PERSISTENCE AND VULNERABILITY OF ISLAND ENDEMIC BIRDS

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ABSTRACT

This thesis investigates the dynamic relationship between the processes of extinction on islands and the traits of oceanic island endemic birds associated with persistence and vulnerability. This is explored using the comparative method and a data set of all birds endemic to oceanic islands. Two case studies are then presented to examine the resilience of the island endemic birds of Príncipe and Boné de Joquei in the Gulf of Guinea.

When comparing closely related oceanic island and mainland birds, clutch size is lower on islands and, within islands it continues to decline as the distribution area of a species decreases. Small birds (<27 cm in body length) tend to get larger, and there is a trend for sexual size dimorphism to increase on oceanic islands.

Recent extinction rates are lower on islands that have been exposed to humans for a long period of time. The birds on such islands are also less threatened by the introduction of exotics. A long period of exposure to humans also reduces the probability that the remaining species are flightless, ground-nesting, or non-forest-restricted endemics.

When comparing island and mainland species that have similar areas of distribution, there is no significant difference in extinction risk. However, island birds are more threatened by introduced species. On oceanic islands, flightless birds, ground-nesting birds, birds with larger body size, and habitat specialists are associated with a greater risk of extinction than other birds. Sexually selected traits such as sexual body size dimorphism and dichromatism are not associated with elevated extinction risk.

The resilience of the island endemic birds on Príncipe appears to be associated with a unique land use history and evolutionary exposure to predators, competitors and disease. Finally, a state of super abundance may be essential for the long-term persistence of endemic birds on small remote oceanic islands.

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DECLARATION

All the work presented in this thesis is my own except the following:

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The analyses and first draft are my own work. Georgina was involved in the development of ideas for the study and made editorial and structural changes to the first draft.

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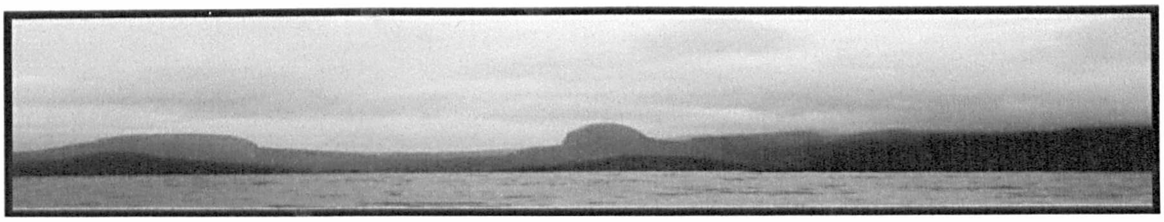
Angus provided information on present land use history and current conservation measures being taken in the region. He also provided the map of Príncipe. The rest of the work is my own.

Appendix

The appendix contains two papers that were written in collaboration while conducting research for my thesis.

Jonathan E M Baillie

TABLE OF CONTENTS



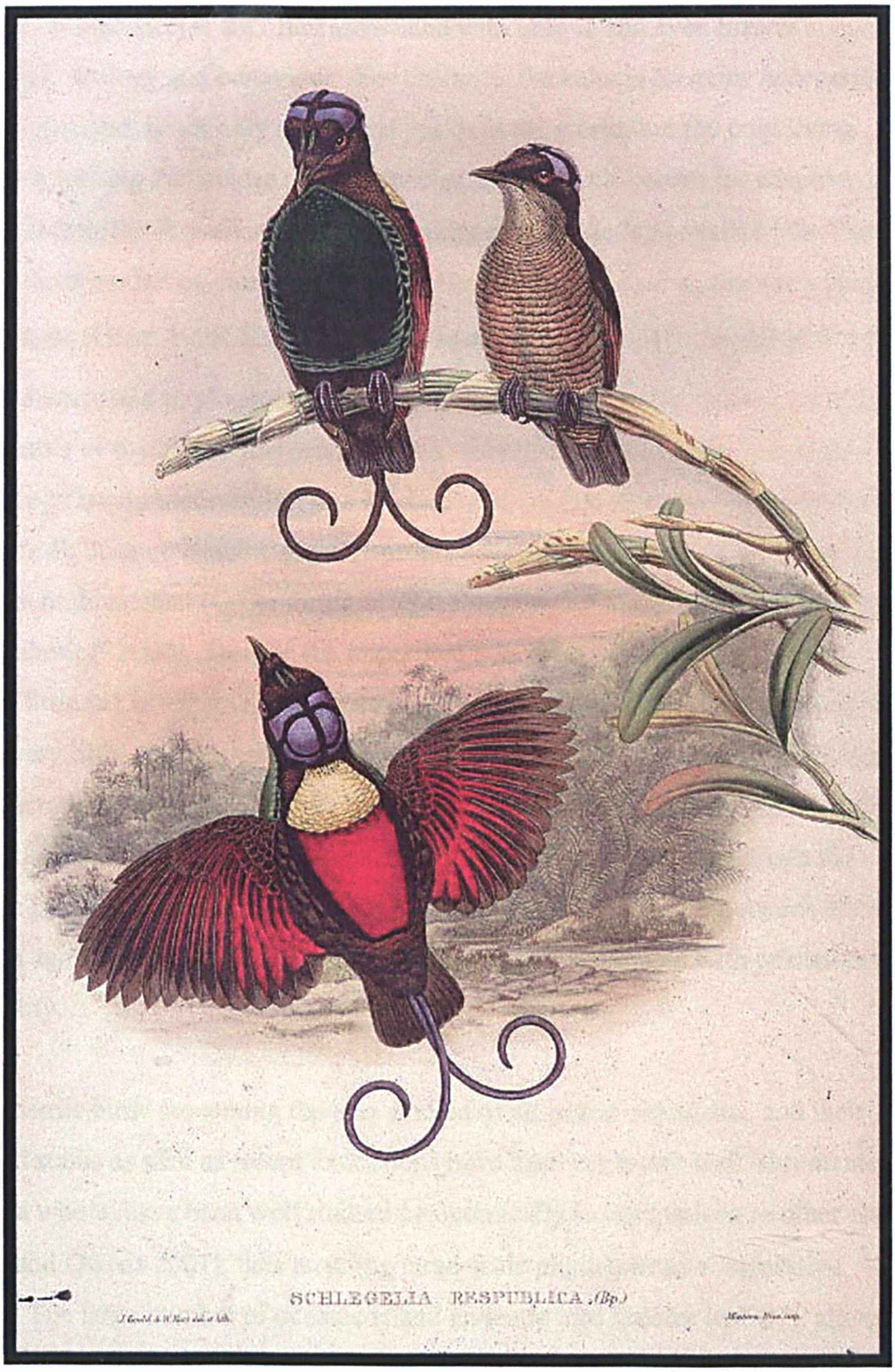
CD This contains the phylogeny used for the analyses in this thesis (Back cover)

