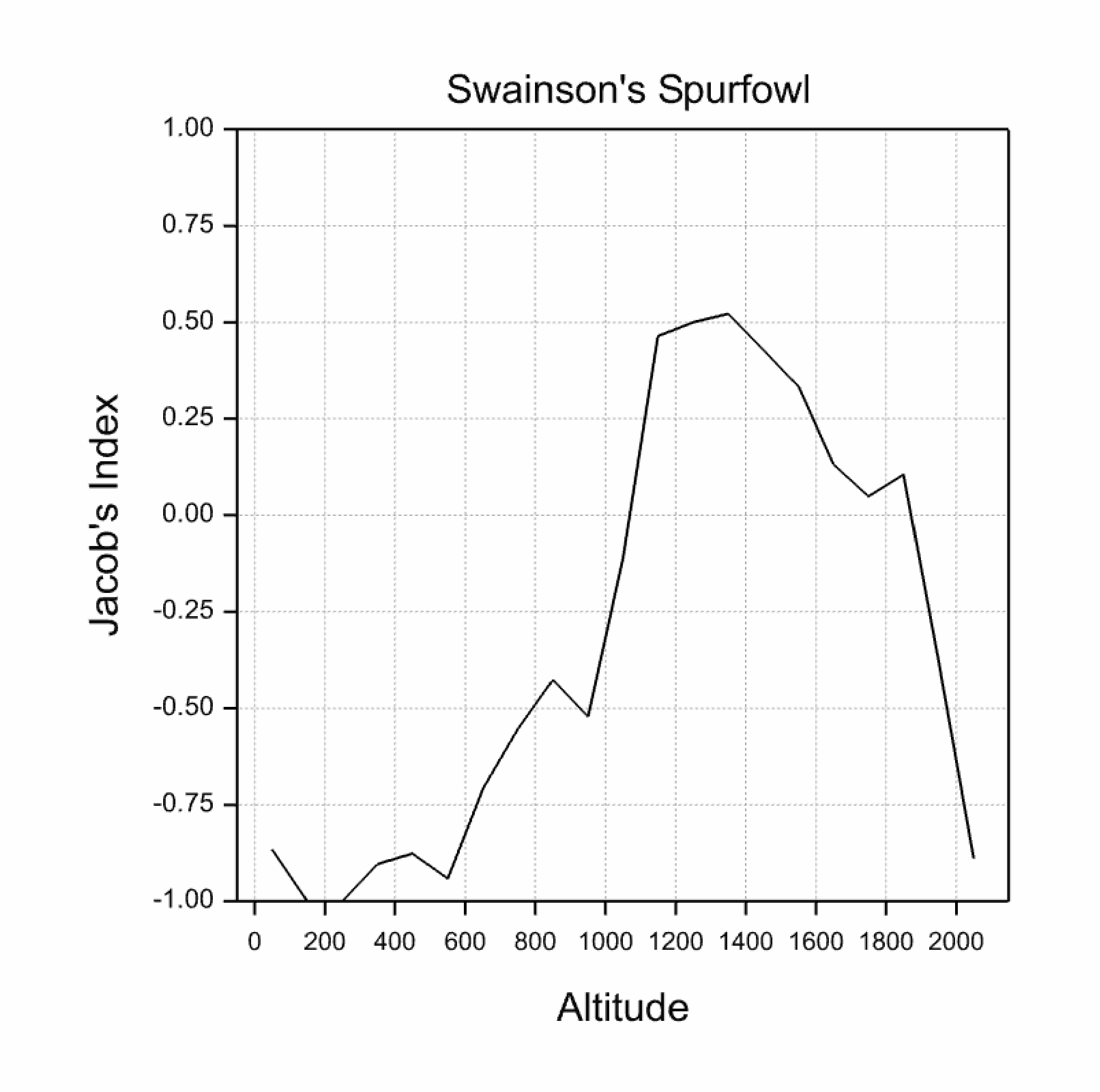


Figure C.5. The altitudinal preference curve for the Shelley’s Francolin and the distribution map for study transect in KwaZulu-Natal.

Swainson's Spurfowl, *Pternistis swainsonii*



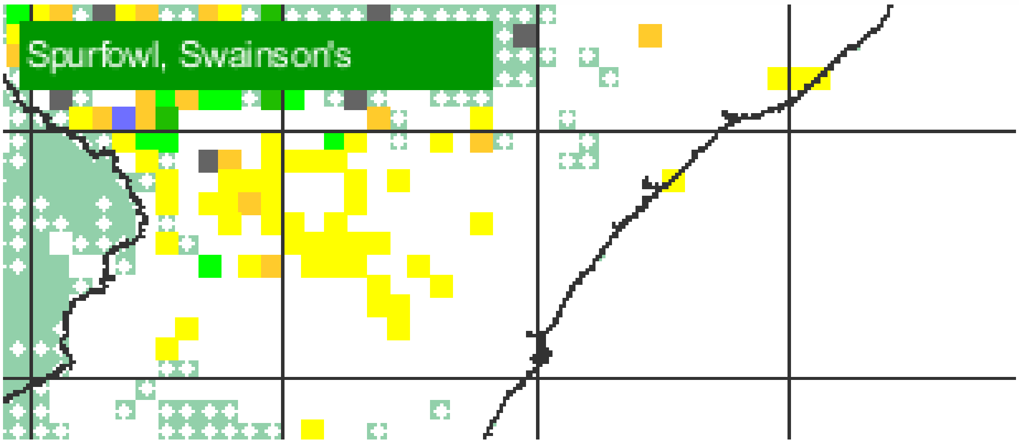


Figure C.6. The altitudinal preference curve for the Swainson's Spurfowl and the distribution map for study transect in KwaZulu-Natal

Appendix D

Summer and winter altitude preference curves for a further 29 species

In Chapter 3, the summer and winter altitude preference plots for 10 carefully selected species occurring in the study area in KwaZulu-Natal were presented (Figures 3.1 to 3.10). The objective of this appendix is to provide these plots, with some interpretive text, for a further 29 species. This enables a better evaluation of the approach than is possible when only 10 species are considered.

African Dusky Flycatcher, *Muscicapa adusta*

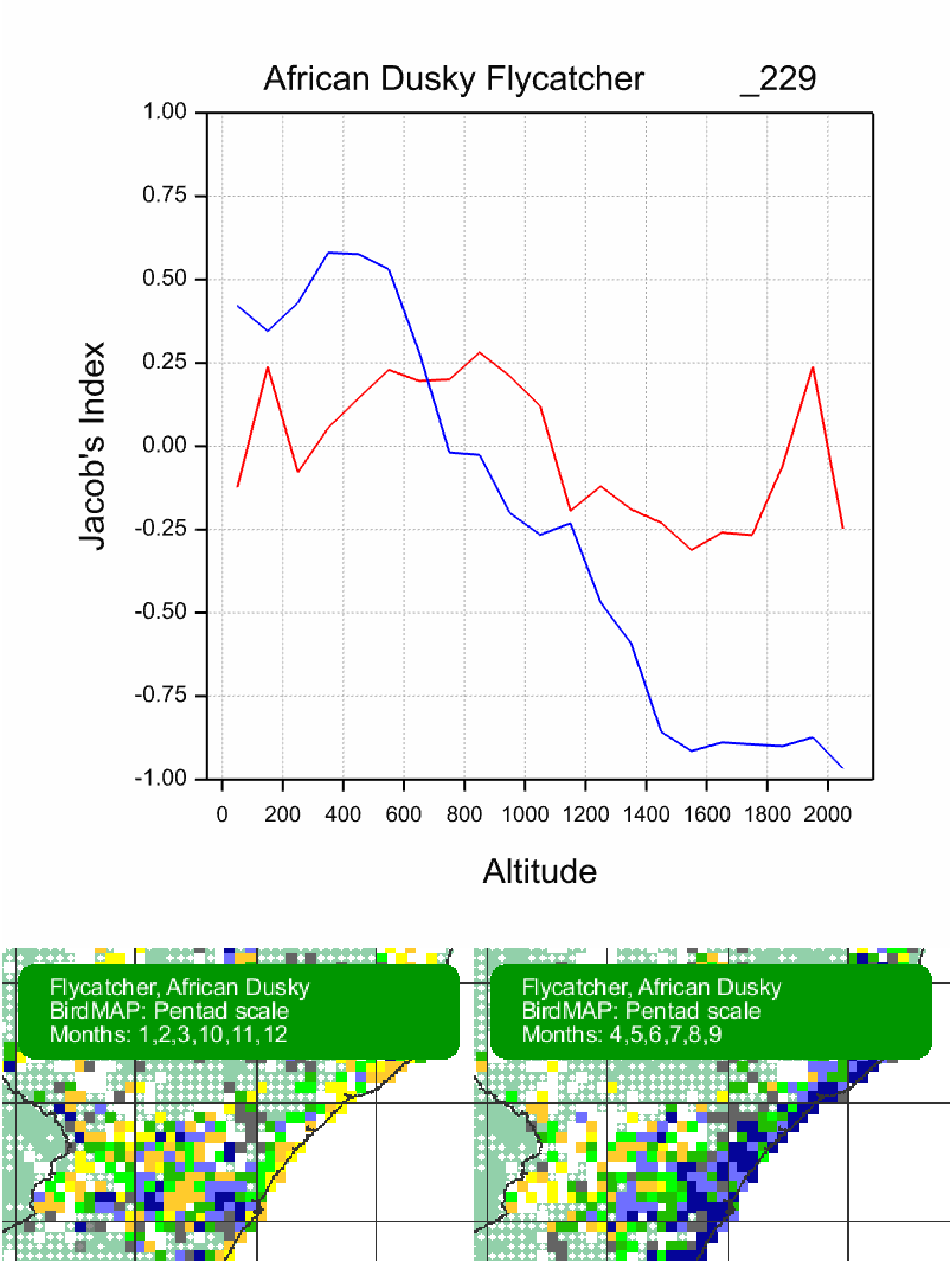


Figure D.1. The altitudinal preference curves for summer and for winter for the African Dusky Flycatcher, and the summer and winter distribution maps for study transect in KwaZulu-Natal.

The summer altitudinal preference line (red line) is fairly flat (Figure D.1). This implies that the distribution of African Dusky Flycatcher in summer is more or less in proportion to the amount of area available at any given altitude. This is confirmed by the summer distribution map (Figure D.1).

In winter (blue line) there is almost total avoidance of areas above 1400 m with scattered records above this altitude; the altitudinal preference line for winter does not reach –1 for these high altitudes, indicating that there are still records at high altitudes, and that the species is a partial migrant (Figure D.1). Below 800 m there are disproportionately more African Dusky Flycatchers than what one would expect given the amount of area available below this altitude. This is confirmed by the winter distribution map (Figure D.1). The most preferred altitude in winter is around 400 m. The preference line does not reach 1.00 at this preferred altitude because not all birds are concentrated at this altitude. The altitude preference is not as strong at sea-level as it is at around 400 m but there is still a clear preference for coastal areas as opposed to higher altitude areas above 800 m in winter.

African Dusky Flycatcher distribution ranges up to about 2000 m on the Drakensberg escarpment during summer in KwaZulu-Natal (Little and Bainbridge 1992). During winter, there is altitudinal movement to the coast (Berruti et al. 1994). In conjunction with this altitudinal movement, this species is also considered to be a coastal migrant from the Western Cape and Eastern Cape spending winter along the warmer east coast (Berruti et al. 1994, Johnson 1997a).

African Stonechat, *Saxicola torquata*

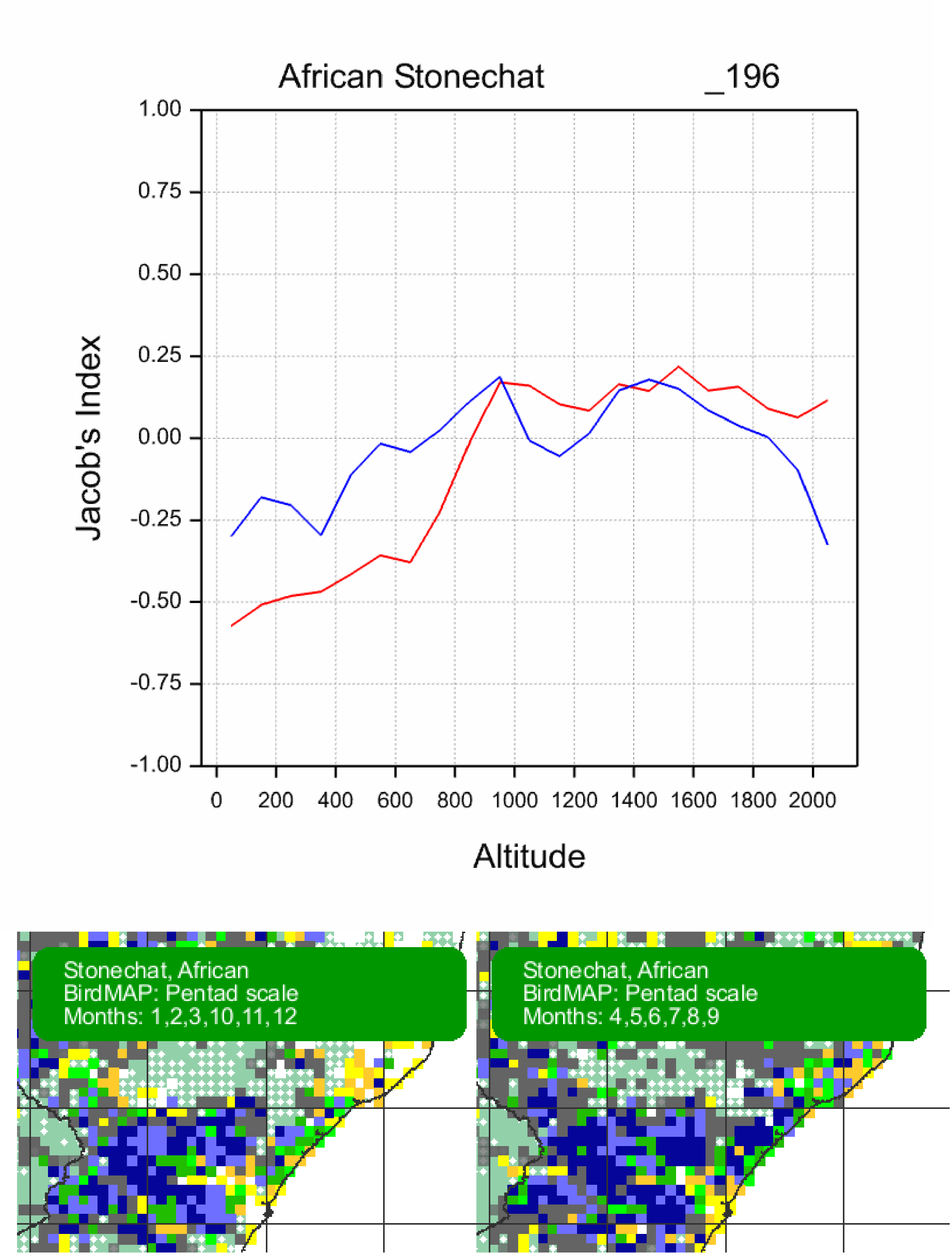


Figure D.2. The altitudinal preference curves for summer and for winter for the African Stonechat, and the summer and winter distribution maps for study transect in KwaZulu-Natal.

African Stonechat occurs from sea-level to higher altitudes above 1000 m throughout the year (Figure D.2).

African Stonechats are preferentially selecting altitudes above 900 m in summer. Above this altitude there are slightly more birds than one would expect given the area of land available. There is not complete avoidance below 900 m. Some birds are present at these lower altitudes but less than one would expect given the area. In winter African Stonechats have a preference for areas at approximately 600–1800 m. Below 600 m and above 1800 m, there are fewer birds than expected given the area.

It is generally regarded as a species of high-altitude grasslands, but in southern Africa it occurs down to sea-level. It is found in relatively moist, open habitats with rank growth of grass and herbs and scattered shrubs (Harrison 1997).

African Stonechat is a partial altitudinal migrant. Osborne and Tigar (1990) noted a decrease in both reporting rate and abundance in winter. An unknown fraction of the population moves to lower altitudes in winter, were it is more readily observed by atlasers in more accessible areas resulting in an increase in reporting rate (Harrison 1997). A study of altitudinal migration in KwaZulu-Natal by Harrison and Navarro (1992) used atlas data and showed that there was a drop in reporting rates at high altitudes in winter. This drop was matched by a simultaneous increase in reporting rates at lower altitudes. They reasoned that this reflected an intolerance of extreme winter conditions on the high escarpment. Oatley (2017) also supports the notion of African Stonechat being an altitudinal migrant: “Populations of this widespread species which spend the summer months and breed at high altitudes in KwaZulu-Natal and Lesotho, swell the numbers of resident populations at lower levels in the winter months.” This statement is clearly supported by the data as displayed in the altitudinal preference curves and distribution maps.

Alpine Swift, *Apus melba*

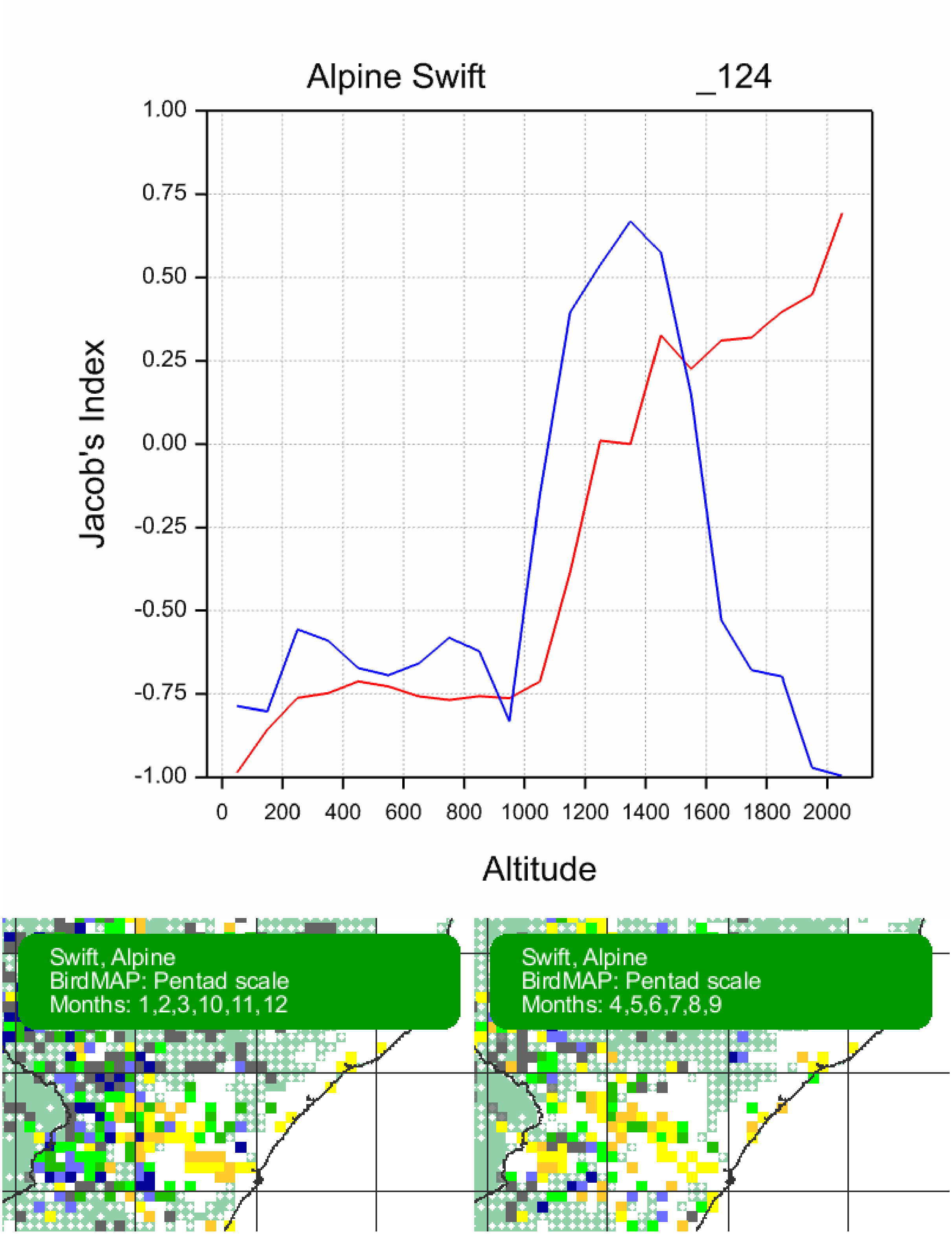


Figure D.3. The altitudinal preference curves for summer and for winter for the Alpine Swift, and the summer and winter distribution maps for study transect in KwaZulu-Natal.

In summer there is total avoidance by Alpine Swifts of areas at sea-level and only handfuls of birds at 100–1000 m (Figure D.3). Above 1000 m the number of Alpine Swifts increases to be in proportion to the amount of land available at around 1300 m. Above 1300 m there are more Alpine Swifts than one would expect given the amount of area available at these high altitudes. Altitude preference increases with increasing altitude above 1300 m.

In winter some Alpine Swifts are present at sea-level to 1000 m, but far less than one would expect given the area available in this altitude range. Alpine Swifts are preferentially choosing altitudes between 1100 m and 1500 m with main altitude preference at 1300–1400 m. Above 1600 m there are far fewer birds than one would expect and there is almost total avoidance of altitudes above 1900 m.

Alpine Swift occurs at all altitudes but is most abundant in Alpine Grasslands, where the majority of its breeding sites lie (Little and Bainbridge 1992, Brooke 1997). It nests colonially in narrow cracks on cliff faces and breeds during summer (Cyrus and Robson 1980). During winter it is absent from the highest sections of the Drakensberg range due to the severe winter conditions that occur there (Brooke 1997). Brown and Barnes (1984) did not record Alpine Swifts in the Alpine Belt (above 2865 m) in winter, although they are likely to breed at this altitude. Only small numbers of birds were recorded at slightly lower altitudes in Giant’s Castle Game Reserve in winter.

Alpine Swift feeds at great heights in winter skies that it often escapes detection, thus resulting in a reduction in winter reporting rates (Brooke 1997), which is visible in the winter distribution map (Figure D.3), with fewer coloured pentads in grid cells 2929 and 2930.

Ashy Flycatcher, *Muscicapa caerulescens*

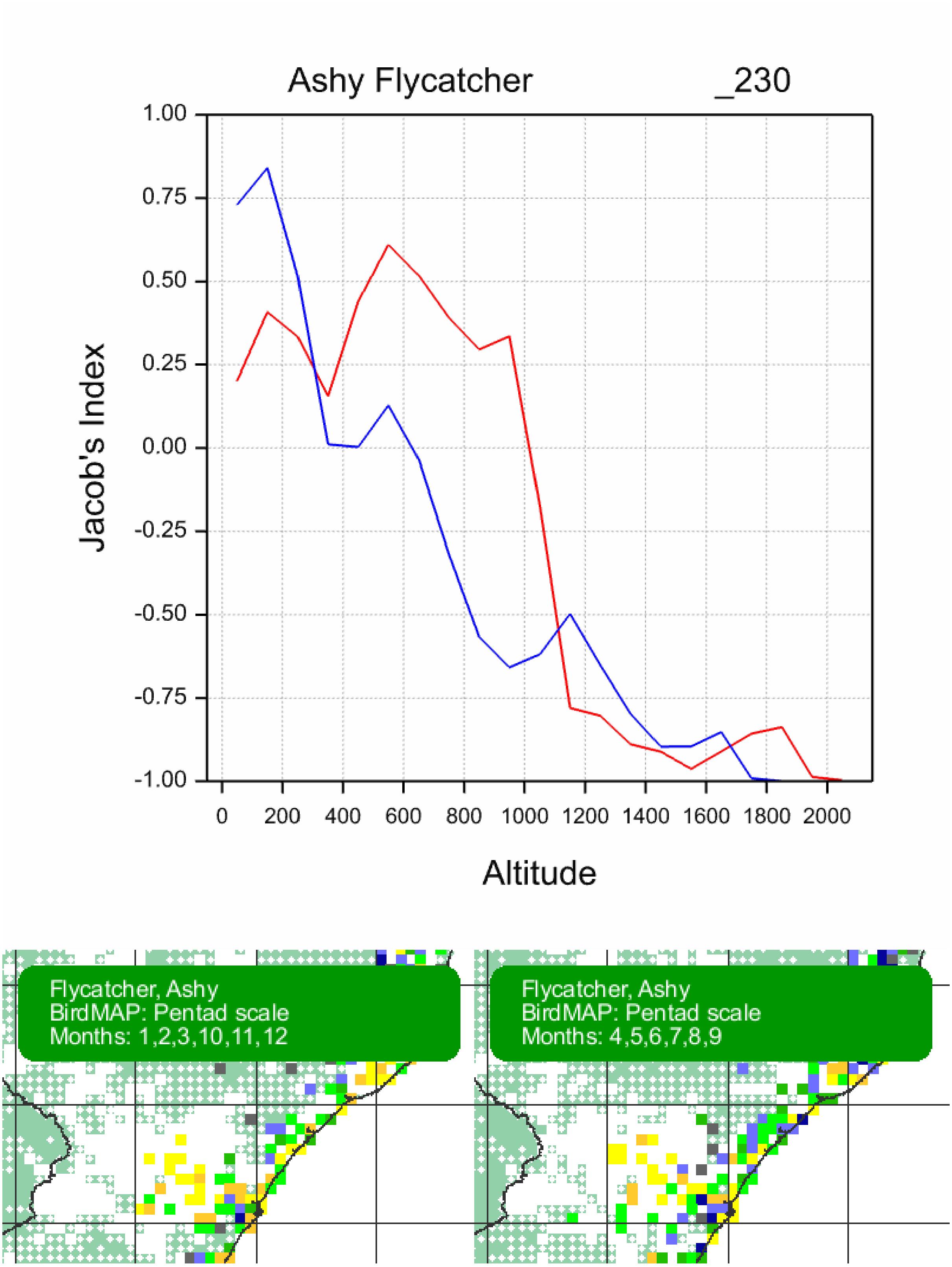


Figure D.4. The altitudinal preference curves for summer and for winter for the Ashy Flycatcher, and the summer and winter distribution maps for study transect in KwaZulu-Natal.

In summer there are more Ashy Flycatchers from sea-level up to 1000 m than one would expect given the amount of the area in this altitude range (Figure D.4). Main altitude preference is 500–600 m. Above 1000 m there are fewer birds than one would expect given the area available and above 1200 m there is almost total avoidance with only a few scattered records. There is complete avoidance of altitudes above 2000 m.

In winter main altitude preference of Ashy Flycatcher is sea-level to 200 m. The general trend in winter is that altitude preference decreases with increasing altitude. The number of birds and the amount of land available are in proportion around 400 m. Above 400 m, there are fewer birds than one would expect given the area. There is total avoidance of areas of 1800 m in winter.

Ashy Flycatcher is found along the coast in coastal forest and riverine woodland. During summer it extends slightly further inland and can be found in evergreen forest (Cyrus and Robson 1980). Breeding takes place during the wet season in summer from October to December (Cyrus and Robson 1980). Due to changes in conspicuousness, there is a small decrease in reporting rate during and shortly after the breeding season (Johnson 1997b). This decrease in reporting rate however does not affect the distribution maps.

The altitudinal preference curves and distribution maps show evidence for altitudinal migration, with birds moving downhill in winter.

Barn Swallow, *Hirundo rustica*

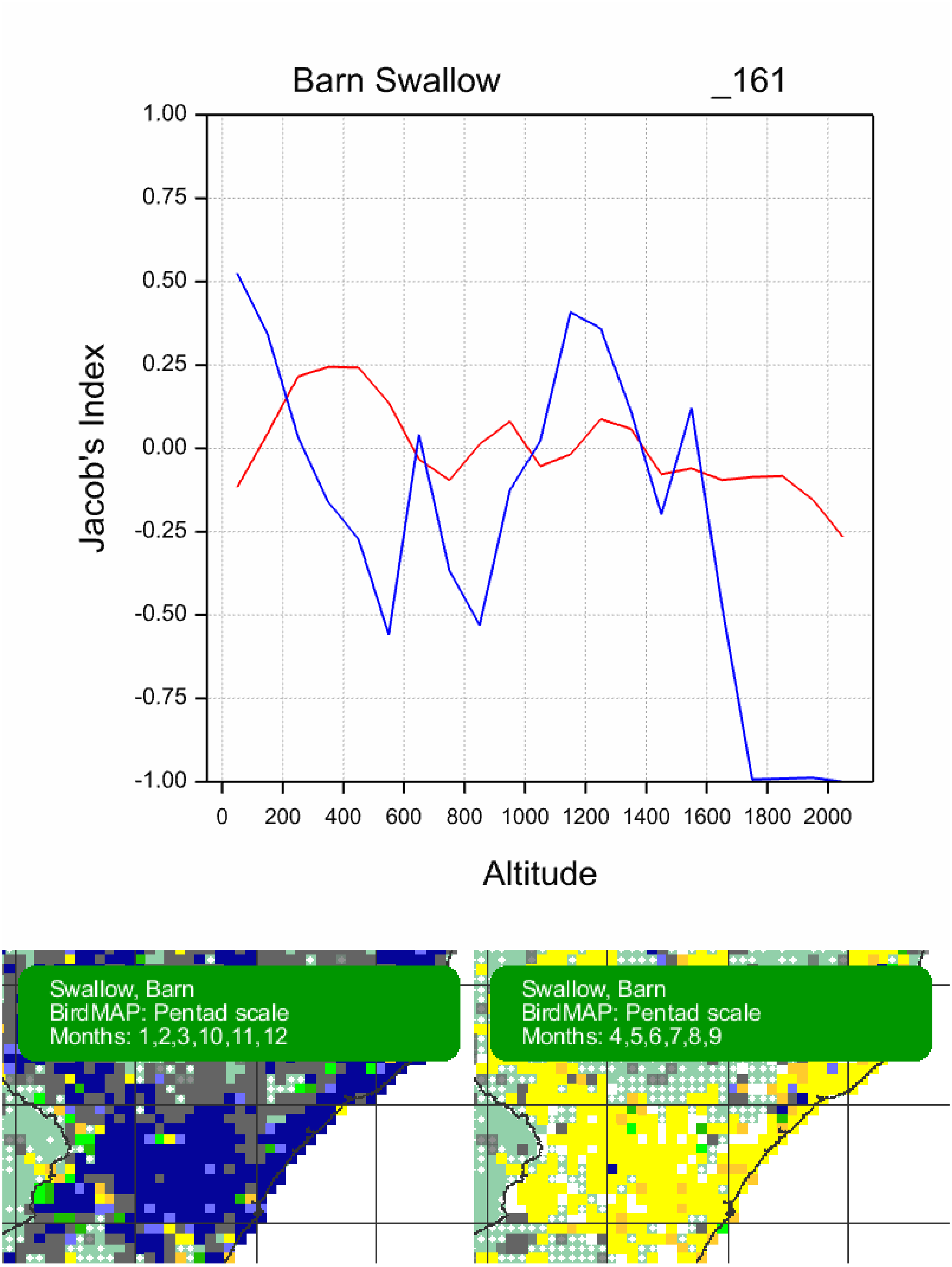


Figure D.5. The altitudinal preference curves for summer and for winter for the Barn Swallow, and the summer and winter distribution maps for study transect in KwaZulu-Natal.

Barn Swallow shows little altitudinal preference in summer. The distribution of Barn Swallow in summer is more or less in proportion to the amount of area available at any given altitude (Figure D.5). There is a slight preference for altitudes 100–600 m in summer.

Barn Swallow is a Palearctic migrant (Little and Bainbridge 1992). It is present in winter in KwaZulu-Natal but there are substantially fewer birds than in summer. Barn Swallow shows little altitudinal preference in winter, as in summer, expect for high altitudes (above 1800 m), which are avoided.

Barratt’s Warbler, *Bradypterus barratti*

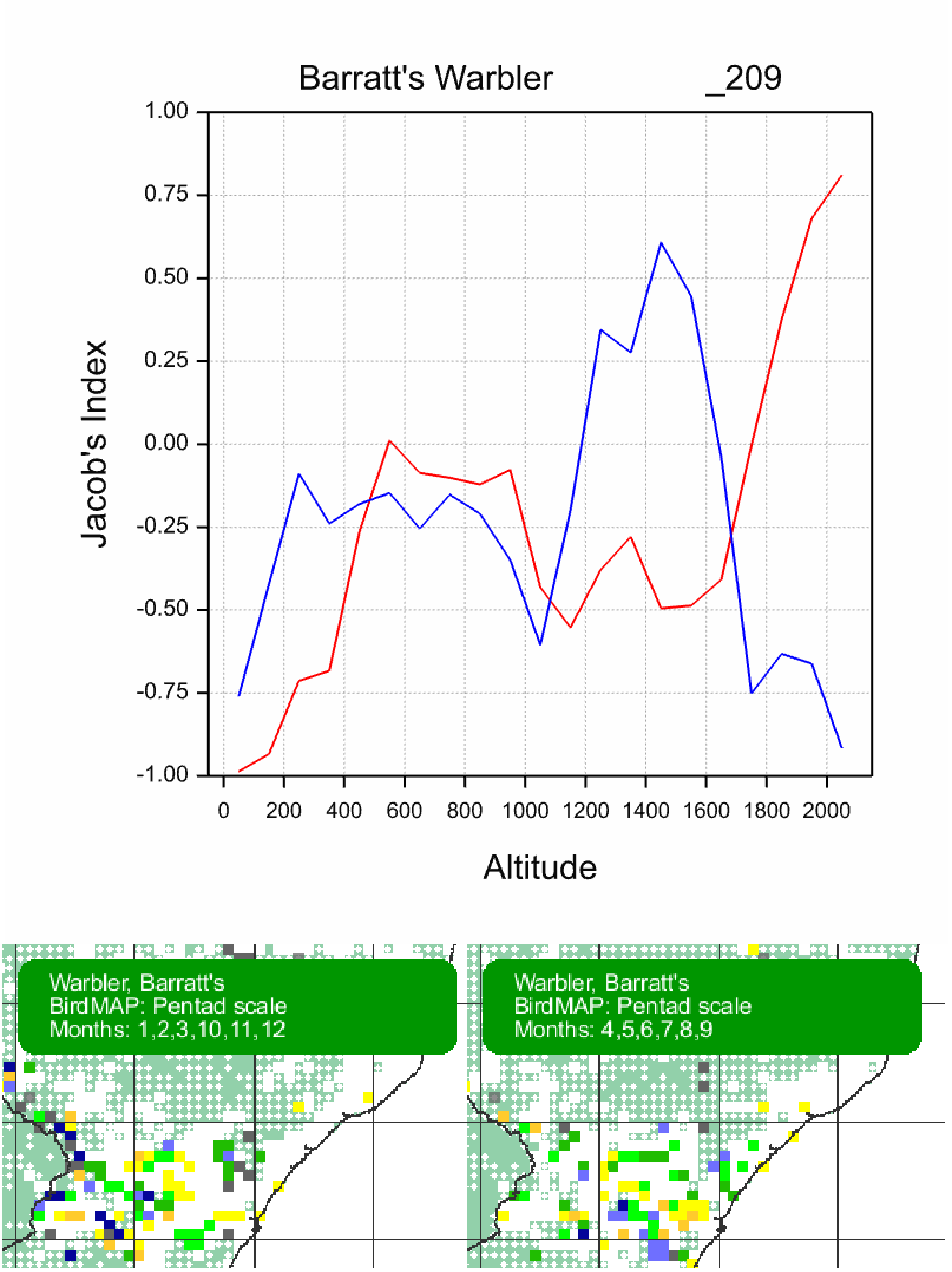


Figure D.6. The altitudinal preference curves for summer and for winter for the Barratt’s Warbler, and the summer and winter distribution maps for study transect in KwaZulu-Natal.

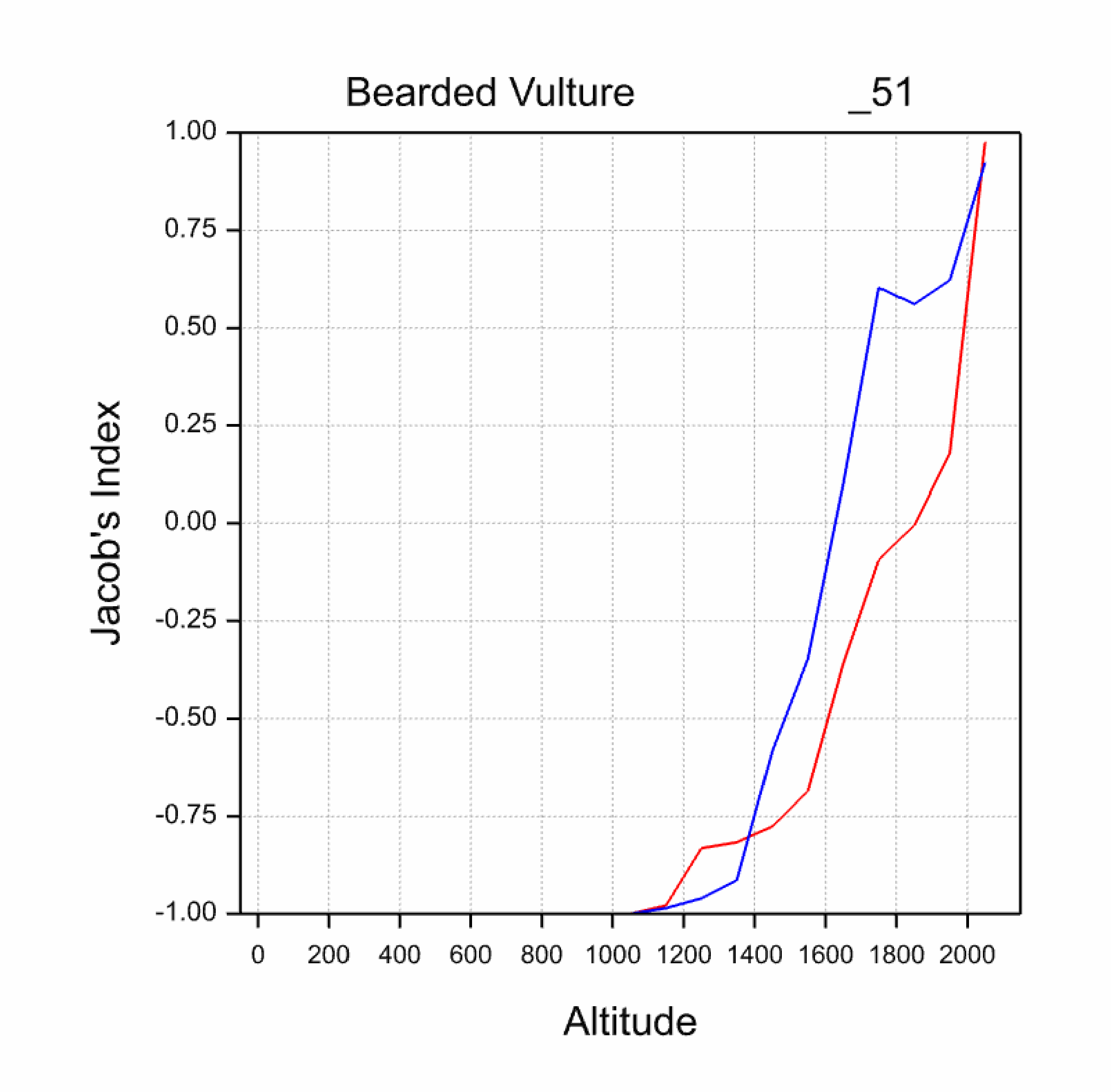
Barratt’s Warbler is preferentially selecting altitudes above 1800 m in summer (Figure D.6). Some birds are present below this altitude but there are fewer than one would expect given the area available. There is almost total avoidance of coastal areas in summer.

In winter there are more Barratt’s Warblers than one would expect given the area at 1200–1600 m, with main preference at 1400–1500 m. Above 1700 m altitude preference drops off markedly to nearly total avoidance of areas at 2000 m. Some warblers do occur between sea-level and 1200 m but there are fewer than one would predict given the land available.

Barratt’s Warbler is a cover-loving species occurring in or near the ground in scrub vegetation on the fringes of evergreen forests, extending in *Leucosidea* scrub to altitudes of 2133 m in KwaZulu-Natal (Oatley 2017, Cyrus and Robson 1980). In the Sani Pass, which lies grid cell 2929 in the study transect, Barratt’s Warbler has been recorded up to 2400 m in summer (Little and Bainbridge 1992). Barratt’s Warbler also occurs in gullies with dense vegetation in the foothills of the Drakensberg Mountains (Cyrus and Robson 1980). Barratt’s Warbler is almost always detected by its frequent calls, especially during summer when it breeds (Berruti 1997a).

Oatley (2017) supports the notion that Barratt’s Warbler is an altitudinal migrant: “There is a strong altitudinal movement in winter, possibly total from the highest levels, to forests between the 900 m contour and the coast.” The data analysis is in agreement with there being an almost complete migration from the highest levels in the Drakensberg to lower altitudes in winter. The analysis suggests that the bird populations at high altitudes are moving into forests and swelling numbers at 1200–1600 m, instead of the lower range suggested by Oatley (2017).