TABLE OF FIGURES

TABLE OF TABLES

TABLE OF ILLUSTRATIONS

INTRODUCTION



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The study of island endemic flora and fauna has been central to the foundation of evolutionary theory (Darwin 1839,1859; Wallace 1870) and continues to be fundamental in our understanding of processes such as speciation, adaptive radiation, competitive exclusion, character displacement, sexual selection, dispersal and extinction. Island species are often associated with unique and even bizarre morphology, ecology and behaviour. For example, the kakapo *Strigops habroptilus* from New Zealand, is not only the largest parrot in the world, but the only living flightless or lekking Psittacidae. Island species are also well known for adaptive radiation such as the Hawaiian silversword alliance, *Partula* land snails of the Pacific, *Anolis* of the West Indies, honey creepers of Hawaii and, of course, Darwin's finches of the Galápagos (Grant 1998; Schluter 2000). In addition, islands have provided a refuge for many ancient and phylogenetically unique lineages such as the tuatara, the sole representative of the family Rhynchocephalia. Given the biological and scientific importance of island biodiversity, it is of great concern that most recent extinctions have taken place on oceanic islands, and a disproportionately large number of island species are at present threatened (Groombridge 1992; Johnson and Stattersfield 1990; Whittaker 1998; Simberloff 2000). Despite the imperilled status of island endemic species, relatively little is known about the process of extinction on islands. More specifically, we have very little understanding of why certain island species or communities appear to be extremely vulnerable to extinction while others are exceptionally resilient. In this thesis, I focus on oceanic island endemic birds to provide greater insight into the extinction process on islands by examining the dynamic relationship between extrinsic extinction agents and traits or conditions of island birds associated with persistence or vulnerability.

Island endemic birds are among the best studied of all island organisms, and their threatened status as well as recent extinctions have been relatively well documented. Birds, as a whole, have been well studied taxonomically in comparison to other classes (Bennett and Owens 2001), thus enabling large-scale phylogenetic comparative analyses. The large number of oceanic island endemic bird species (n=987), allows the exploration of global patterns and processes. The vulnerability to extinction of island birds also makes them an important group on which to focus (King 1985; Mountfort 1988, Johnson and Stattersfield 1990). Thirty five percent of oceanic island endemic bird species are at risk of extinction compared to 9% of non-oceanic island birds. In addition, 88% of recent bird extinctions have occurred on oceanic islands (data from

BirdLife International 2000). Greater insight into the process of extinction associated with this group may therefore have important and immediate implications for their conservation.

Species that have become restricted to isolated island environments are often hypothesised to be uniquely susceptible to extinction (Williamson 1981; Atkinson 1989; Vermeij 1991; Paulay 1994). However, it has been suggested that the greater vulnerability of island endemic birds is largely a result of their very small distributions (Simberloff 1995; 2000). Thus, they may be primarily susceptible to processes associated with the small population paradigm (reviewed by Caughley 1994; Simberloff 1998) such as demographic stochasticity, environmental stochasticity, and reduced heterozygosity. Thus, if oceanic island and mainland birds with similar distributions are compared, island endemic birds may not be more threatened to processes of extinction such as overkill, habitat destruction and fragmentation, impacts of introduced species, and chains of extinction. These processes of extinction have been coined by Diamond (1984b, 1989b) as the 'evil quartet'.

Manne *et al.* (1999) recently demonstrated that passerine island birds off the coast of the Americas were no more vulnerable to extinction than their mainland relatives, when they controlled for species' distributions. In fact, when only passerines with distributions between 1,000 and 100,000 km^2 were considered, and montane species were excluded from the analysis, then island birds were less threatened than mainland species. Thus, it is unclear whether oceanic island birds are especially susceptible to extinction, or whether there are specific processes of extinction to which they are particularly prone or resilient.

To understand why island birds might be more extinction prone or resilient to specific processes of extinction, we must establish how island species consistently differ from their mainland relatives. There is great variation in the size of oceanic islands, their distance from the mainland, latitude, and habitat types. Thus, adaptations of species may be expected to be specific to individual islands. However, species that colonise oceanic islands tend to find themselves in a species poor environment with fewer competitors or predators. Thus, island species may be subjected to certain common selection pressures resulting in particular ecological, evolutionary or behavioural adaptations (see MacArthur *et al.* 1972; Diamond 1975; Williamson 1981; Stamps and Buechner 1985; Grant 1998; Blondel 1991, 2000).

Examples of documented trends associated with island endemic birds are flightlessness (Diamond 1981; Roff 1994; McNab1994a), a change in body size (Amadon 1953; Grant 1968; McNab 1994b), long bills and tarsi (Murphy 1938; Grant 1965a), reduced clutch size (Cody 1966; Lack 1970; Grant 1998), increased sexual size dimorphism (Selander 1966), decreased dichromatism (Mayr 1942, Amadon 1953; Sibley 1957; Grant 1965b; Herremans 1990), increased fidelity (Griffith *et al.* 1999; Griffith 2000; Møller 2001), island tameness (Atkinson 1985; Grant 1998), and niche expansion as well as population inflation (MacArthur *et al.* 1972; Blondel 1991). However, few of the island patterns have been rigorously tested and modern comparative methods are required to determine if these observed island trends can truly be generalised (Grant 1998).

The high extinction risk associated with island endemic birds is not a recent phenomenon. The first human colonists on oceanic islands have been implicated in extensive prehistoric island bird extinctions (Diamond 1982, 1984a, 1989a; Olson and James 1982; Cassels 1984; Steadman and Pregill 1984; Dye and Steadman 1990; Milberg and Tyrberg 1993; Pimm *et al.* 1994; Benton and Spencer 1995; Wragg 1995; James 1995; Steadman 1995; Steadman *et al.* 1999). Subfossil remains of extinct endemic birds continue to be detected on most islands that are surveyed (James 1995). On the tropical Pacific islands, Steadman (1991, 1995) has estimated that more than 2,000 species of birds went extinct during the period of prehistoric human colonisation (most of which were flightless rails). If this estimate is correct, then at least one fifth of all birds extant during the early Holocene are now extinct (Milberg and Tyrberg 1993).

Pimm *et al.* (1994) observed that birds inhabiting Pacific islands that have been colonised by humans for a long period of time are at present less threatened, and have experienced fewer recent extinctions than those species on islands colonised more recently. It is, therefore, possible that prehistoric human-caused extinctions have resulted in some island bird communities appearing less susceptible to extinction simply because the vulnerable species have already been driven to extinction. This process is known as the "extinction filter effect" (Coope 1995; Balmford 1996). An extinction filter occurs when a region's biota is faced with a novel extinction process. Initially, extinction rates may be high but, once the particularly vulnerable subset of species has been removed, the remaining birds are less susceptible to the same or similar extinction processes. If past patterns of human-caused extinction truly influence present patterns of susceptibility, then understanding the extent and location of past extinction filters may help to identify potential extinction-prone or resilient island communities.

Thus, it may be important to have an understanding of the various dominant processes of extinction in the distant past and how they have changed over time. Unfortunately, it is difficult to infer the dominant causes of extinction during prehistoric times. However, it is clear that exploitation by humans (Diamond 1984a; Milberg and Tyrberg 1993; Holdaway 1999), introduced species (Atkinson 1985; Diamond 1984ab; Keegan and Diamond 1987) and habitat destruction (Olson and James 1982; Flenley and King 1984; Holdaway 1989; Steadman 1995) were all contributing factors. The dominant processes of extinction over the past 500 years are also poorly understood. However, a literature review for a subset of recent extinctions suggests that introduced species and human exploitation were previously the dominant causes of extinction (Johnson and Stattersfield 1990). Identifying present processes of threat is also challenging (Green 1994, 1999), but assessments of the conservation status of all oceanic island birds suggest that habitat loss followed by introduced species are now the dominant processes of extinction (Stattersfield *et al.* 1998).

If extinction filters have occurred, it may be possible to identify species with specific life history, morphological or ecological traits that have been selectively removed from the island system by humans. If species with specific traits are extremely extinction-prone, then they should be rare or absent where humans have been present for a long period of time. Examples of island endemic species with traits that are well represented in the subfossil record are flightless birds (Olson and James 1982; Steadman 1995; Olson and Jouventin 1996; Rando *et al.* 1999; Steadman *et al.* 1999), ground nesting birds (Duncan and Blackburn submitted) and large bodied birds (James 1995; Duncan and Blackburn submitted). Although many of the particularly extinction prone species may have already been removed from the island system, there may be specific life history, morphological or ecological traits of some species or groups of species, that make them more prone to extinction than others. Identifying extinction prone traits of island endemic birds is important because it may help to identify species that are less well adapted to persistence within a restricted-range environment. It may also help to identify whether there are truly specific traits associated with island endemic birds that make them especially susceptible to human related threats.

While many traits have been hypothesised to be associated with increased extinction risk on islands, such as flightlessness (Diamond 1984b; King 1985; Johnson and Stattersfield 1990, Roff 1994; McNab1994a), larger body size (Duncan and Blackburn submitted) and heightened secondary sexual characteristics (McLain *et al.* 1995; Sorci *et al.* 1998; McLain 1999), the only conditions that have been consistently linked to greater extinction risk, are species with small distributions or populations (Diamond 1984b; Pimm *et al.* 1988). However, until now, a large-scale comparative analysis of traits that may be correlated with greater extinction risk of island endemic birds has not been conducted.

Analyses of all birds or studies primarily focusing on mainland species have identified a few traits associated with increased extinction risk. Birds at greater risk of extinction tend to have a smaller clutch size (Bennett and Owens 1997) and larger body size than those at lower risk (Bennett and Owens 1997; Gaston and Blackburn 1995; Pimm *et al.* 1988). However, a recent study by Owens and Bennett (2000) has demonstrated that large and small species may be susceptible to different threat processes. Specific groups of birds that are associated with increased extinction risk are species found in deep-rooted lineages (Gaston and Blackburn 1997) or species poor taxa (Russell *et al.* 1998; Hughes 1999; Lockwood *et al.* 2000; Purvis *et al.* 2000).

Given the present threat level and past extinction rate of oceanic island endemic birds, it is ironic that we might learn about traits or conditions associated with persistence or resilience from this group of species. However, a few island endemic bird communities, such as the endemic birds of Príncipe in the Gulf of Guinea, appear to have escaped extinction and remained abundant despite extensive habitat destruction, the introduction of exotic species, and human exploitation. Many species of island endemic bird are also remarkable for their ability to persist within extremely restricted distributions. The Lord Howe white-eye *Zosterops tephropleururs*, Razo lark *Alauda razae*, Noronha vireo *Vireo gracilirostris* and Nihoa finch *Telespiza ultima* are examples of birds that persist within distributions of less than 20km^2. A subspecies of the Príncipe seedeater *Serinus rufobrunneus fradei*, has persisted on an islet less than 1 km^2 for thousands of years. Understanding the conditions, traits, or mechanisms associated with persistence in a restricted-range environment, will help to identify communities of species that may be more resilient to escalating human-related threats. It will also enable conservationists to manage for conditions necessary for the future persistence of island endemic birds.