Bearded Vulture, *Gypaetus barbatus*



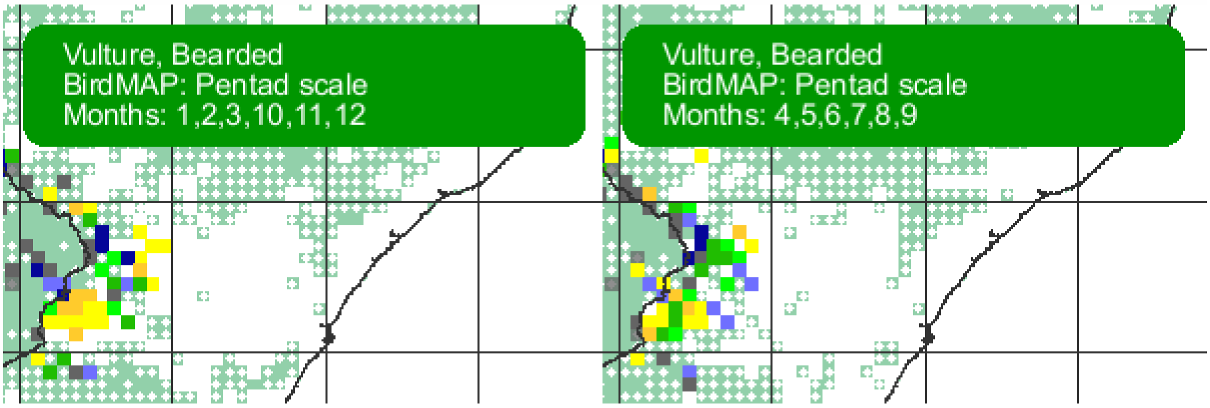


Figure D.7. The altitudinal preference curves for summer and for winter for the Bearded Vulture, and the summer and winter distribution maps for study transect in KwaZulu-Natal.

There are disproportionately more Bearded Vultures above 1900 m in summer and above 1600 m in winter (Figure D.7). There is almost complete avoidance of altitudes 1000–1300 m and there is total avoidance of altitudes below 1000 m throughout the year.

Bearded Vulture is resident and occurs at high altitudes in the Drakensberg Range (Cyrus and Robson 1980). It breeds mainly in caves high up on large cliffs in midwinter. Pairs nest at the same site each year and use this area as a roost outside the breeding season (Brown 1997). Bearded Vulture occasionally ranges to lower altitudes to feed (Cyrus and Robson 1980).

Bush Blackcap, *Lioptilus nigricapillus*

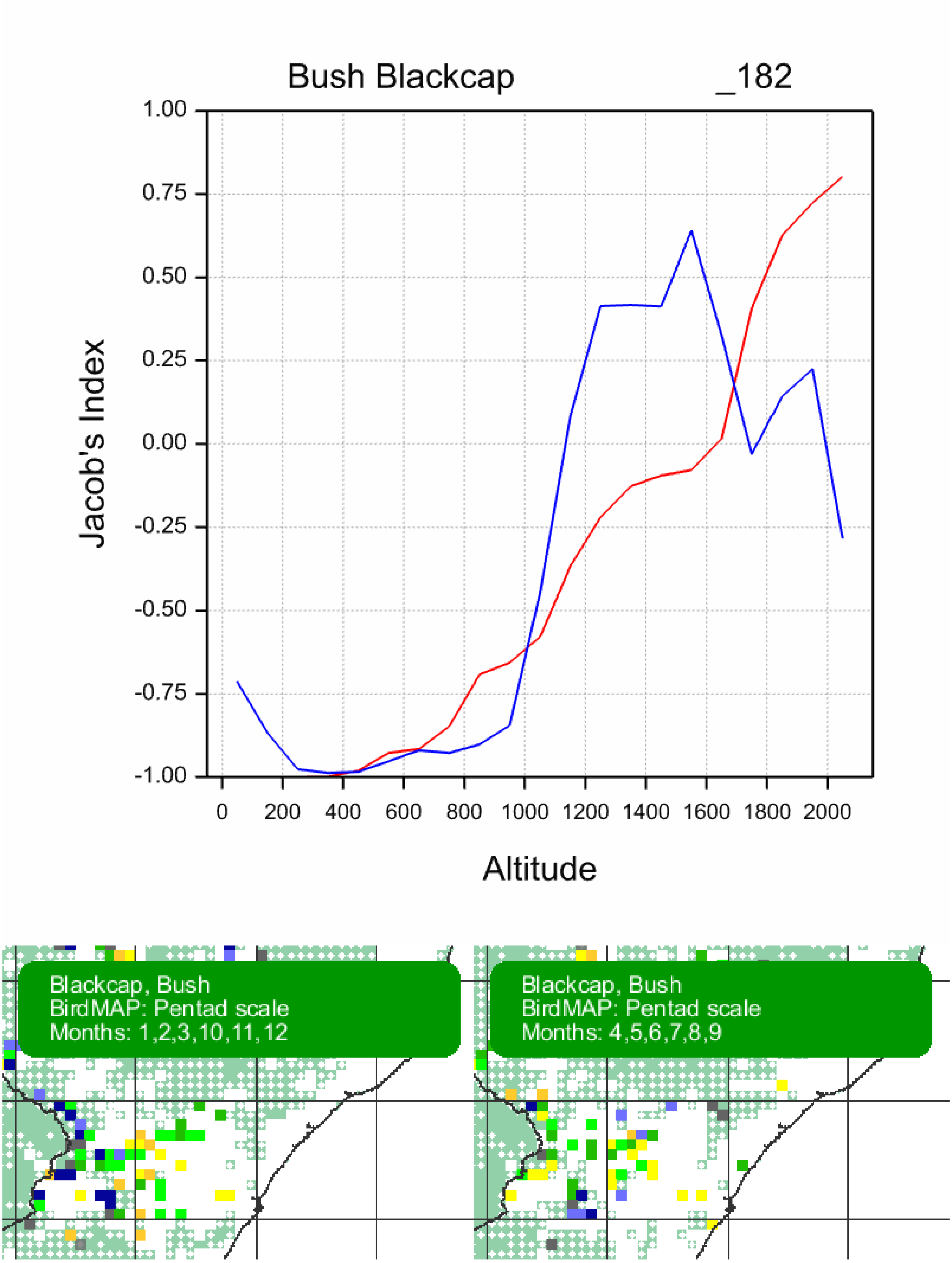


Figure D.8. The altitudinal preference curves for summer and for winter for the Bush Blackcap, and the summer and winter distribution maps for study transect in KwaZulu-Natal.

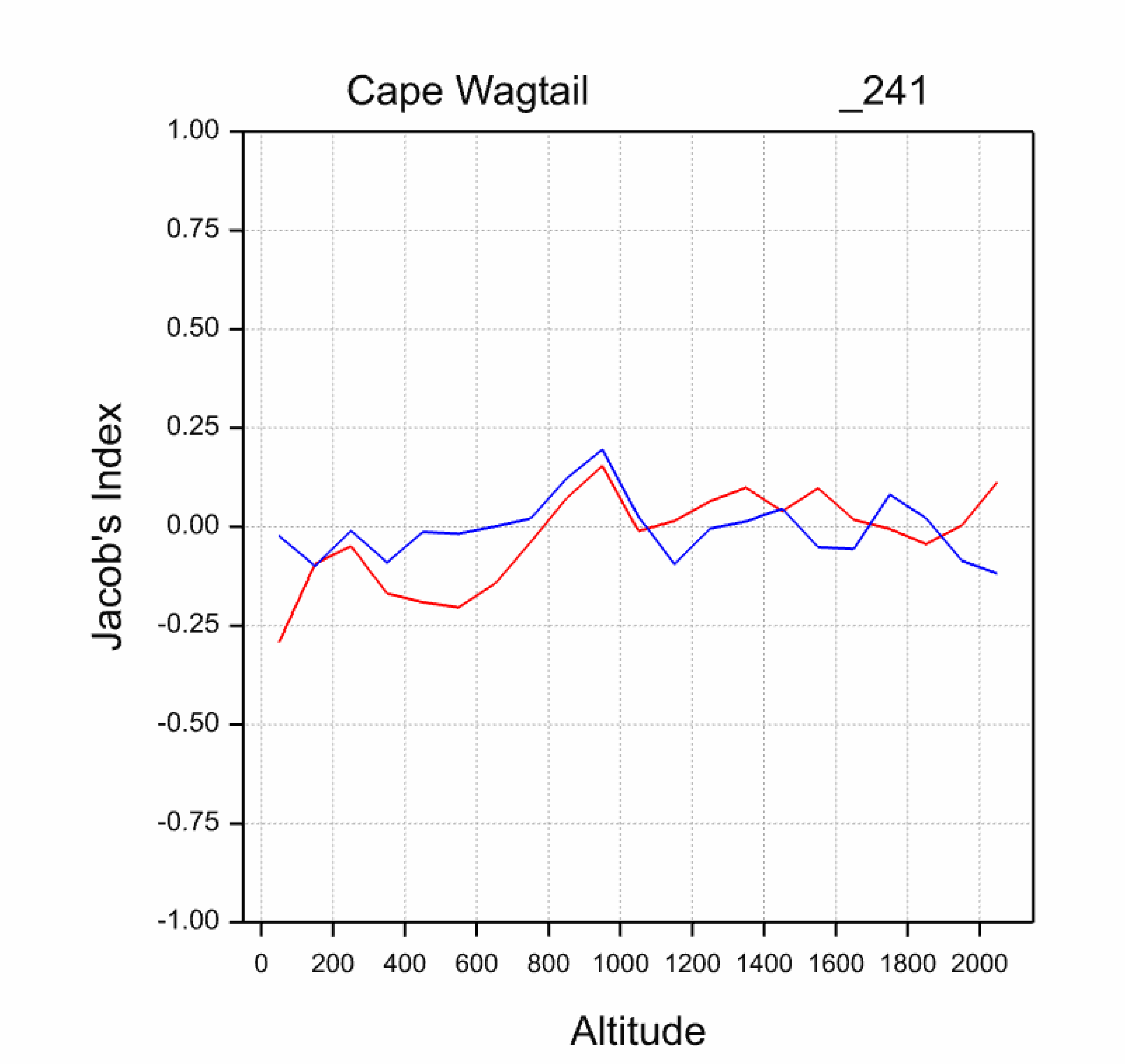
In summer Bush Blackcaps completely avoid altitudes below 400 m (Figure D.8). There are handfuls of birds above 400 m increasing to be in proportion to the land available at around 1600 m. There are more Bush Blackcaps than one would predict given the amount of area. Altitude preference increases with increasing altitude.

In winter some Bush Blackcaps are present from sea-level to 1000 m but far less than one would expect given the area. The number of birds increases to be in proportion to the land available at approximately 1100 m. Blackcaps are preferentially choosing altitudes 1100–2000 m with main preference 1500–1600 m. Above 2000 m there are fewer birds than one would predict given the area.

Bush Blackcap occurs mainly in *Leucosidea* thickets bordering montane forest patches in narrow ravines. These small, isolated forests and *Leucosidea* tree patches are surrounded by sour grasslands on the slopes of the Drakensberg escarpment (Oatley 1997c). It is a partial altitudinal migrant. In summer it can be found in the highest Afromontane forests up to about 2000 m and comes down to the lower mistbelt forests (lower forest edge at 1100 m) and occasionally valley bushveld in winter (Little and Bainbridge 1992). It breeds during summer (Cyrus and Robson 1980). The reporting rate for Bush Blackcap is highest in summer when this species is most vocal. It seems to not sing at all during the non-breeding season (Oatley 1997c).

Oatley (2017) writes: “A species endemic to South Africa. In KwaZulu-Natal in summer it is found in high forest in the Drakensberg foothills and fringing *Leucosidea* thickets up to altitudes of 1800 m. It visits forests at lower levels down to about 1000 m in KwaZulu-Natal midlands … and may linger in these haunts well into October, later than most other altitudinal migrants. It seems never to reach the coast, and some birds may be found in the highest forests even in winter.”

Cape Wagtail, *Motacilla capensis*



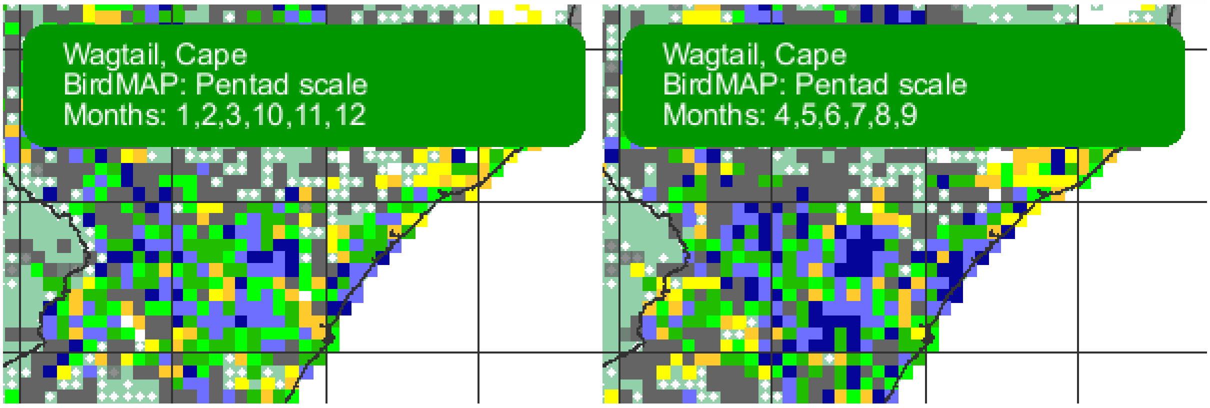
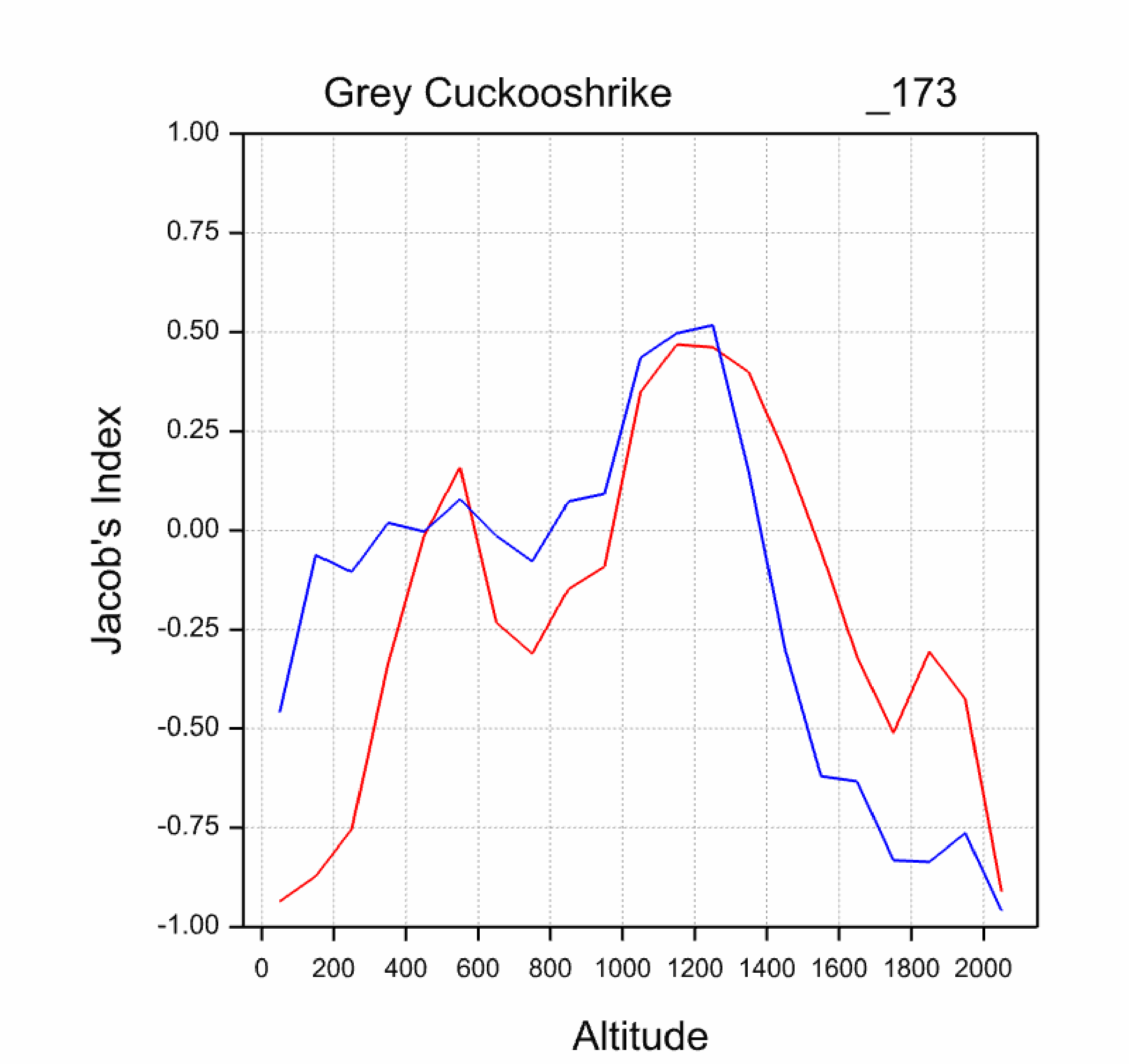


Figure D.9. The altitudinal preference curves for summer and for winter for the Cape Wagtail, and the summer and winter distribution maps for study transect in KwaZulu-Natal

The distribution of Cape Wagtail in summer and in winter is more or less in proportion to the amount of land available at any given altitude (Figure D.9). The availability of land and use of land by Cape Wagtail essentially match up.

Cape Wagtail is largely sedentary. It is ubiquitous throughout KwaZulu-Natal occurring at all altitudes (Little and Bainbridge 1992). During the winter months, at least part of the population remains at high altitudes, while some may move to lower altitudes (Little and Bainbridge 1992). In Lesotho, Osborne and Tigar (1990) noted that little seasonal variation in reporting rates, and considered that “there is no evidence that it leaves the uplands in winter.” Cape Wagtail is commonly found in the vicinity of water (Piper 1997, Cyrus and Robson 1980). Cape Wagtail is common in a wide range of natural habitats and has also adapted to suburban and urban environments occurring commensally with humans (Piper 1997). Figure D.9 supports this consensus view of a resident species (Table 3.1).

Grey Cuckoo-shrike, *Coracina caesia*



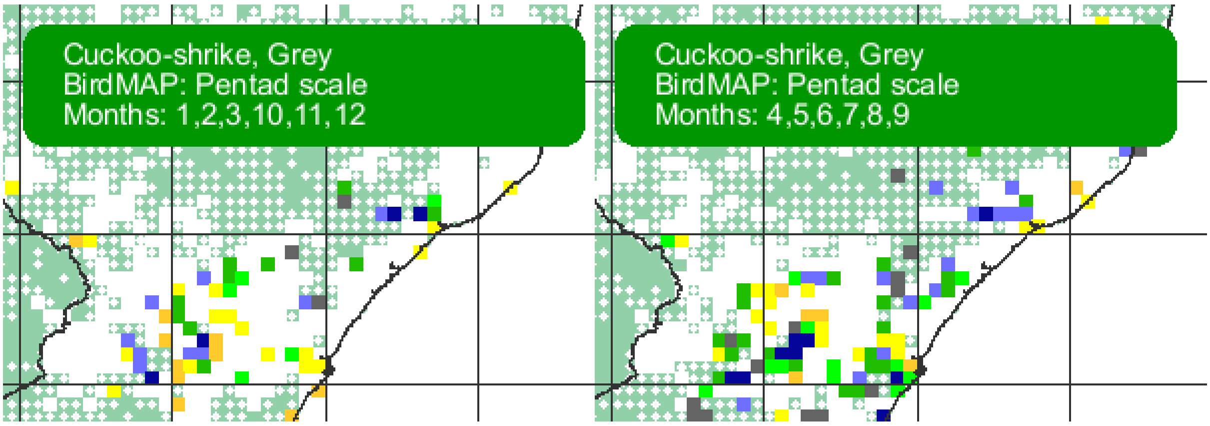


Figure D.10. The altitudinal preference curves for summer and for winter for the Grey Cuckoo-shrike, and the summer and winter distribution maps for study transect in KwaZulu-Natal.

In summer there are more Grey Cuckooshrikes at 1000–1500 m than one would expect given the area, with main altitude preference at 1100–1300 m (Figure D.10). Below 1000 m and above 1500 m altitude preference declines and there are fewer birds than one would expect given the area available. The numbers of birds decreases in proportion to the area until almost complete avoidance of areas at sea-level and at 2000 m.

Grey Cuckooshrikes are preferentially selecting altitudes 800–1400 m in winter, with main preference at 1200–1300 m. The number of birds is roughly in proportion to the area of land available at 100–800 m. Below 100 m there are some birds present but less than one would expect given the area. Above 1400 m, altitude preference declines drastically to there being only handfuls of birds present above 1700 m. There is almost total avoidance of areas at above 2000 m.