The aim of this thesis is to provide insight into the extinction process on oceanic islands, both in terms of the changing processes of extinction as well as the traits or conditions associated with persistence or vulnerability. A phylogeny has been constructed for all birds so that the comparative approach can be employed, with controls for the non-independence of closely related species. I have addressed nine main questions in this thesis: Are there unique traits associated with island endemic birds? Have prehistoric human-caused extinctions influenced present patterns of avian extinction risk? Has the process of extinction changed from prehistoric times to the present? Have humans been responsible for the selective removal of specific life history or ecological traits on islands? Are island or mainland bird species with similar distributions at greater risk of extinction? Are the extinction processes on islands and the mainland the same? Which life history, ecological, or morphological traits are associated with species that are more vulnerable to extinction? What is the status and distribution of the endemic birds of Príncipe and why has this community of species been so resilient to extinction? What traits or conditions have enabled the Príncipe seedeater *Serinus rufobrunnea fradei* to persist on an islet of less than 1km^2 for thousands of years?

This thesis is arranged as follows:

Chapter 1 introduces the oceanic island data set, endemic bird data set, the phylogeny constructed for all birds, and the comparative methods employed for chapters 2, 3, 4, and 5. General patterns in the data are also described.

Chapter 2 identifies life history or morphological traits of oceanic island endemic birds that differ consistently from their mainland relatives. The traits considered are clutch size, body size and sexual size dimorphism. The variation in these traits is also examined within islands. This is in relation to biogeographic features of a species, such as its distance from the mainland, total area of geographic distribution, and latitude.

Chapter 3 explores patterns of recent extinction and threat to oceanic island birds in order to test whether early human colonists to oceanic islands have acted as an extinction filter. If humans have acted as an extinction filter, then fewer recent extinctions and threatened species should be found on islands having a long history of human occupation. The relationship between the date of first human colonisation and levels of susceptibility to specific extinction processes such as human exploitation, habitat loss, and introduced species are also explored.

Chapter 4 examines whether humans have caused the selective extinction of specific avian life history, morphological or ecological traits on oceanic islands. This is tested by comparing birds on islands recently or never colonised by humans with birds inhabiting islands colonised in the distant past, to determine if specific avian traits are less frequent or absent on islands with a longer exposure to humans. Clutch size, body size, flight ability, ground nesting, and forest specialism are the five traits examined.

Chapter 5 first addresses whether island or mainland birds are more threatened with extinction. Threat types are then broken down into introduced species, exploitation, and habitat loss to see whether island or mainland birds are particularly susceptible to a specific threat process. Second, life history, ecological and morphological traits of island endemic birds are analysed to determine whether they are correlated to high levels of extinction risk. The traits considered are body size, clutch size, sexual size dimorphism, dichromatism, flight ability, nest site, and habitat specialisation. The analyses are first conducted for all oceanic island birds, and then restricted to birds that inhabit islands or island groups that have been colonised by humans for less than 1000 years. The latter approach has been employed to reduce the extinction filter effect, caused by the selective removal of species with vulnerable traits, on islands that have been colonised by humans for a long time. The relationship between the above traits and species threatened specifically by introduced species, is also examined.

Chapter 6 is a case study of the extremely resilient endemic birds of Príncipe in the Gulf of Guinea. Despite facing threats common to many islands, such as habitat destruction and introduced species, there have been no recorded extinctions. The endemic birds are not particularly threatened and they remain the most abundant species on the island. Research, carried out in the mountain and southern-lowland forest, along with historic and recent studies, are combined to estimate the total distribution and present conservation status of the poorly-known endemic birds. The conditions that have enabled the remarkable persistence of these restricted-range endemics are discussed.

Chapter 7 focuses on an endemic subspecies of seedeater, *Serinus rufobrunneus fradei*, restricted to an islet located less than 3 km away from Príncipe that is less than 1 km^2 in area. An estimate of the population is given, using distance sampling and new observations are made of its morphology, song, and ecology. Mechanisms and factors enabling this subspecies to persist within such a small distribution are addressed, and the implications of this for the management and conservation of isolated, restricted-range birds are discussed.

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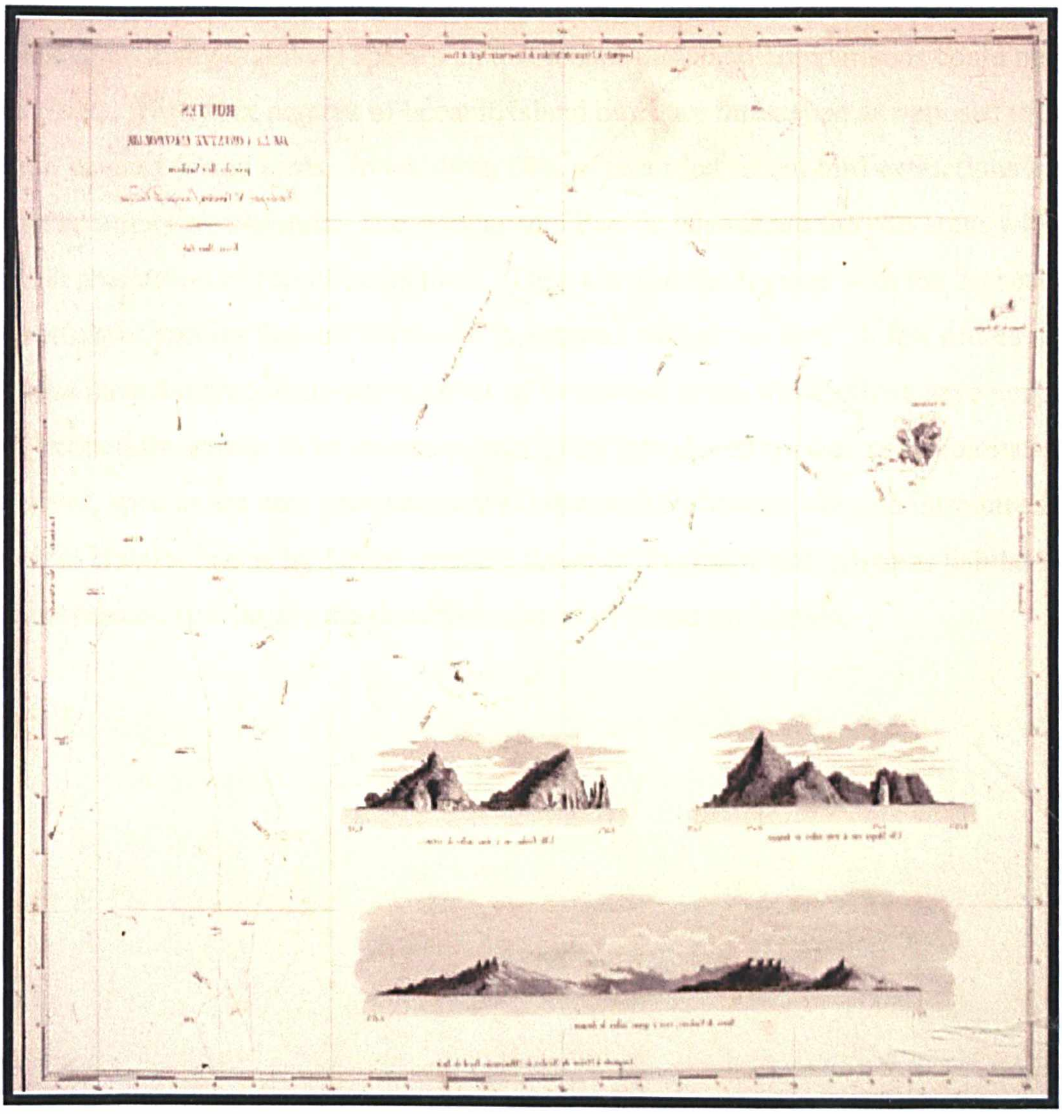
CHAPTER 1

INTRODUCTION TO THE DATABASE AND GENERAL METHODS



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Abstract

A phylogeny of all extant and recently extinct birds has been constructed to allow comparative analyses that control for the non-independence of closely-related species. A database has been built where each oceanic island bird has been assigned a total area of geographic distribution, minimum distance from the mainland, and average latitude. Data is also collected on the habitats occupied by species, their threat status, and an estimate of the date when they were first exposed to human colonists. Information on species life history, ecology and morphology has also been collected for many of the island endemic birds. In addition, life history and morphological data has been collected for many mainland species so that island-mainland comparisons could be conducted. Thirty six percent of oceanic island birds are threatened as opposed to 9% of non-oceanic island birds. In addition, 88% of recorded recent bird extinctions have occurred on oceanic islands. The African and Pacific islands are the two areas with the highest proportion of recent extinctions. They are also the regions with the highest proportion of species that are at present threatened with extinction. A few orders and families have a disproportionate number of threatened birds while others have very few. Past extinctions appear to be caused primarily by introduced species and exploitation. However, species are now predominantly threatened by habitat loss and introduced species. Habitat loss is by far the greatest threat on the mainland, whereas habitat loss and introduced species are the dominant causes of threat on islands.

Introduction to the database

Island database

Ultimately, the definition of an oceanic island is somewhat arbitrary in terms of the size, limit and extent to which the island has been isolated from the mainland. In this database, oceanic islands are defined as islands that are smaller than 200,000 km^2 and are separated from the mainland by a sea depth of greater than 200 m. This definition is consistent with recent large-scale studies of oceanic island birds (McCall 1997; Stattersfield *et al.* 1998). The largest island in the database is Celebes (180,680 km^2) and the smallest is Cousine (0.25 km^2). The database contains area, distance from the mainland, latitude, longitude and, for many, the date of first human colonisation for over 500 oceanic islands or island groups. Information is also provided on whether the landmass is an island or archipelago, the ocean basin in which it is located, the nearest continent, other given names, and the political country affiliation.

The total area of each island or island group was obtained using the UNEP Regional Seas Directories and Bibliographies, provided by WCMC (Dahl 1991), UNEP/IUCN Vol 1-3 (1988a,b,c) or BirdLife International (2000). ArcView 3.1 and VMAP Level 0 data were used to determine the area of islands or island groups where no reference could be found. Distance is defined as the minimum distance of an island or archipelago from the nearest continental land mass (Madagascar has been included as a continent due to its large size). These distance measurements are from McCall (1997) supplemented by measurements from Encarta World Atlas (1998b). Data on latitude and longitude are based on Dahl (1991) also supplemented with data from Encarta World Atlas (1998b). The date of first colonisation refers to the time when human beings first arrived to an island. Estimates of the date of first colonisation are obtained from Webster (1972), Olson and James (1982), Steadman *et al.* (1984), Munro (1988), Jones *et al.* (1992), Milberg and Tyrberg (1993), Pimm *et al.* (1994), Wragg (1995), Steadman (1991, 1995), Vianna (1997), Encyclopaedia Britannica (1998a) Microsoft Encarta Encyclopaedia (1998a) and Steadman *et al.* (1999).

Bird database

The bird database includes all extant birds recognised by Sibley and Monroe (1990, 1993). For recently extinct birds the taxonomy follows IUCN (2000) and BirdLife International (2000). Recent extinctions are defined as species that have become extinct within the past 500 years. Order, family, tribe, and common names are also given for each species based on Sibley and Monroe (1990, 1993) for extant species, and BirdLife International (2000) for recently extinct species. The threat status of a species and the dominant processes of threat are based on BirdLife International (2000). Species are classified as lower risk, least concern (LRlc), lower risk, near threatened (LRnt), lower risk, conservation dependent (LRcd), vulnerable (VU), endangered (EN), critically endangered (CR), extinct in the wild (EW), extinct (EX), or data deficient (DD) (see IUCN 1994; BirdLife 2000). Threat types have been summarised into three major categories - those threatened by introduced species, by exploitation, or by habitat loss (BirdLife 2000). The threat from introduced species includes introduced predators, competitors, habitat modifiers, and potentially species that transmit disease. Exploitation refers to persecution by humans whether, for subsistence, sport hunting or the pet trade. Habitat loss is most often associated with deforestation, but may also result from events such as drainage or pollution. Data from Stattersfield *et al.* (1998) is used to classify birds into broad-range or restricted-range species. Restricted-range species are those with breeding distributions of less than 50,000 km^2, and broad-range species those greater than 50,000 km^2 (see Stattersfield *et al.* 1998). Finally, I distinguish oceanic island endemic birds as those species with distributions restricted to oceanic islands. Species that inhabit islands separated from the mainland by a sea level of less than 200 m, which do not breed on the mainland, are considered continental island species. A species' with any part of its breeding distribution on the mainland is also considered a mainland species.