Grey Cuckooshrike is an evergreen forest bird (Cyrus and Robson 1980) that undergoes a small altitudinal migration. Grey Cuckooshrike has only been recorded up to about 1800 m (Little and Bainbridge 1992). As the altitudinal preference curves suggest, it is regularly encountered in the midlands forest of KwaZulu-Natal, where it breeds (Oatley 2017). It is not a common or conspicuous species, and with its soft vocalisation, silent flight and habit of visiting the forest canopy (Oatley 2017, Oatley 1997b) it is probably overlooked by many observers.

Ground Woodpecker, *Geocolaptes olivaceus*

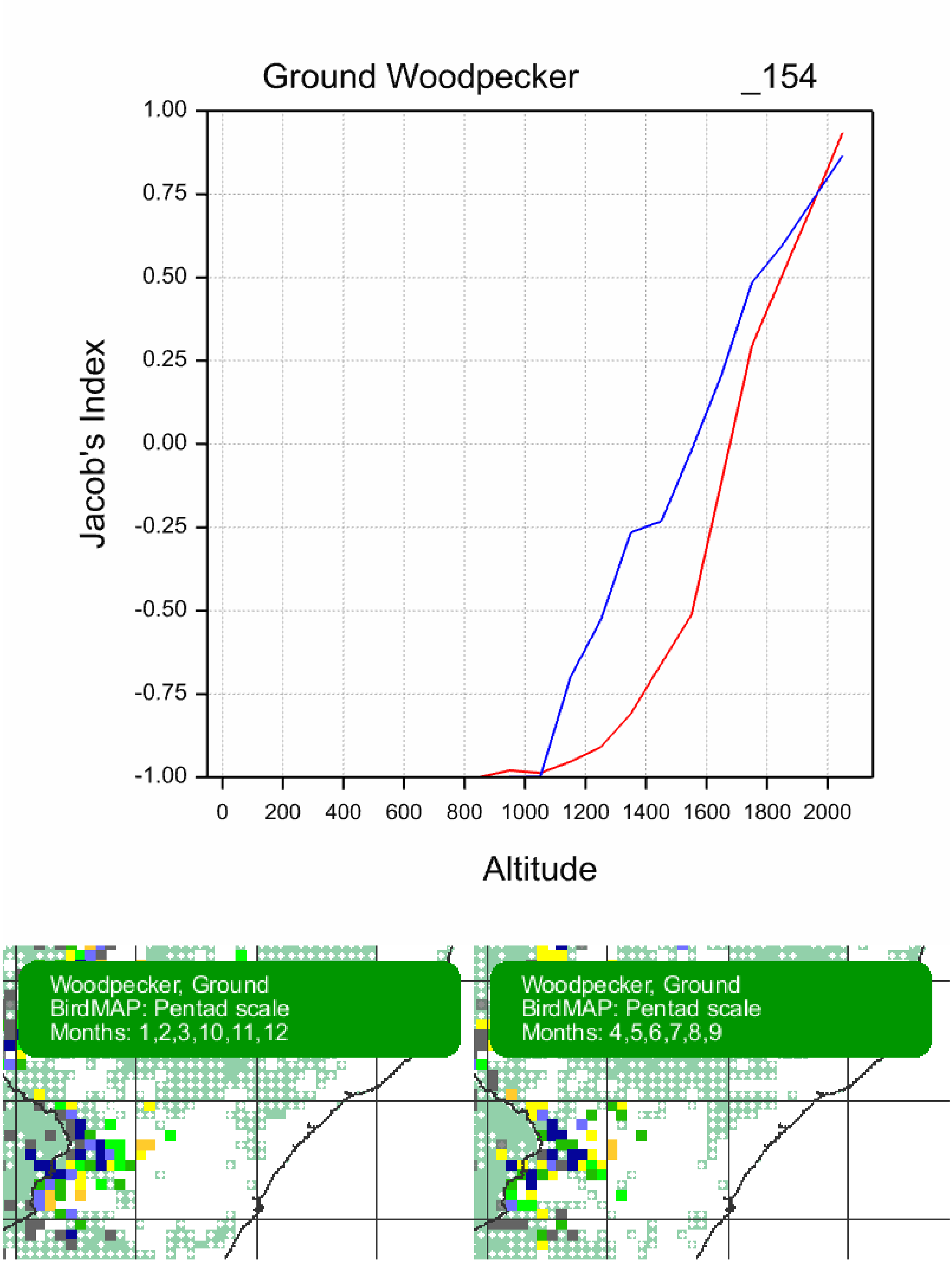


Figure D.11. The altitudinal preference curves for summer and for winter for the Ground Woodpecker, and the summer and winter distribution maps for study transect in KwaZulu-Natal.

In summer Ground Woodpeckers avoid areas below 900 m (Figure D.11). There is almost complete avoidance of areas at 900–1200 m with only a few scattered records in this altitude range. Above 1200 m there are handfuls of birds present up to 1400 m. Bird numbers continue to increase with increasing altitude but there are still far fewer than the amount expected given the area of land available. Numbers of Ground Woodpeckers are in proportion to area of land at 1700 m. Above 1700 m there are many more birds than expected. Altitude preference increases with increasing altitude with main altitude preference at 2000+ m.

Ground Woodpeckers completely avoid altitudes below 1000 m in winter. The number of birds increases to be in proportion with land available at approximately 1600 m. Above 1600 m there are disproportionately more Ground Woodpeckers than land.

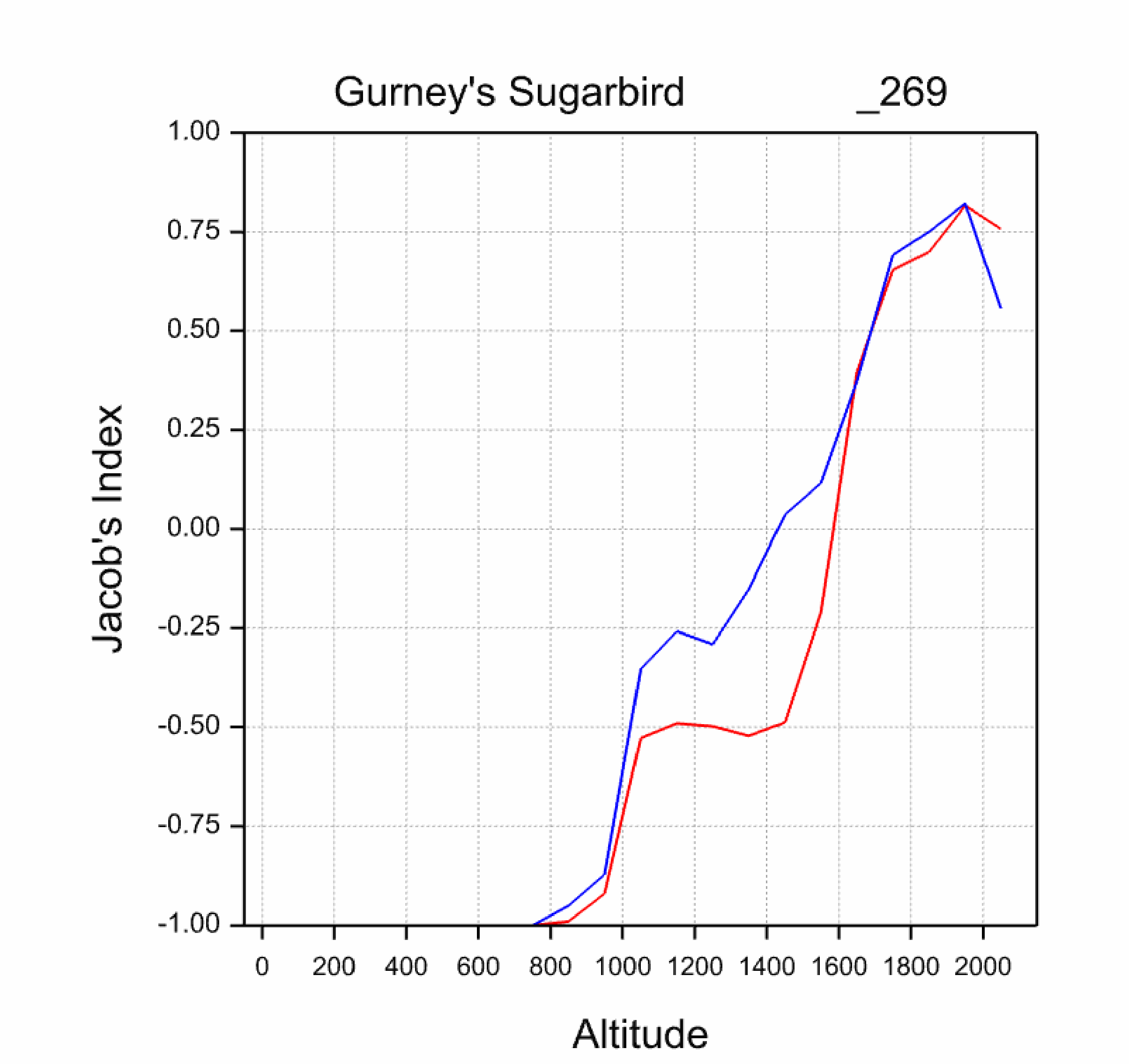
Ground Woodpecker occurs in the high altitude Drakensberg region. Landform is a primary determinant of the distribution of this species, favouring the steep rocky slopes. Ground Woodpecker is a terrestrial forager and avoids densely vegetated areas (Oatley 1997a).

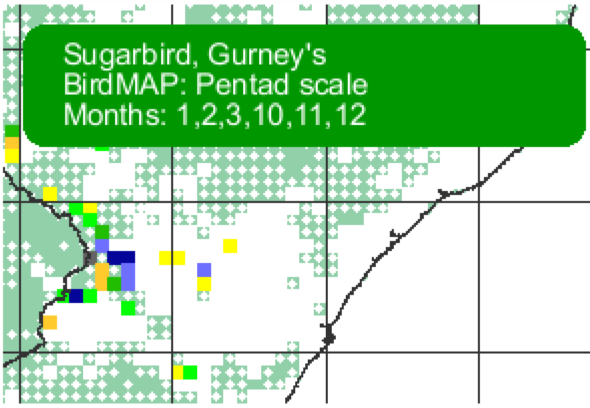
The Ground Woodpecker has been recorded along the Drakensberg above 2865 m in the summer months only (Brown and Barnes 1984, Little and Bainbridge 1992). Brown and Barnes (1984) also observed breeding at this altitude.

Oatley (2017) found Ground Woodpecker to be present throughout the Drakensberg foothills and above the escarpment in the summer months, where it may be found nesting in December and January. It is absent from the higher altitudes in winter but at that time may be encountered on rocky hilltops in the KwaZulu-Natal midlands from which it is normally absent in summer. Osborne and Tigar (1990) found them throughout the uplands of Lesotho, but make no mention of altitudinal movements.

Brown and Barnes (1984), Little and Bainbridge (1992) and Oatley (2017) provide evidence for this species being an altitudinal migrant. This may well be the case as this analysis does not have data for the highest altitudes where this species has been recorded by other authors.

Gurney’s Sugarbird, *Promerops gurneyi*





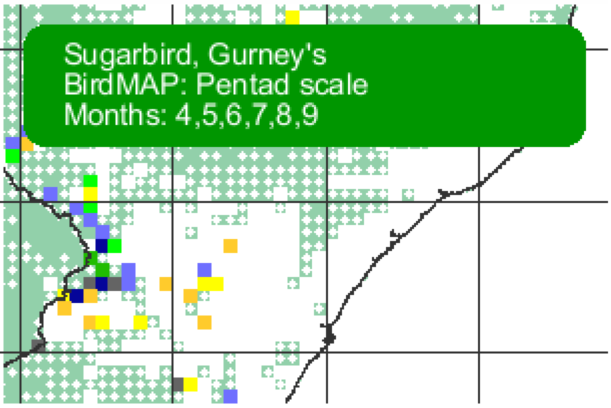


Figure D.12. The altitudinal preference curves for summer and for winter for the Gurney's Sugarbird, and the summer and winter distribution maps for study transect in KwaZulu-Natal.

Gurney's Sugarbird has a slightly lower preference for the highest altitude (above 2000 m) in winter than in summer, but there are more birds at 1000–1600 m in winter than in summer (Figure D.12). Number of Gurney's Sugarbirds decreases with decreasing altitude and there is total avoidance of altitudes below 700 m throughout the year.

Gurney's Sugarbird is a known altitudinal migrant farther north in the Lydenberg district (De Swardt 1991). The same birds were found in the town and surrounding mountains. The altitudinal difference of 480 m gives us an idea of the extent of altitudinal migration.

In KwaZulu-Natal, Gurney's Sugarbird occurs on *Protea* slopes in summer at high altitudes up to about 2400 m (Little and Bainbridge 1992), and moves down to gardens in smaller towns and around resorts and campsites in winter where it is seen more regularly by observers.

Dawie de Swardt ringed Gurney's Sugarbirds at Sani Pass (1890 m a.s.l.) in midsummer 2013 (February). The birds were concentrated on the Silver Sugarbush *Protea roupelliae* which has November to April as its main flowering period (in the Drakensberg the altitudinal range is mostly above 1600 m with the highest recorded altitude being 2440 m) (Rebelo 2007).

Hadeda Ibis, *Bostrychia hagedash*

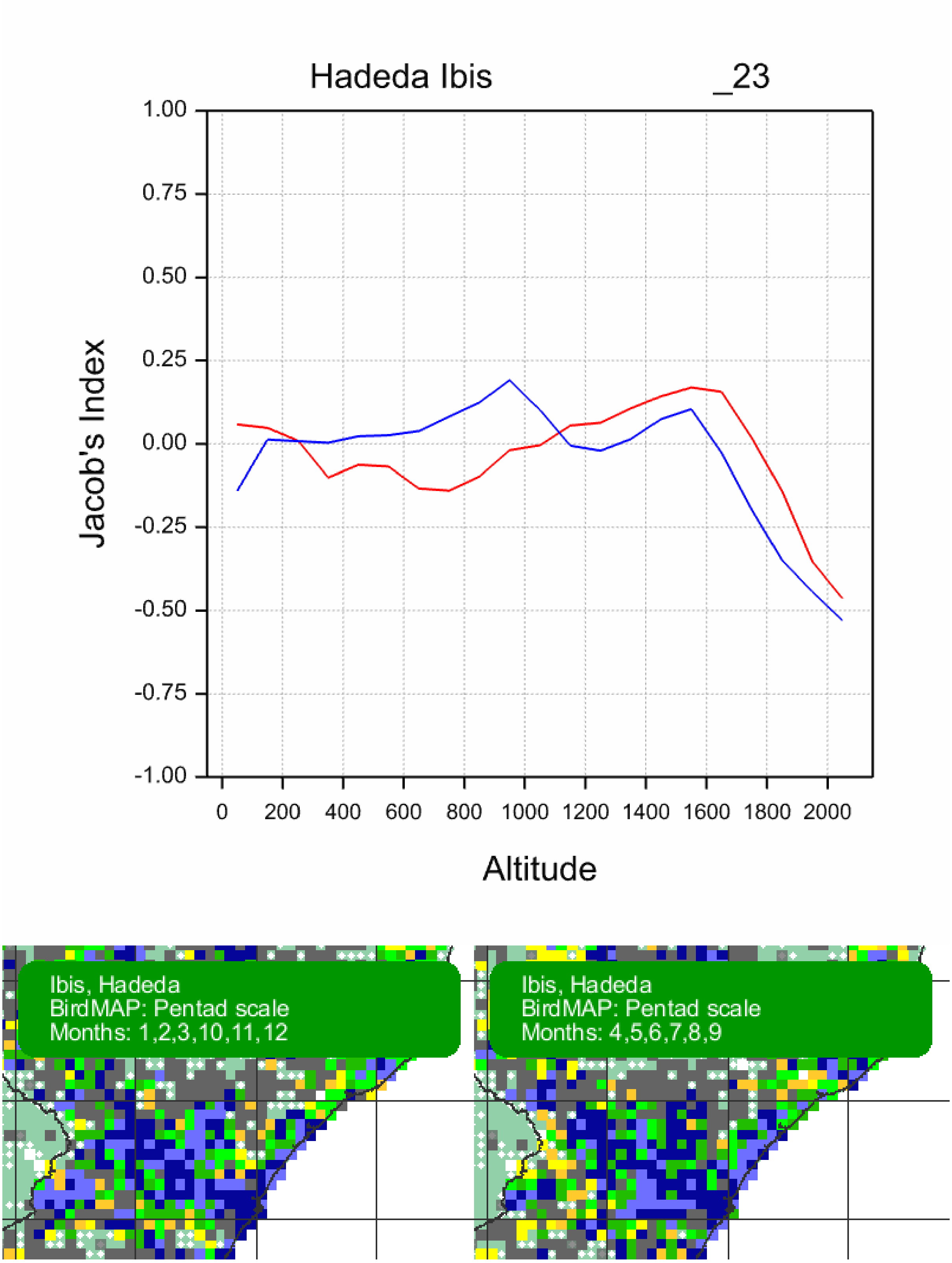
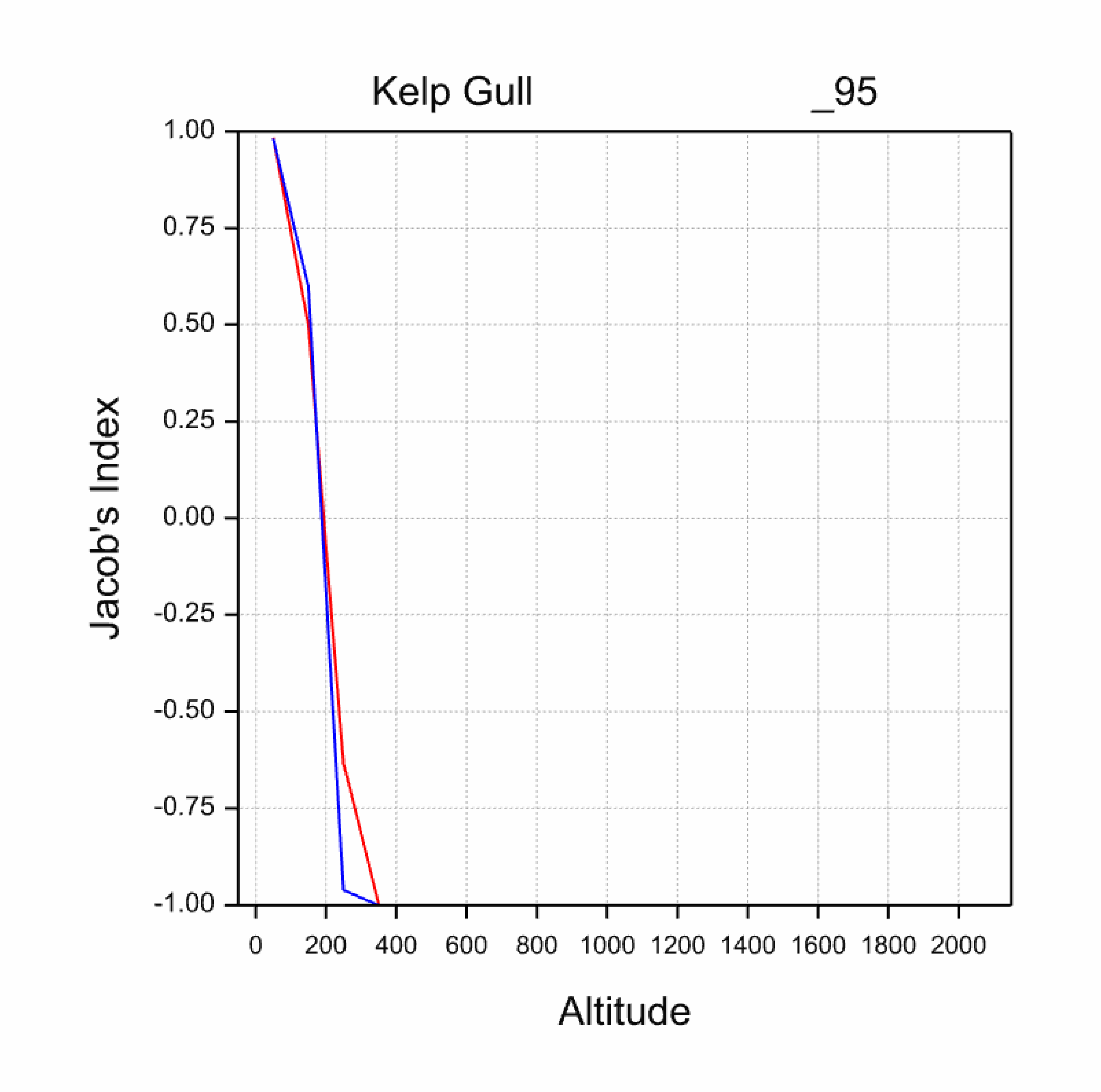


Figure D.13. The altitudinal preference curves for summer and for winter for the Hadeda Ibis, and the summer and winter distribution maps for study transect in KwaZulu-Natal.