More detailed data have been collected for oceanic island endemic birds (excluding seabirds). For each such species, the island(s) on which they have been observed to breed are listed. The list of islands occupied by each species is based on Howard and Moore (1984,1991), McCall (1997), Sibley and Monroe (1990,1993), Stattersfield *et al.* (1998) and, for the extinct species, on IUCN (2000) and BirdLife International (2000). These islands correspond with those listed in the island database. The number and type of habitats occupied by each species is also given for all oceanic island endemic terrestrial birds, based on Collar *et al.* (1994), Stattersfield *et al.* (1998), Sibley and Monroe (1990,1993). Male body mass, female body mass, body length, clutch size, flight ability, nest site, and dichromatism are recorded for many of the oceanic island bird species. Body mass, body length and clutch size, has also been collected for many mainland species. The definitions of these traits and the extent of data collection are discussed in the relevant chapters.

Island and bird database

The island database and bird database are merged so that each island endemic species may be assigned a total land distribution, minimum distance from the mainland, average latitude, and an estimate of the date when humans first colonised an island within their distribution. For the analyses, the total area for a species is the sum of the area of the islands where a bird is found. Mapping the exact distribution of species would have been preferable, but the precise distribution of many island birds is unknown, and this measure provides a rough surrogate. Minimum distance is defined as the minimum distance of a species range from the nearest continental landmass (including Madagascar). A species is assigned a latitude score from an average of the latitudes of the islands where the bird is found. Finally, first human colonisation is an estimate of how long before the present (BP) humans arrived on an island or archipelago within a species' range. For the analyses, total area and distance are transformed using natural logarithms and for first colonisation, I use the natural logarithm of date (BP) +1.

Comparative approach

When using the comparative approach, species data can not generally be treated as independent data points for statistical analyses because species share associations among characteristics by decent from common ancestors rather than independent evolution (Felsenstein 1985; Harvey and Pagel 1991; Pagel 1992). Previous comparative studies of birds have shown that many of the traits studied in this thesis show such phylogenetic pattern, necessitating phylogenetic analysis: (see Cotgreave and Harvey 1992; Roff 1994; Barraclough *et al.* 1995; Cotgreave 1995; Bennett and Owens 1997; MacCall 1997; Russell *et al.* 1998; Hughes 1999; Lockwood *et al.* 2000; Bennett and Owens 2001). To control for the effect of phylogenetic non-independence, analyses have been performed on evolutionarily independent contrasts calculated using the Comparative Analyses by Independent Contrasts (CAIC) software package (Purvis and Rambaut 1995). The CAIC program calculates comparisons between the descendants of each node in the phylogeny and produces 'contrasts'. The contrast at each node assesses the correlation between the y and x variable (i.e. are big values of y associated with big values of x, or with small values?). These comparisons are technically linear contrasts and can be pooled in a meta-analysis to determine if there is an overall relationship between the traits or characteristics of interest.

A phylogenetic hypothesis is required for this approach. I used the avian molecular phylogeny of Sibley and Ahlquist (1990) that is based on DNA-DNA hybridisation experiments, with classification below the level of tribe following Sibley and Monroe (1990, 1993). Although contentious, Sibley and Ahlquist's (1990) is the only comprehensive attempt, based on molecular data, to reconstruct a phylogeny for the entire class of birds (Bennett and Owens 2001) and remains the most objective avian phylogeny to date (Mooers and Cotgreave, 1994; Cotgreave and Pagel 1997). Branches in the phylogeny are assumed to be of equal length, as molecular estimates of lengths have not been determined for most taxa below the tribe level.

There are two algorithms in CAIC that may be used for calculating contrasts: CRUNCH and BRUNCH. Generally, CRUNCH is used when all the variables in the model are continuous, and BRUNCH is used when the predictor variable is categorical. CRUNCH uses species values to provide average estimates at higher nodes in the phylogeny. This enables CRUNCH to make contrasts both between very closely related species (e.g. sister taxa) and among higher nodes in the phylogeny. BRUNCH on the other hand, compares only the tips of the tree using the values of each species only once. Thus, CRUNCH has greater statistical power, but makes more assumptions (Purvis and Rambaut 1995).

For the analyses in this thesis where one of the variables is categorical, the BRUNCH algorithm has been employed. Using this approach, the only evolutionary assumption made for the categorical variable is that, if two sister taxa have the same character state, their ancestor is presumed to have shared that state too. The contrasts in the continuous variable are tested for normality and a one-sample t-test is used to determine significance. All contrasts were also analysed using Wilcoxon's test which assumes neither normality nor homogeneity of variance (Siegel and Castellan 1988).

For comparative analyses with continuous variables, the CRUNCH algorithm was first explored. However, the ecological variables consistently did not conform to the evolutionary and statistical assumptions of CAIC. The CAIC program assumes equal rates of evolutionary change per unit branch length. If traits do not conform to Felsenstein's (1985) model of evolution then the scaling will be incorrect resulting in inappropriate standardised contrasts. In my analyses, this problem appears to be exacerbated when the average state of a node is estimated at higher levels in the phylogeny. If the nodal estimates are not relatively accurate then the model of evolution is violated and the contrasts lose evolutionary independence. Thus, the BRUNCH algorithm has been used for continuous variables as contrasts are only conducted at the tips of the phylogeny and therefore each contrast maintains evolutionary independence. This more conservative approach resulted in fewer violations of the assumptions. However, it does not completely resolve the issue of ecological variables being less likely to conform to assumptions about evolutionary process. Thus, the regressions through the origin, including ecological variables, should be interpreted with caution.

All sets of contrasts were assessed to determine if they violated the evolutionary or statistical assumptions, as outlined by Purvis and Rambaut (1995). First I test whether the rate of evolution is independent of a trait's current value (e.g. is the rate of body size evolution comparable across the body size spectrum?). This is tested by regressing the absolute values of the contrasts on the estimated nodal values, and testing whether the slope differs significantly from zero (Purvis and Rambaut 1995). If it does, data transformation and/or branch length transformations are in order (Garland *et al.* 1992). This requirement provides the rationale for logarithmic transformation of many continuous variables: while absolute changes in body size are likely to be greater in large-bodied than in small-bodied lineages (e.g. ostrich vs hummingbird), proportional changes are more likely to be equal across the whole range. Second I test whether the standardised contrasts are appropriate for regression analysis. This has been done by plotting the absolute values of the contrasts against the square root of the variance of the unstandardised contrasts (Purvis and Rambaut 1995). In the few cases where the assumptions are not met the residuals of the regression have been assessed to assure that they approximate a normal distribution. All contrasts for each analysis have also been plotted to ensure that the results are not driven by one or more influential observations.

To determine whether a categorical trait is related to a continuous trait, independent of other continuous variables, the control variables must be tested individually (see Purvis and Rambaut 1995). This has been done by first analysing the continuous variable and the control variable in CAIC using the CRUNCH algorithm, with the control variable as the predictor. The dependent variable has then been regressed on the control variable through the origin. The slope of this relationship is then fitted to the raw species data set and the residuals taken from the line (Purvis and Rambaut 1995). The residuals and the original categorical variable are then analysed using the BRUNCH algorithm.

All extant oceanic island birds recognised by Sibley and Monroe (1990, 1993) were used in this phylogeny with the exception of 20 species within the families Brachypteraciidae, Mesitornithidae, Pluvianellidae, Philepittidae, Callaeatidae, Picathartidae, Hypocoliidae, as the affiliation of these families within the phylogeny are uncertain (Sibley and Ahlquist 1990). Species driven extinct over the past 500 years or species that are extinct in the wild were only included in analyses if they could be placed in a genus recognised by Sibley and Monroe (1990, 1993). This resulted in the exclusion of 16 of the 116 extinct or extinct in the wild oceanic island species recognised by BirdLife International (2000). For extinct species, where Sibley and Monroe (1990, 1993) and BirdLife (2000) include the same species with different nomenclature, the taxonomy of Sibley and Monroe is followed.

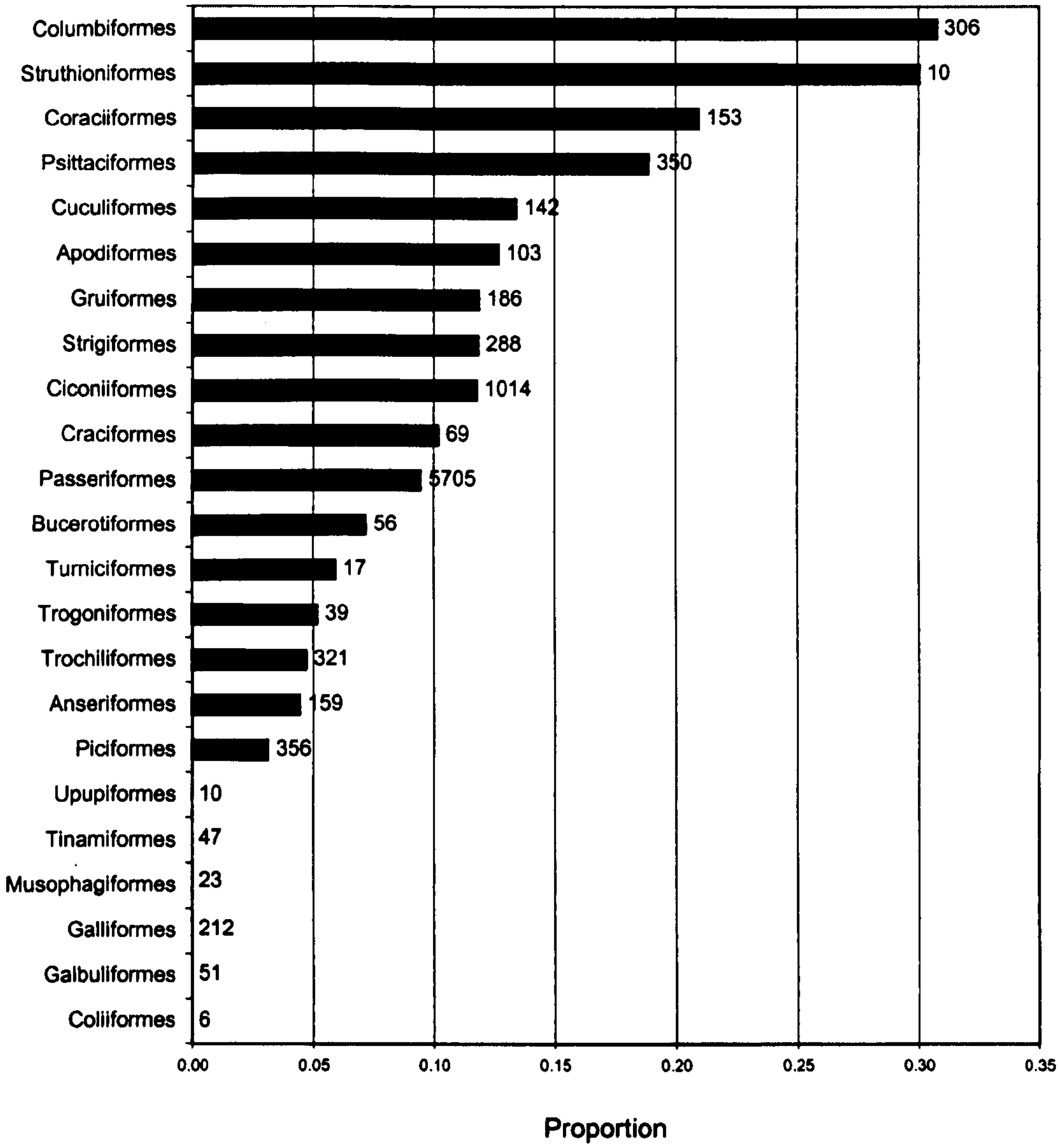
General patterns in the database

The data set includes 9623 extant birds from 145 families and 23 orders Sibley and Monroe (1990, 1993). Of the 9623 species, 987 are restricted to oceanic islands. Of these 987, 84 have been classified as seabirds. In addition to the 9623 extant species, there are an estimated 128 birds that have gone extinct in the past 500 years (BirdLife International 2000), 112 of which were restricted to oceanic islands.