The distribution of Hadeda Ibises in summer and in winter is more or less in proportion to the amount of land available at any given altitude from sea-level up to 1700 m (summer) and 1600 m (winter) (Figure D.13). Above these altitudes, altitude preference declines and there are fewer Hadeda Ibises than what one would expect given the area available for use. The seasonal distribution maps show lower reporting rates in winter than in summer in degree square 2929. This apparent altitudinal shift is faithfully portrayed in the altitudinal preference plot, with the blue winter line to the left of the red summer line for altitudes above 1100 m.

Hadeda Ibis is regarded as largely sedentary and inhabits open, moist grasslands and savannas, particularly along well-vegetated river channels. It can also be found in marshes, flooded grasslands, along the edges of large wetlands, irrigated farmlands and garden lawns (Anderson 1997). Little and Bainbridge (1992) regard the Hadeda Ibis as essentially a forest species. Individuals have been recorded up to about 2000 m (Little and Bainbridge 1992). This study suggests that it is partial altitudinal migrant at high altitudes in KwaZulu-Natal.

Kelp Gull, *Larus dominicanus*



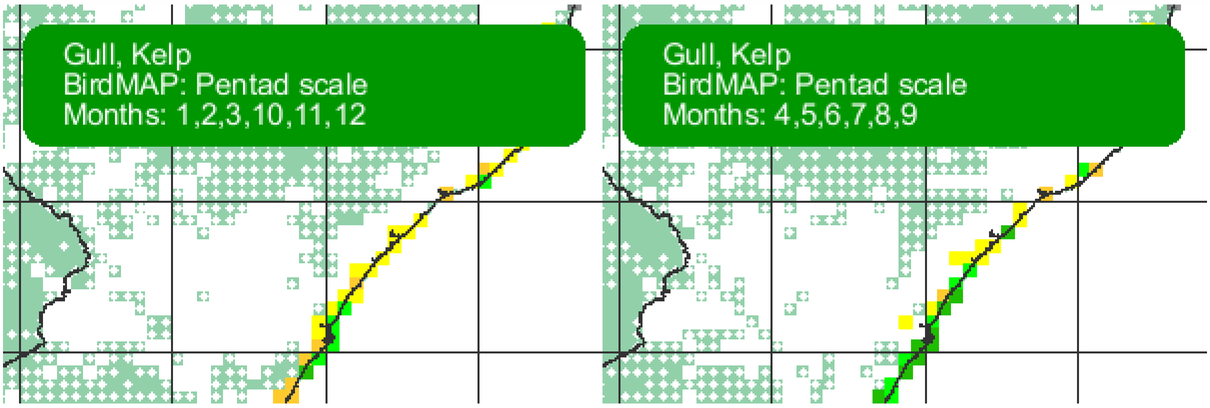


Figure D.14. The altitudinal preference curves for summer and for winter for the Kelp Gull, and the summer and winter distribution maps for study transect in KwaZulu-Natal.

Kelp Gulls are an almost exclusively coastal species, which explains why the altitude preference curve has a value of almost +1.0 for the height class 0–100 m, which includes the coastline (Figure D.14). The seasonal distribution maps (Figure D.14) show that there are higher reporting rates, and consequently disproportionately more Kelp Gulls along the coast in winter than in summer (Figure D.14). This winter presence is attributable to the "sardine run", and Kelp Gull migrates eastward occurring along the KwaZulu-Natal coast. This movement coincides with many other marine predators that move eastwards following the sardine run which occurs in mid-winter along this section of shore, and attracts a large number of avian predators (Allan et al. 1997). The summer and winter altitudinal preference curves are almost identical; although there are more Kelp Gulls present in winter than in summer, their altitudinal distributions are the same.

The altitudinal preference curve does not immediately drop to –1 for the height classes immediately above the 0–100 m class, because some of the coastal pentads include areas with altitudes 100–200 m, and even 200–300 m. This distortion is an artefact of the analysis approach.

Lazy Cisticola, *Cisticola aberrans*

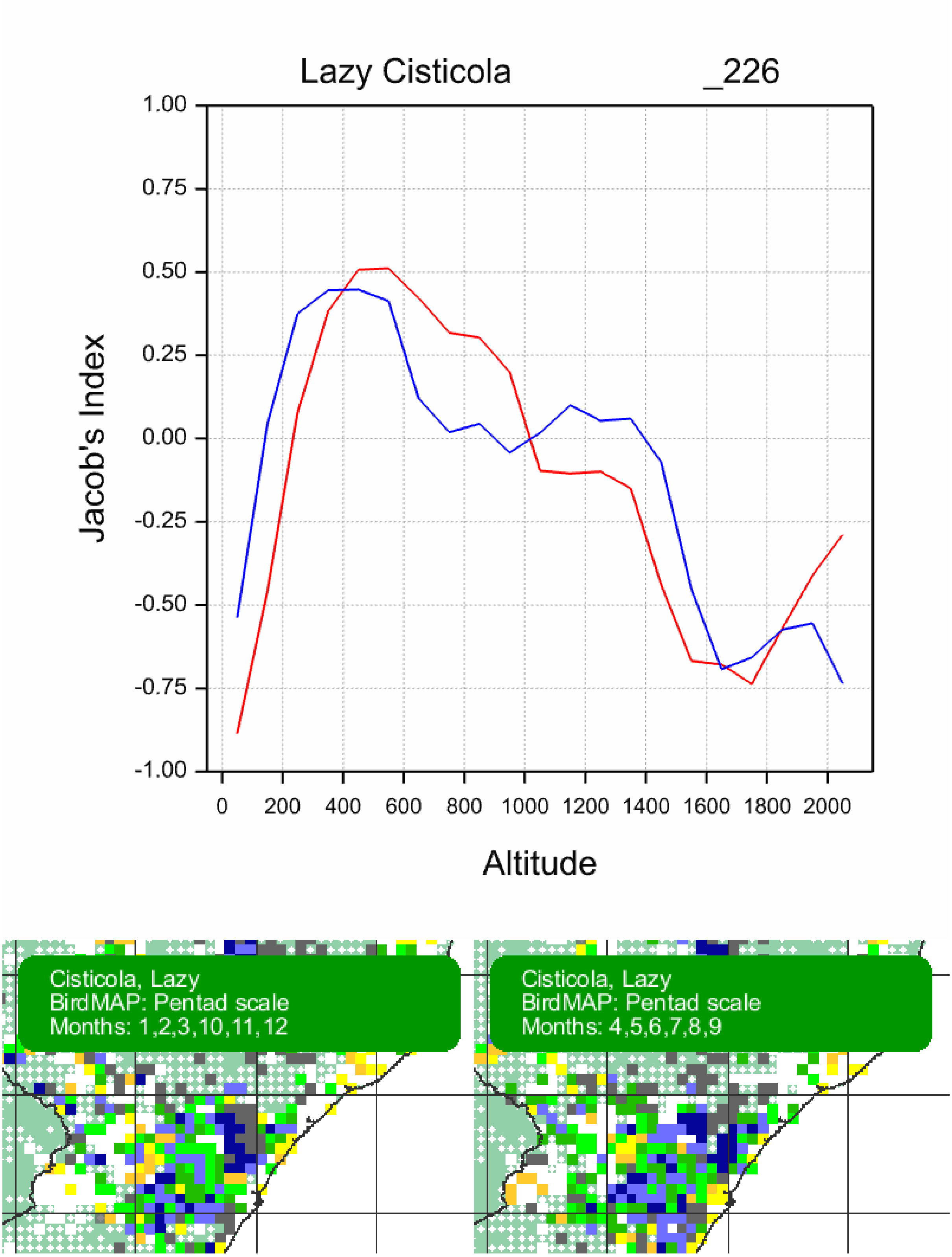


Figure D.15. The altitudinal preference curves for summer and for winter for the Lazy Cisticola, and the summer and winter distribution maps for study transect in KwaZulu-Natal.

In summer there are more Lazy Cisticolas than one would expect at altitudes 300–1000 m (Figure D.15). Above 1000 m there are fewer cisticolas than expected given the amount of area available for use, but there is not total avoidance of these higher altitudes.

In winter Lazy Cisticolas are preferentially selecting altitudes 100–700 m with main preference 300–500 m. Between 700 m and 1400 m, the number of birds is more or less in proportion to the area available. Above 1400 m, there are considerably fewer birds than predicted given the area.

Lazy Cisticola expresses a strong avoidance of coastal areas throughout the year.

Lazy Cisticola is resident with minor seasonal change in distribution. It is closely associated with rocky outcrops with grass, scrub and intermittent trees and thickets (Little and Bainbridge 1992, Berruti 1997e). Lazy Cisticola forages low down in vegetation or on the ground (Berruti 1997e). This species has been recorded up to about 2440 m (Little and Bainbridge 1992).

Long-tailed Widowbird, *Euplectes progne*

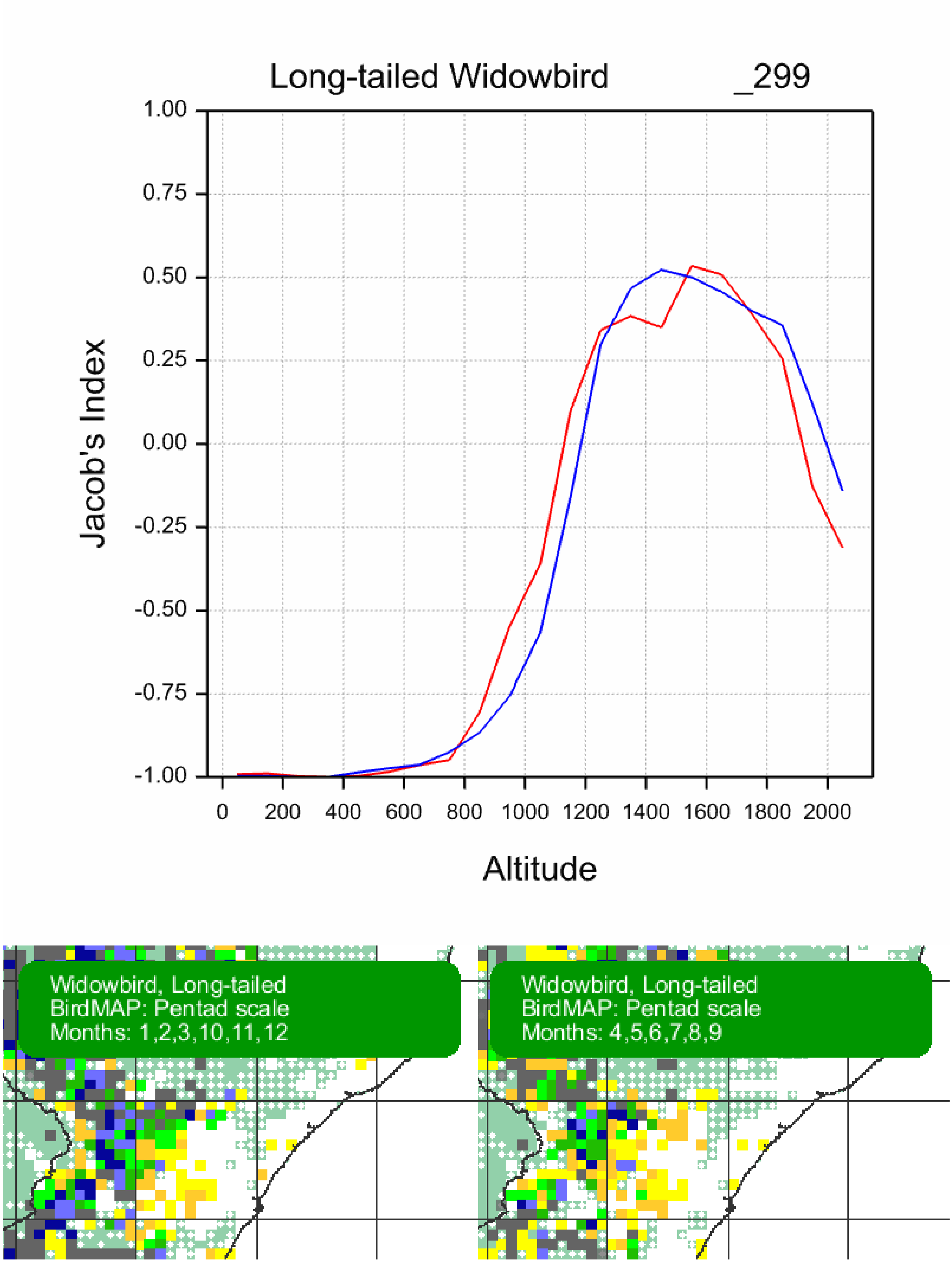


Figure D.16. The altitudinal preference curves for summer and for winter for the Long-tailed Widowbird, and the summer and winter distribution maps for study transect in KwaZulu-Natal.

The summer and winter altitudinal preference curves for the Long-tailed Widowbird match up closely (Figure D.16).

In summer there are more Long-tailed Widowbirds than one would expect given the amount of area available at altitudes 1100–1900 m. Main altitude preference is 1500–1600 m. There is almost complete avoidance of altitudes below 800 m.

In winter Long-tailed Widowbirds are preferentially selecting altitudes 1200–2000 m with main preference 1400–1500 m. As is summer, there is almost complete avoidance of altitudes below 800 m.

Little and Bainbridge (1992) have recorded this species up to about 2300 m. It is a high-altitude species occurring predominantly in open grassland and vlei habitats (Little and Bainbridge 1992, Craig 1997b). There is no evidence of seasonal altitudinal movements.

The Long-tailed Widowbird has a recognisable non-breeding plumage and a very distinctive breeding plumage resulting in the seasonality of reporting rates to be less noticeable than that of other widowbirds (Craig 1997b).

Malachite Kingfisher, *Alcedo cristata*

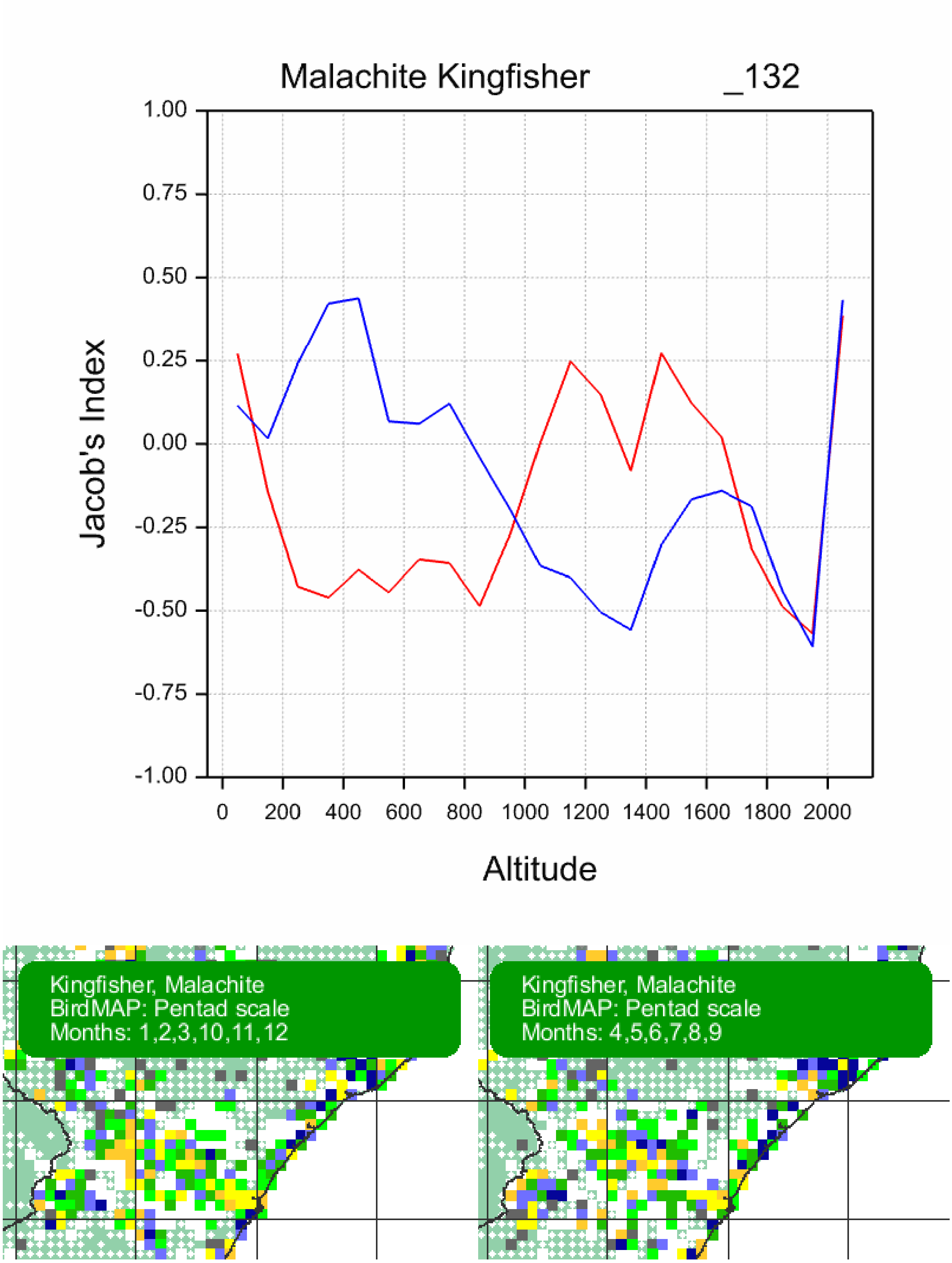


Figure D.17. The altitudinal preference curves for summer and for winter for the Malachite Kingfisher, and the summer and winter distribution maps for study transect in KwaZulu-Natal.

A visual inspection of the summer and winter distributions of the Malachite Kingfisher suggests fairly similar distributions (Figure D.17). However the altitudinal preference graph shows a small preference for altitudes between 1000 m and 1700 m in summer and a small preference for altitudes less than 800 m in winter. A more careful assessment of the two distribution maps shows a more widespread presence in the northeastern corner of degree cell 2929 in summer than in winter.

Malachite Kingfisher is mainly piscivorous and is closely associated with aquatic habitats, usually below 2000m. Many favoured sites are only seasonally available after the arrival of the main rains and are generally situated at higher altitudes. The breeding season coincides with the wet season. When the seasonal streams and wetlands dry out at the onset of the dry season, the birds are forced to find new hunting grounds and move to lower altitudes to exploit food availability and can also be found along the KwaZulu-Natal coast (Clancey 1997).

Pied Crow, *Corvus albus*

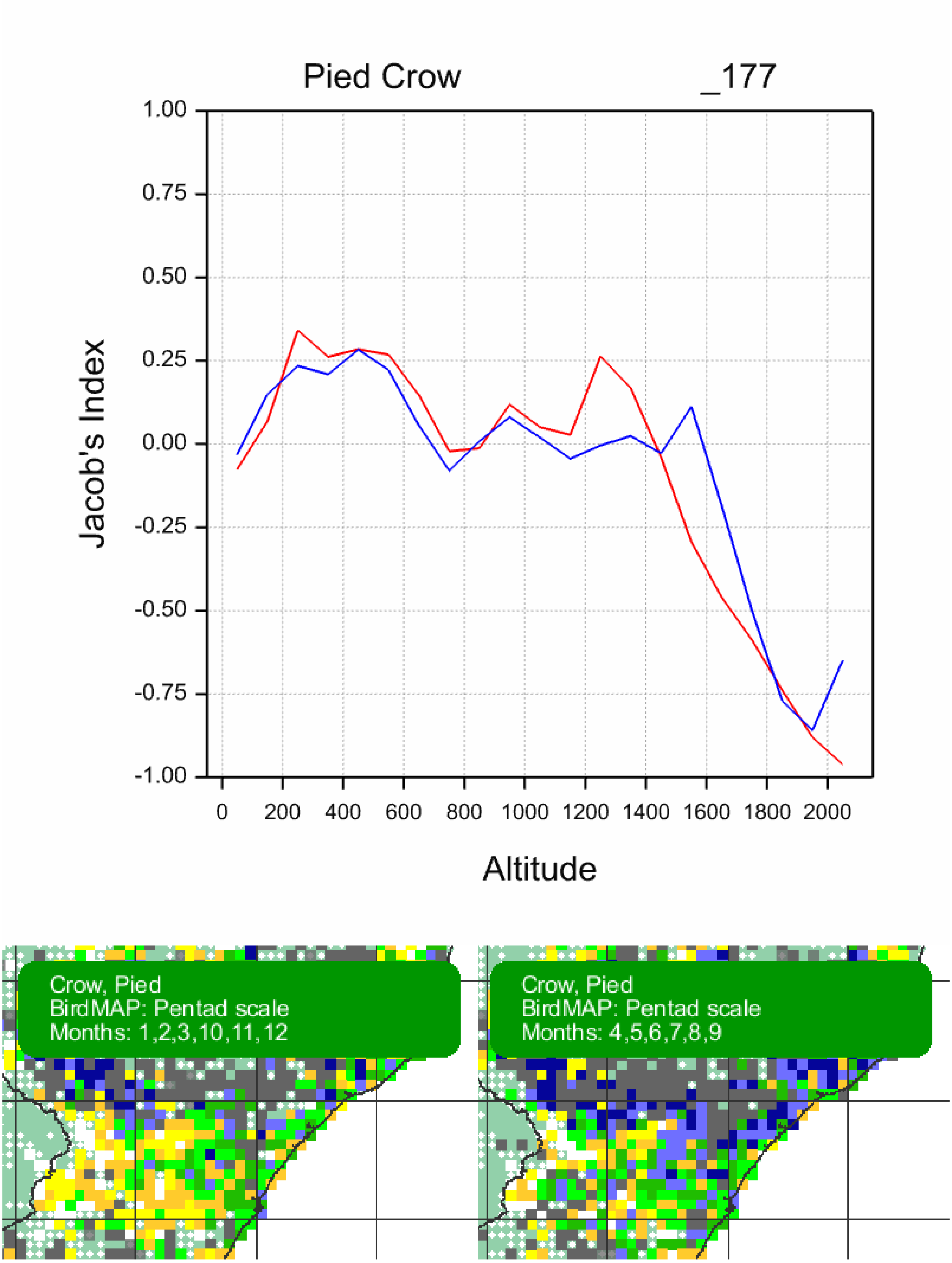


Figure D.18. The altitudinal preference curves for summer and for winter for the Pied Crow, and the summer and winter distribution maps for study transect in KwaZulu-Natal.

The distribution of Pied Crow is roughly in proportion to the amount of land available at any given altitude from sea-level up to 1400 m in summer and from sea-level up to 1600 m in winter (Figure D.18). Above these altitudes, altitude preference declines sharply in both seasons and there are substantially fewer crows than expected given the amount of area available for use.

Pied crow is an omnivorous bird found in a wide range of habitats (Jenkins and Underhill 1997). In KwaZulu-Natal it occurs from the coast to the lower portions of the Drakensberg. It is scarce in the higher-altitude grasslands (Cyrus and Robson 1980). There are seasonal changes in the conspicuousness of this species which are thought to be associated with the onset of breeding (Jenkins and Underhill 1997).

Red-billed Quelea, *Quelea quelea*

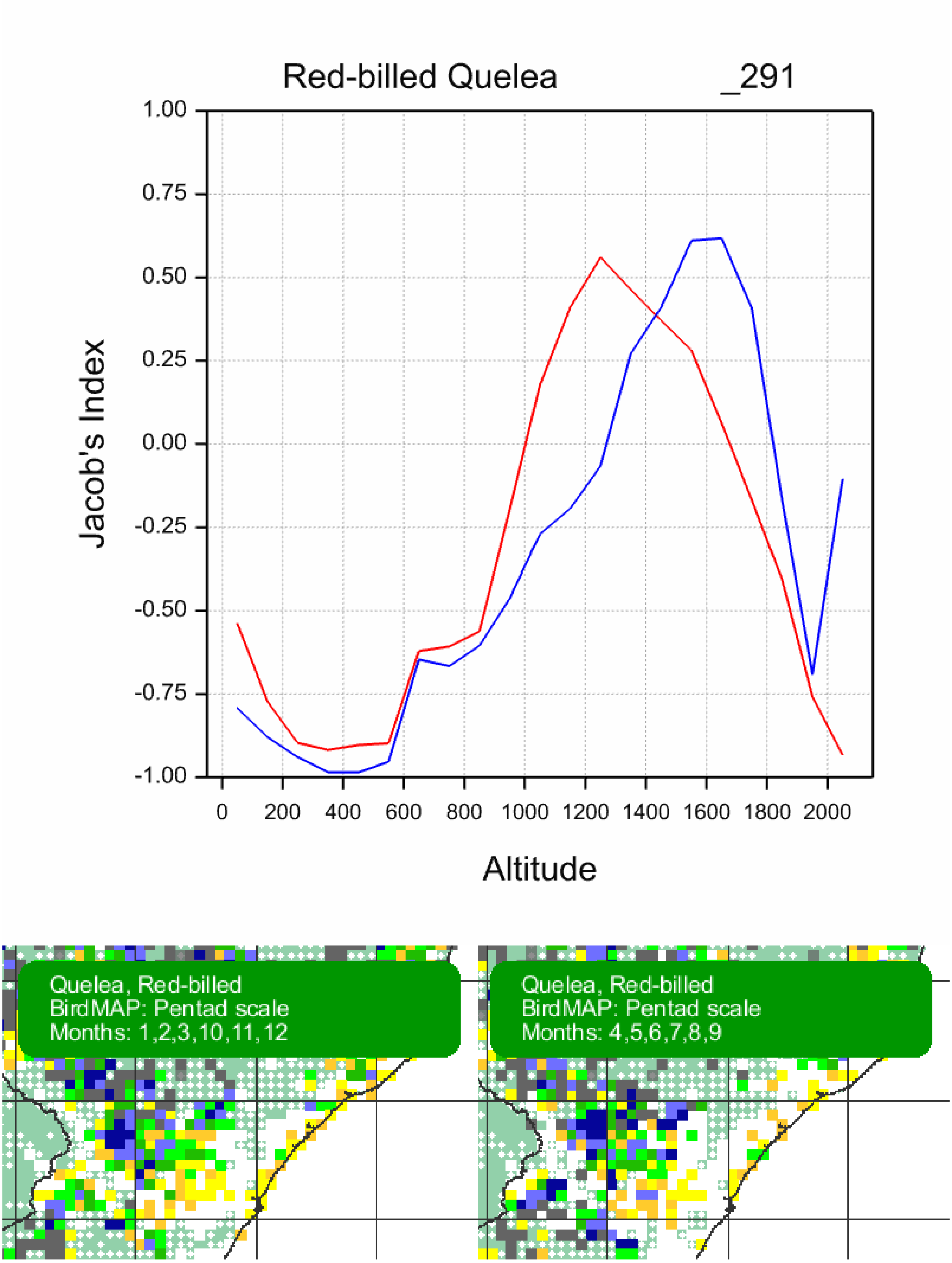


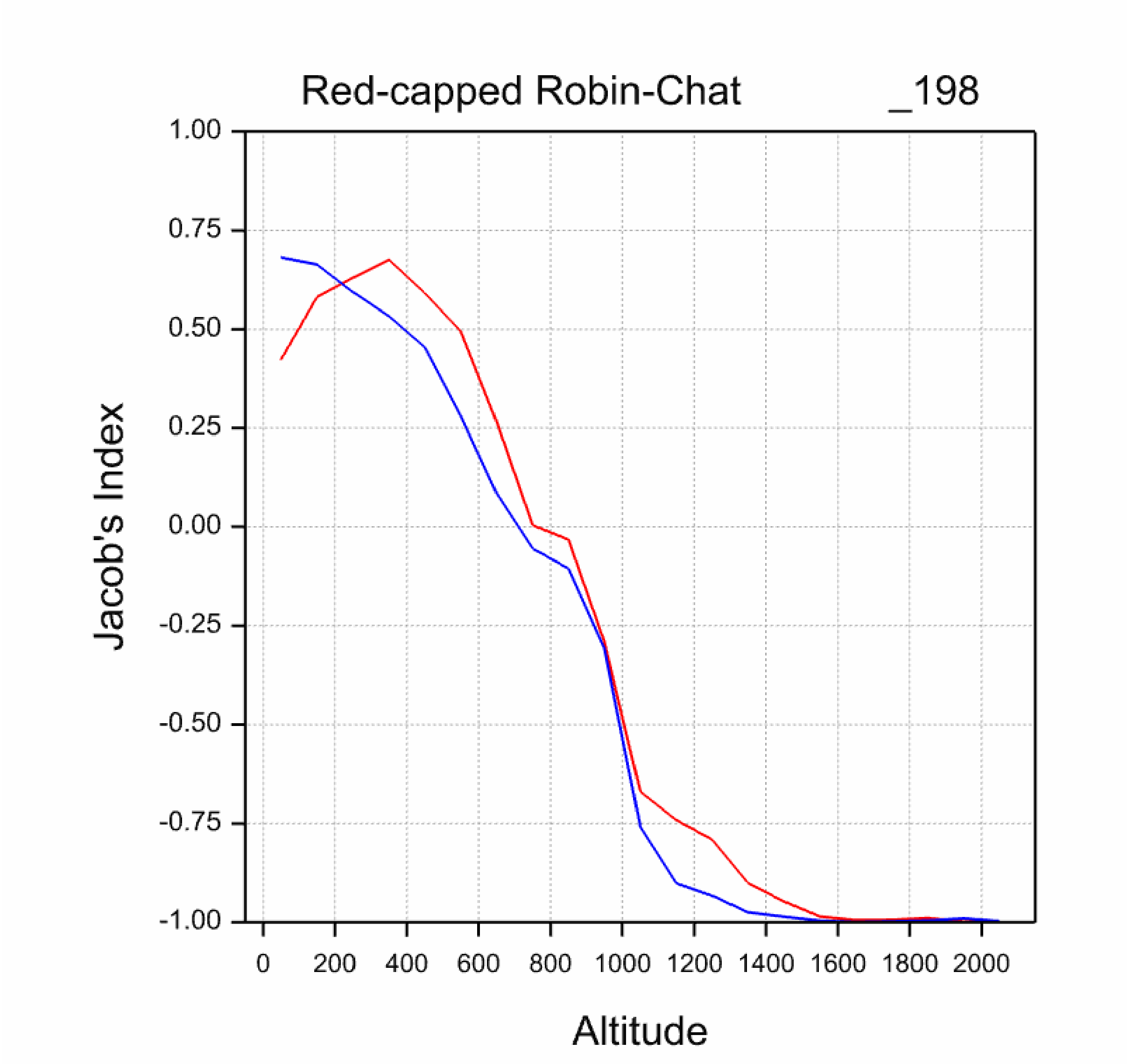
Figure D.19. The altitudinal preference curves for summer and for winter for the Red-billed Quelea, and the summer and winter distribution maps for study transect in KwaZulu-Natal.

Between sea-level and 1000 m in summer there are fewer Red-billed Queleas than one would expect given the amount of area (Figure D.19). At 1000 m the number of queleas and the amount of area are in proportion. From 1000 m to approximately 1700 m there are more Red-billed Queleas than expected with main altitude preference at 1200–1300 m. Above 1700 m Jacobs Index is negative indicating that there are fewer birds than area available, with almost complete avoidance of areas above 2000 m.

The winter altitudinal preference curve and distribution map follow a similar pattern to the summer plots. There are fewer birds than expected between sea-level and 1300 m in winter. At altitudes 1300–1800 m there are more Red-billed Queleas than one would expect given the amount of area available. Main altitude winter preference is 1500–1700 m. Above 1800 m, there are varying levels of avoidance.

Red-billed Quelea occurs in most vegetation types but has a preference for woodlands and grasslands below 2000 m and cultivated lands. It is a summer breeder and its preferred breeding habitat is thorny or spiny vegetation. Red-billed Quelea feeds on annual grasses and drinks at least twice a day so access to surface water is important (Cyrus and Robson 1980; Mundy and Herremans 1997).

Red-capped Robin-Chat, *Cossypha natalensis*



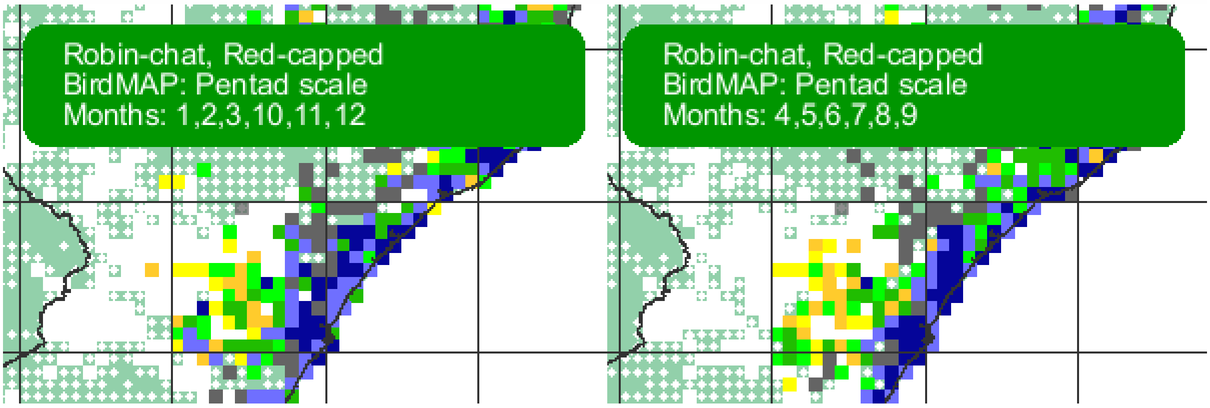


Figure D.20. The altitudinal preference curves for summer and for winter for the Red-capped Robin-chat, and the summer and winter distribution maps for study transect in KwaZulu-Natal.

Red-capped Robin-Chat is present on the KwaZulu-Natal coast throughout the year (Oatley and Arnott 1998). Red-capped Robin-Chat is preferentially choosing altitudes below approximately 700 m in summer and in winter (Figure D.20). Main altitude preference in summer is 300–400 m. There is still a preference at sea-level but this preference is not as strong as at 300–400 m. Winter altitude preference is 0–100 m. Above 700 m there are fewer Red-capped Robin-Chats than one would predict given the area. There are small numbers of birds above 1200 m and virtually complete avoidance of areas above 1400 m.

Red-capped Robin-Chat is characteristic of coastal evergreen forest and scrub. It is also common in gardens in KwaZulu-Natal coastal towns (Cyrus and Robson 1980, Oatley 1997e). Its distribution extends up river valleys occurring in riverine forest and woodland and can be found in escarpment forests below the mistbelt-forest level (Cyrus and Robson 1980, Oatley 1997e).

It is a partial altitudinal migrant, meaning not all of the individuals in the population migrate (Oatley and Arnott 1998). Resident Red-capped Robin-Chats breed in the KwaZulu-Natal coast belt at or close to sea-level (Oatley and Arnott 1998). In spring the migrants move inland up river valleys to take advantage of seasonally suitable habitat, dispersing into thornveld and bushveld habitats where they breed. In winter they are absent from these areas having returned to the coast in autumn (Oatley and Arnott 1998). This is confirmed by ringing data suggesting some birds are only winter visitors to coastal areas and disappear from these areas in summer (Cyrus and Robson 1980; Oatley 1997e). The number of Red-capped Robin-Chats in coastal forest habitats increases in the winter months after the arrival of migrants from further inland. This increase can be seen in the pentads in the coastal areas in grid cells 2930 and 2931 being darker blue in winter than in summer (Figure D.20).

According to Oatley (1997e), Red-capped Robin-Chat does not commonly occur above 400 m in KwaZulu-Natal. Cyrus and Robson (1980) however stated that it occurs up to about 600 m which is in better agreement with the altitudinal preference curves depicting this species to have a preference for altitudes up to about 700 m.

Oatley (2017) writes extensively on the Red-capped Robin-Chat: “In Natal, *Cossypha natalensis* is characteristically a bird of the dune forest of the littoral and of lowland forest remnants and evergreen thickets of the coast hinterland. The species breeds in these haunts in the period October to February, but is more numerous in winter than in summer. It also breeds in riparian thickets well inland along the major river systems and their tributaries, but is present in these valleys only during the summer months of October to March. There is a seasonal movement inland along the river valleys in spring and coastwards in autumn. Red-capped Robin-chats ringed in winter in suburban gardens in Durban and environs disappear in summer and return again the following winter. Although the movement inland is along incised drainage line, altitudinal increment inevitably results and some birds are found breeding in wooded gullies some 1100 m a.s.l. The density of cover in such localities fluctuates markedly between summer and winter due to dominance of deciduous elements in the flora and the dryness of the habitat in July and August. To a cover-loving species such as the Red-capped Robin-chat, this factor may well be a significant one …”

Although the summer and winter lines for this species are fairly similar, this difference is adequate to describe a partial altitudinal migrant.

Red-faced Cisticola, *Cisticola erythrops*

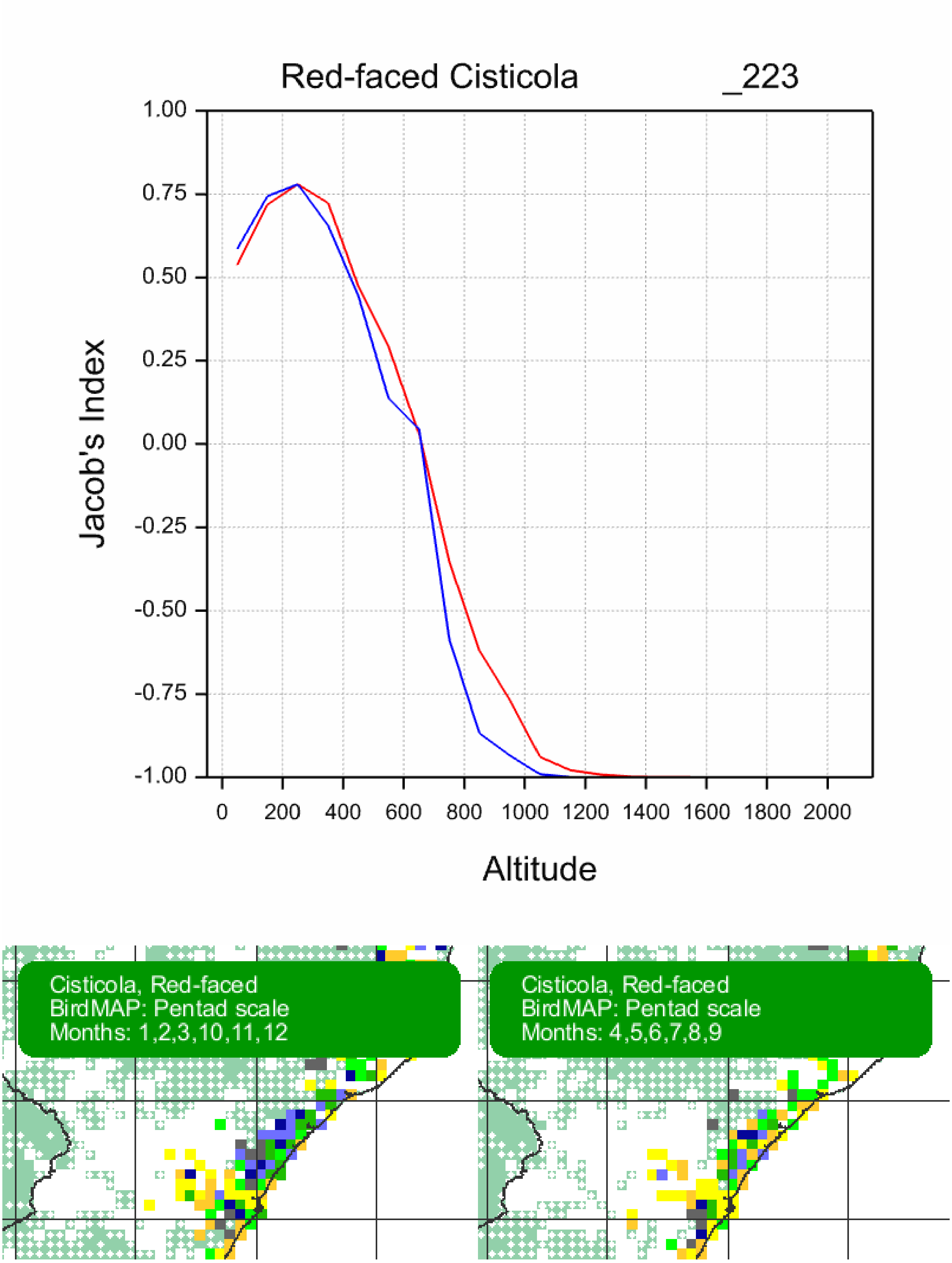


Figure D.21. The altitudinal preference curves for summer and for winter for the red-faced Cisticola, and the summer and winter distribution maps for study transect in KwaZulu-Natal.

The summer and winter altitudinal preference curves and seasonal distribution maps are closely similar (Figure D.21). There are disproportionately more Red-faced Cisticolas from sea-level up to 600–700 m than land available at these altitudes throughout the year, both summer and winter. Main altitude preference is 200–300 m. Altitude preference at sea-level is not as strong as at 200–300 m but there is still a definite preference. Above 700 m altitude preference drops markedly and there are fewer cisticolas than one would expect given the area. There is almost total avoidance at 1000 m and complete avoidance above 1400 m.

Red-faced Cisticola is resident occurring mainly at altitudes below 700 m in KwaZulu-Natal. It is primarily associated with wetland habitat inhabiting rank growth and reeds. In KwaZulu-Natal, Red-faced Cisticola also inhabits the fringes of sugarcane fields bordering wetlands (Cyrus and Robson 1980; Berruti 1997d).

Rock Kestrel, *Falco tinnunculus*

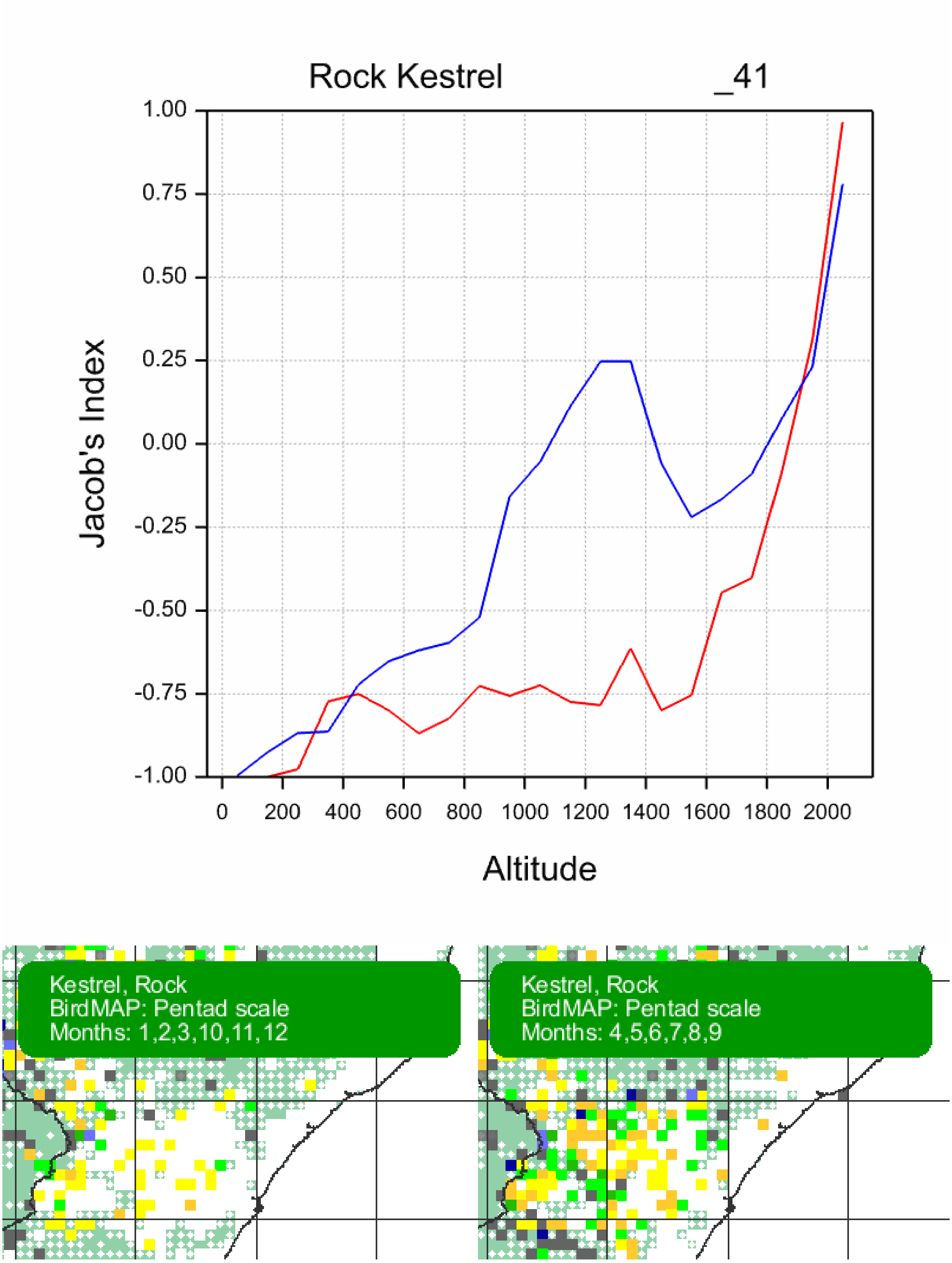


Figure D.22. The altitudinal preference curves for summer and for winter for the Rock Kestrel, and the summer and winter distribution maps for study transect in KwaZulu-Natal.

In summer there is complete avoidance of areas from sea-level up to approximately 200 m (Figure D.22). Some Rock Kestrels are present at 200–1600 m but far less than one would expect given the area. Numbers of birds increase to be in proportion to area available at approximately 1900 m. Above 1900 m there are disproportionately more Rock Kestrels than area. Altitude preference increases with increasing altitude. Main altitude preference is above 2000 m.

In winter, Rock Kestrel moves off the escarpment to lower altitudes in KwaZulu-Natal.

Rock Kestrel is a versatile species able to exploit a wide variety of habitats. The breeding distribution is strongly influenced by the distribution of mountainous areas. During the breeding season (September– January, peaking October–December), Rock Kestrel hunts closer to nest sites which are mainly situated on cliff rock faces (Cyrus and Robson 1980, Van Zyl 1997). This is illustrated in the altitudinal preference curves where Rock Kestrel ranges to lower altitudes during winter but is largely confined to high altitudes during the summer breeding season.

Rock Martin, *Hirundo fuligula*

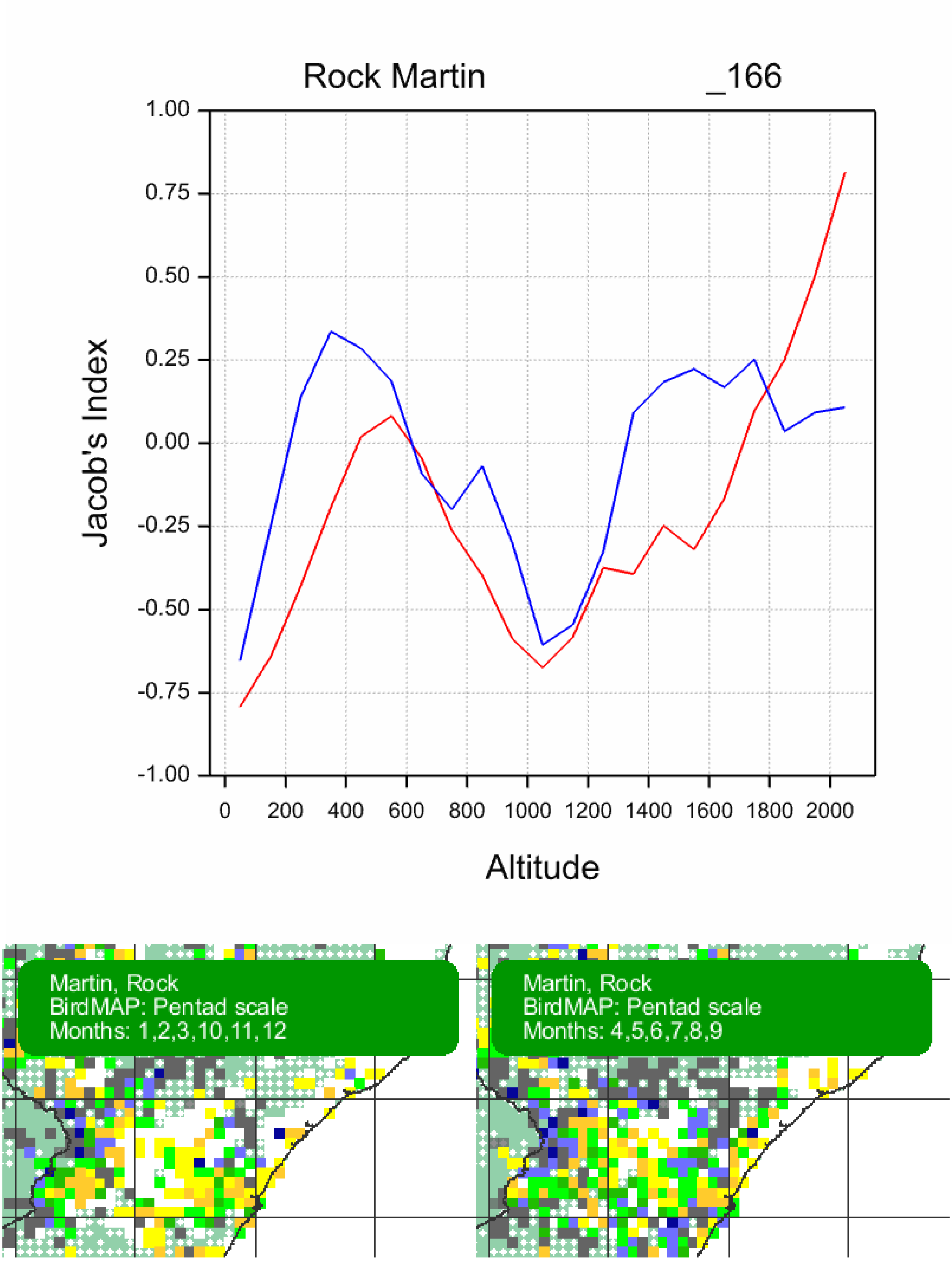


Figure D.23. The altitudinal preference curves for summer and for winter for the Rock Martin, and the summer and winter distribution maps for study transect in KwaZulu-Natal.

Rock Martin is common at all altitudes throughout the year (Little and Bainbridge 1992). In summer Rock Martin has a strong preference for altitudes above 1700 m (Figure D.23). Rock Martin moves off the escarpment to lower altitudes in KwaZulu-Natal in winter (Figure D.23). Interestingly, Rock Martin appears to show a degree of avoidance of altitudes 900–1200 m in summer and in winter (Figure D.23). This avoidance is illustrated in the summer and winter distribution maps in grid cell 2930 (Figure D.23).

Rock Martin is most common in rocky terrain in hilly and mountainous areas, especially along ridges on the escarpment. The distribution of Rock Martin is determined by the availability of suitable nesting sites, which include sheer rock faces, gorges and small rock faces. It has also adapted to breeding on man-made structures, such as bridges and buildings, in urban and farming areas. Rock Martin breeds from spring to early summer with a peak September–January (Cyrus and Robson 1980; Earlé 1997).

The degree of avoidance of altitudes 900–1200 m illustrated in figure D.23 coincides with the mistbelt evergreen forest region in the study transect. This can be understood in terms of possible lack of rocky habitat in the region.

.

Sombre Greenbul, *Andropadus importunus*

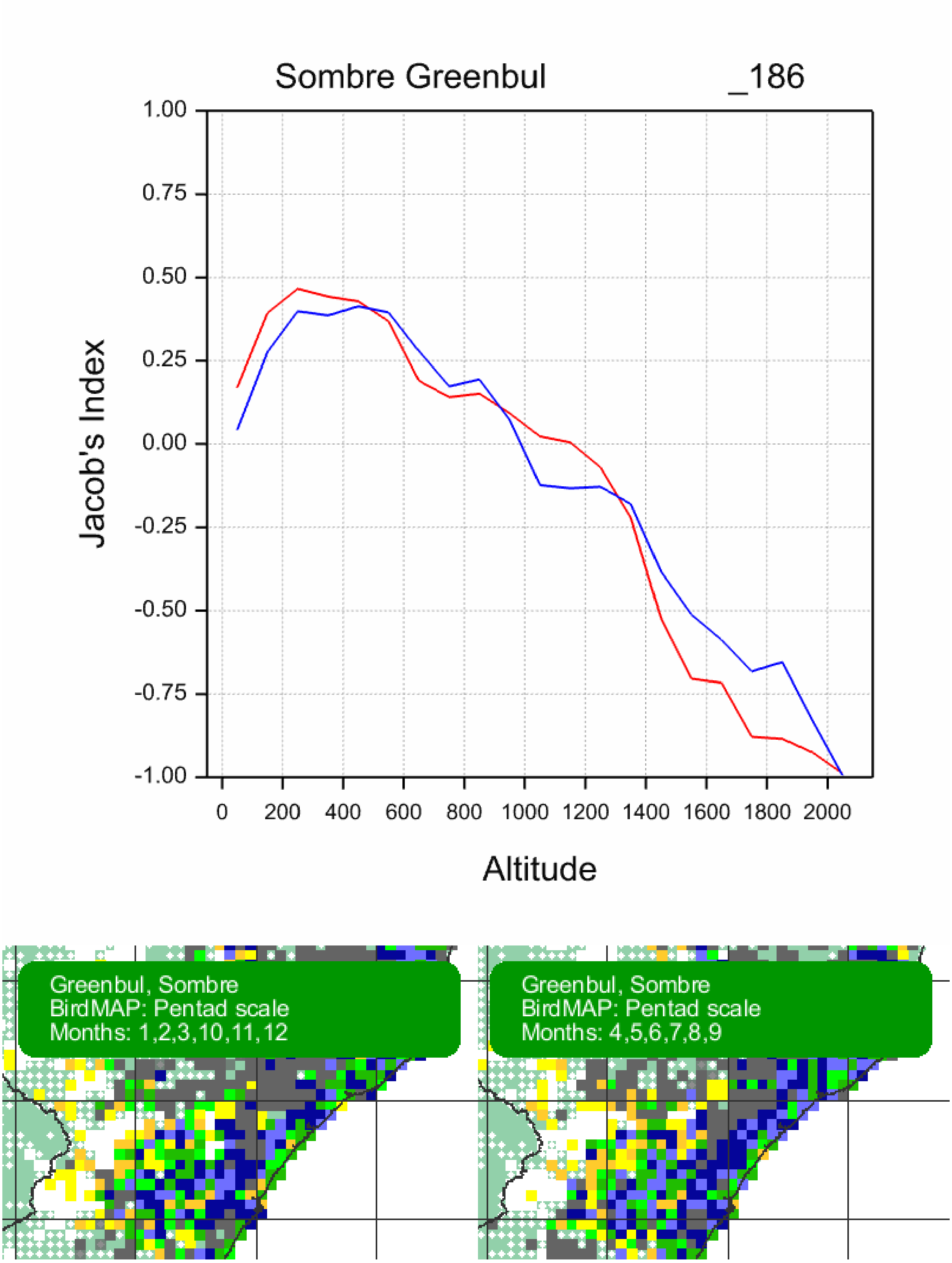


Figure D.24. The altitudinal preference curves for summer and for winter for the Sombre Greenbul, and the summer and winter distribution maps for study transect in KwaZulu-Natal.

Summer and winter altitudinal preference curves and distribution maps of Sombre Greenbuls follow the same trend (Figure D.24). In summer there are more Sombre Greenbuls than one would expect at altitude 0–1100 m. Main altitude preference is 200–300 m. In winter Sombre Greenbuls are preferentially choosing altitudes 0–1000 m with main preference at 400–500 m. Above 1100 m in summer and 1000 m in winter there are fewer birds than one would expect given the area. Numbers of birds decrease with increasing altitude. There is virtually complete avoidance above 2000 m.

Sombre Greenbul is sedentary occurring along the KwaZulu-Natal coastal region and ranging slightly inland along river valleys. It inhabits coastal scrub, coastal and lowland forest, riverine woodland, thornveld and thickets in wooded valleys up to mistbelt evergreen forest (Cyrus and Robson 1980; Oatley 1997d).

Swift Tern, *Sterna bergii*

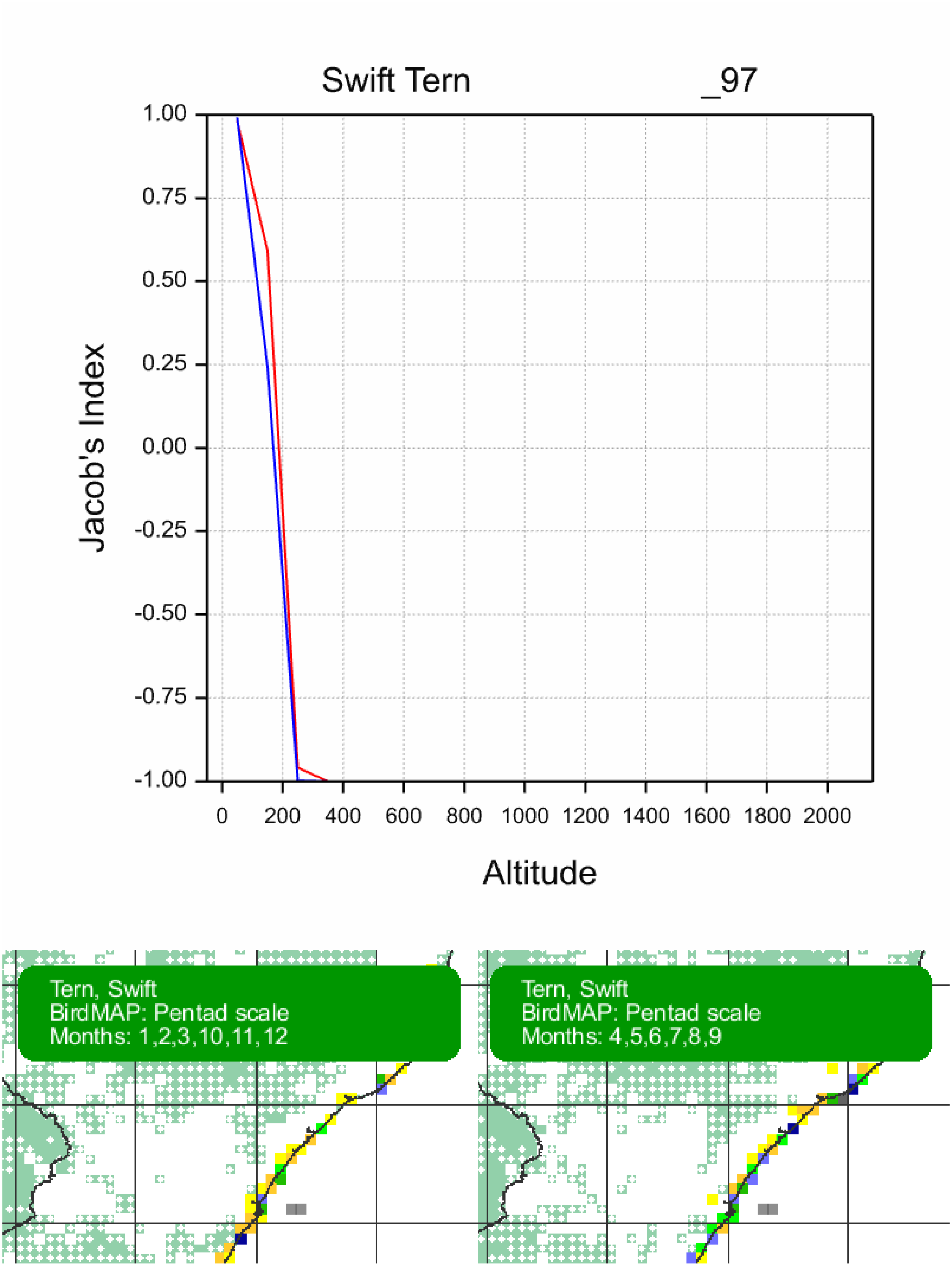
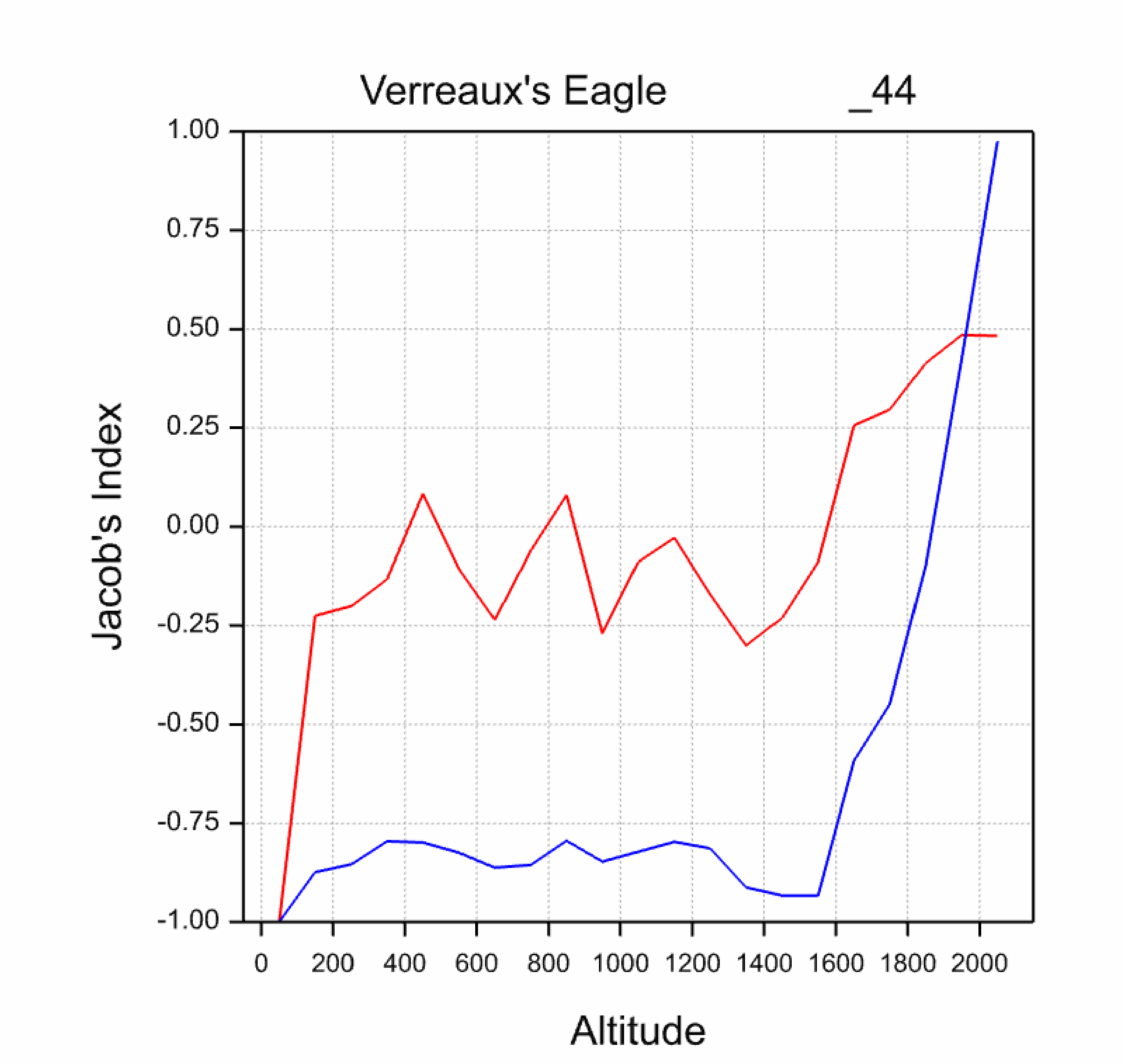


Figure D.25. The altitudinal preference curves for summer and for winter for the Swift Tern, and the summer and winter distribution maps for study transect in KwaZulu-Natal.

The Swift Tern is almost entirely a coastal species; they occur throughout the year in KwaZulu-Natal with an influx in winter (Harrison et al. 1997). The winter influx occurs because Swift Tern breeds in late summer on the offshore islands of the Western Cape and disperses to KwaZulu-Natal in winter (Cyrus and Robson 1980, Cooper et al. 1990, Crawford 1997). This species rarely moves inland (Cooper et al. 1990). Along with the Kelp Gull (Figure D.14), the Swift Tern (Figure D.25) was the only coastal bird species included in this analysis. The caveats written in the text for Kelp Gull (above) apply to Swift Tern as well.

Verreaux’s Eagle, *Aquila verreauxii*



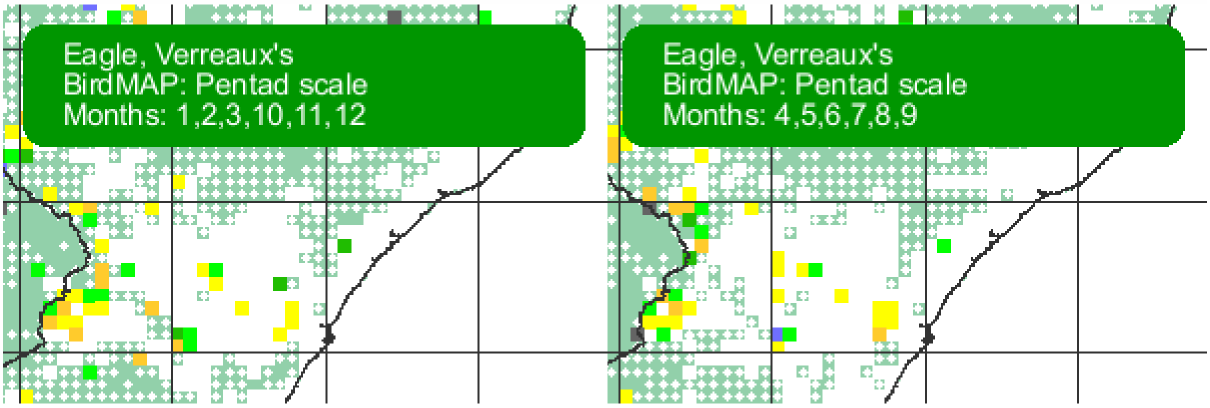


Figure D.26. The altitudinal preference curves for summer and for winter for the Verreaux’s Eagle, and the summer and winter distribution maps for study transect in KwaZulu-Natal.

Verreaux’s Eagle shows little altitudinal preference for altitudes 100–1600 m in summer (Figure D.26). There is strong avoidance of coastal areas and preference for altitudes above 1600 m (Figure D.26). In winter Verreaux’s Eagle has a strong altitude preference of altitudes above 1900 m (Figure D.26). Verreaux’s Eagle is present at lower altitudes as well, but there are only handfuls of birds at these lower altitudes (sea-level to 1600 m).

Verreaux’s Eagle is resident in rocky mountainous habitat throughout the year. It breeds mid- to late winter on mountain cliffs, which tends to hinder movement of any significant distance at that time. The young fledge in late spring, after which they leave their natal territories enabling adults to roam more freely in summer (Davies and Allan 1997). These movements related to breeding are clearly reflected in the summer and winter altitudinal preference curves.

White-bellied Sunbird, *Nectarinia talatala*

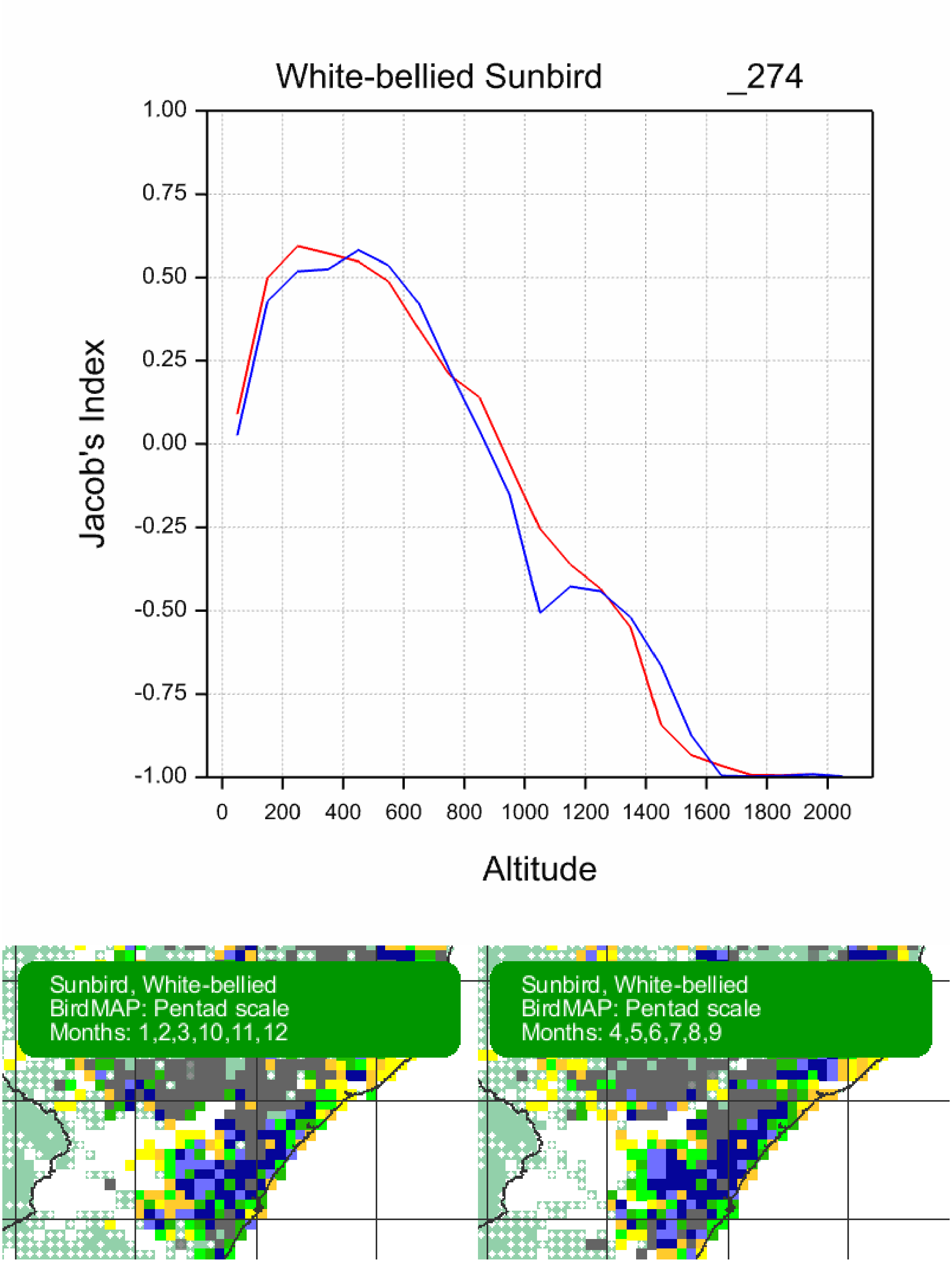


Figure D.27. The altitudinal preference curves for summer and for winter for the White-bellied Sunbird, and the summer and winter distribution maps for study transect in KwaZulu-Natal.

There are more White-bellied Sunbirds than one would expect given the amount of area available from sea-level up to approximately 900 m in summer and winter (Figure D.27). Main summer altitude preference is 200–300 m and main winter altitude preference is 400–500 m. At approximately 900 m the number of sunbirds and the amount of area are in proportion. Above 900 m there are fewer White-bellied Sunbirds than one would predict given the area. The number of birds decreases with increasing altitude with only handfuls present at 1500 m. There is essentially complete avoidance of areas above 1800 m.

White-bellied Sunbird is predominantly a thornveld species but also occurs in mixed woodland, coastal scrub, thickly-wooded valleys, open bush and gardens. When nectar-bearing flowers are most abundant, large numbers of White-bellied Sunbirds are likely to be attracted to these nectar sources regardless of the woodland type (Cyrus and Robson 1980, Tree 1997).

White-starred Robin, *Pogonocichla stellata*

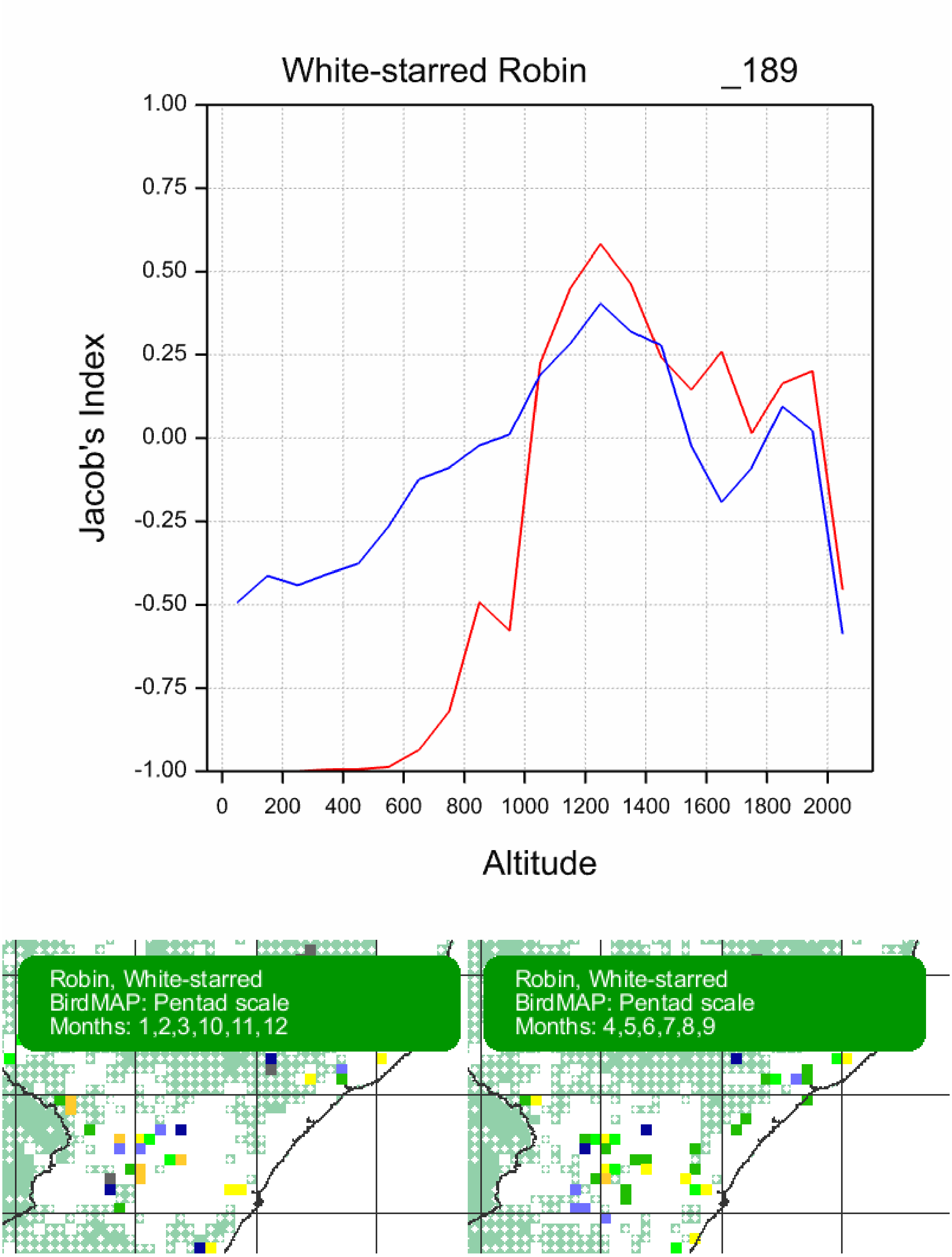


Figure D.28. The altitudinal preference curves for summer and for winter for the White-starred Robin, and the summer and winter distribution maps for study transect in KwaZulu-Natal.

White-starred Robin has a definite altitude preference for altitudes between 1000 m and 2000 m in summer (Figure D.28). There are virtually no birds below 500 m and only a minute portion of the population at 600 m (Figure D.28). In winter there are substantially more birds at lower altitudes, from the coast up to 1000 m, than in summer (Figure D.28). White-starred Robin still preferentially chooses altitudes above 1000 m, but below 1500 m, in winter, indicating that a large portion of the population remains at higher altitudes during winter. Interestingly, the peak altitude preference of 1200–1300 m remains the same for summer and winter (Figure D.28 and Table 3.1). This peak altitude preference occurs towards the upper extent of the Mistbelt Evergreen Forest region.

White-starred Robin occurs throughout evergreen forests in the study area; lowland and coastal forests, interior mistbelt forest and high-altitude forest on the slopes of the Drakensberg up to approximately 1800 m in some places (Cyrus and Robson 1980, Oatley 1982). White-starred Robin breeds from October to December in evergreen forests mainly above 900 m (Oatley 2017). White-starred Robin undertakes a notable altitudinal migration of both young and adult birds and is a winter visitor to coastal and lowland forests (Cyrus and Robson 1980, Oatley 2017, Oatley 1982, Oatley 1997g, Oatley and Arnott 1998). Birds undertaking altitudinal migration follow riverine forest and woody cover along streams and rivers to their lowland localities (Oatley 1997g). This migration is only a partial migration as some individuals remain in the main breeding areas throughout the year (Oatley 1982, Oatley 1997g, Oatley and Arnott 1998). This particularly applies to adult males that are part of the breeding population. They remain at higher altitudes to defend their territories (Oatley 1982, Oatley 1997g, Oatley and Arnott 1998).

White-starred Robin is an example of the method working with rather limited data. It was recorded in 20 pentads in summer and 22 pentads in winter (Table 3.1)

Yellow-throated Woodland Warbler, *Phylloscopus ruficapillus*

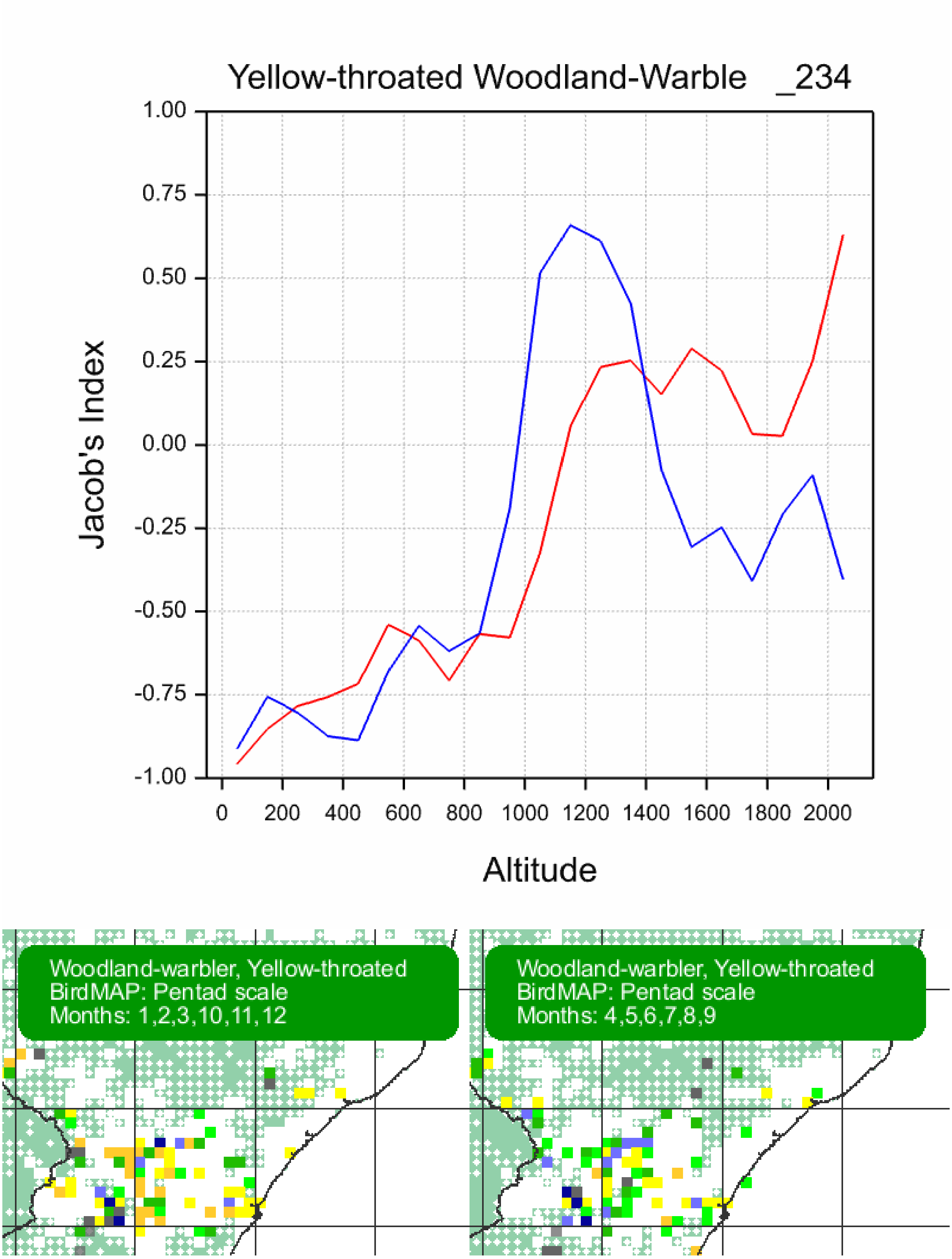


Figure D.29. The altitudinal preference curves for summer and for winter for the Yellow-throated Woodland Warbler, and the summer and winter distribution maps for study transect in KwaZulu-Natal.

In all months of the year Yellow-throated Woodland Warblers are sparsely distributed in lowland areas (Figure D.29). In summer there are only handfuls present at the coast with numbers increasing to be in proportion to the area of land available at 1100 m. Altitude preference continues to increase with there being more birds than expected given the area at 1100–2000+ m. There appears to be a preference for areas in the altitude range 1300–1600 m, but the main preference in areas at 2000+ m.

In winter, like in summer, there are only handfuls of warblers present at the coast. The number of birds increases to be in proportion to the area at 1000 m. There is a definite altitude preference of 1000–1400 m, with main preference at 1100–1200 m. Above 1400 m, altitude preference decreases and there are fewer birds than one would predict given the area. There is not total avoidance of these high altitudes in winter but there are substantially fewer birds present than in summer.

Yellow-throated Woodland Warbler is an evergreen temperate forest species that is able to live in fairly small patches of this habitat (Berruti 1997b). In KwaZulu-Natal the Yellow-throated Woodland Warbler is largely confined to evergreen forests from the Drakensberg range, through the mistbelt region (where it is most common) and sparsely to the coast (Cyrus and Robson 1980). It is a relatively inconspicuous species but forages actively and calls frequently (Berruti 1997b). According to Johnson and Maclean (1994) it is not known to undertake altitudinal migrations although our data suggests otherwise. Oatley (2017) states that Yellow-throated Woodland Warbler is indeed a regular altitudinal migrant from the high forests of KwaZulu-Natal to lower levels, reaching the coast where suitable forest exists.