Oceanic island birds

For all bird species, orders that contain the highest proportion of species restricted to oceanic islands are the Columbiformes (pigeons and doves), Struthioniformes (kiwis), Coraciiformes (kingfishers, todies, and rollers), Psittaciformes (parrots, cockatoos, lories, and macaws), and Cuculiformes (cockoos, and coucals). Orders that are noticeably rare or absent from oceanic islands, given their relatively high number of species, are Galliformes (francolins, quails, pheasants, peafowl), Piciformes (woodpeckers, toucans, barbets), Trochiliformes (hummingbirds), and Galbuliformes (jacamars and puffbirds) (Figure 1.1).

Figure 1.1. The proportion of species in different avian orders found on oceanic islands. The numbers at the end of the columns represent the total number of species in the order.



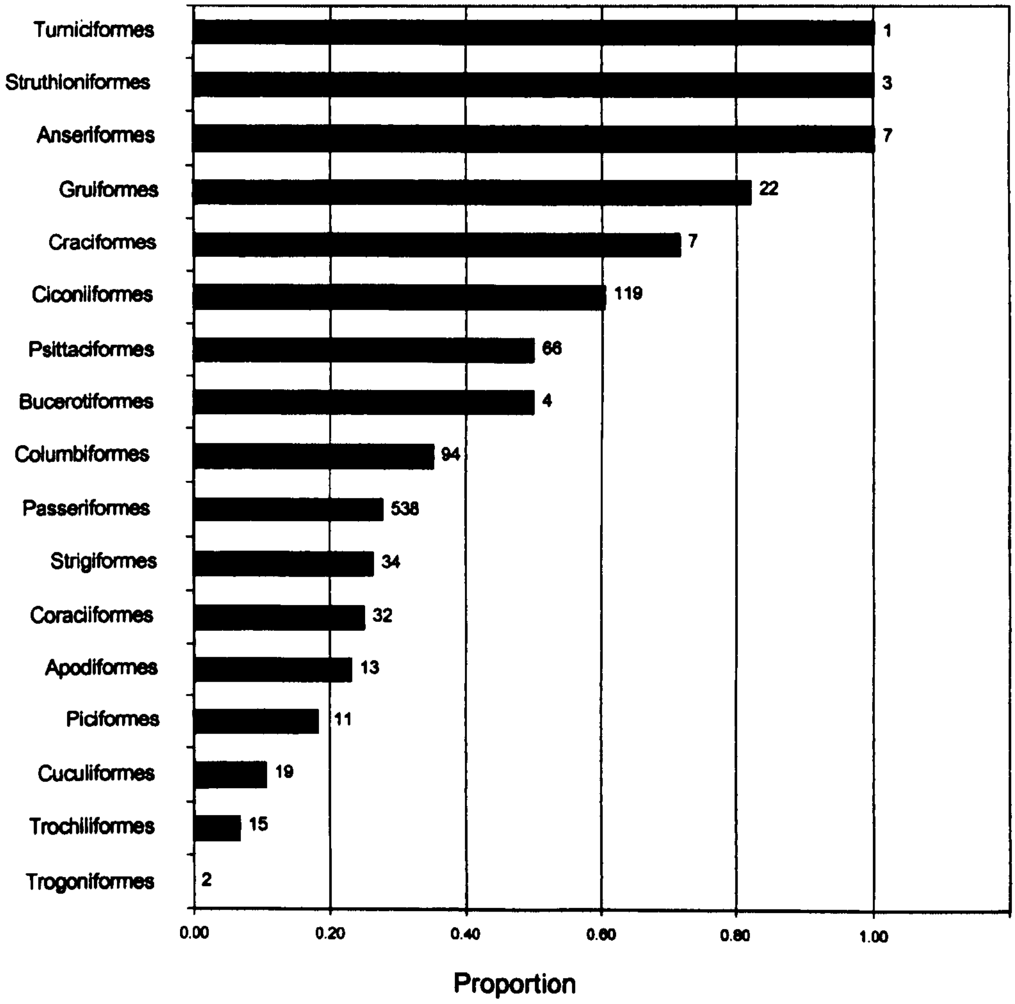
Many small families are entirely restricted to oceanic islands such as Rhynochetidae (kagu), Acanthisittidae (New Zealand wrens), Callaeatidae (New Zealand wattlebirds), Apterygidae (kiwis), and Todidae (todies). Larger families with at least 15% of their species restricted to oceanic islands are Zosteropidae (white-eyes), Procellariidae (petrels, shearwaters), Halcyonidae (kingfishers), Columbidae (pigeons, doves), and Meliphagidae (honey-eaters), Sturnidae (starling), Corvidae (e.g. monarchs, cockoo-shrikes, crows, and fantails), Psittacidae (parrots, cockatoos, lories, macaws), and Rallidae (rails, crakes, coots) (Appendix 1.1). For a discussion of families that tend to produce island endemic birds see McCall (1997). He found that overall species richness, the number of islands available in a region, and dispersal ability were the dominant factors in explaining the number of endemic oceanic island birds per family.

Threatened and extinct species

Oceanic island birds account for roughly one tenth of all birds, of which 35% are considered threatened with extinction. This is relatively high when compared to the 9% of non-oceanic island birds threatened with extinction (Appendix 1.1). In addition 88% of the 128 recent extinctions have occurred on oceanic islands.

For three orders, the Turniciformes (buttonquails), Struthioniformes (kiwis), and Anseriformes (ducks), every oceanic island representative is threatened with extinction. However, these orders are only represented by a few island species (Figure 1.2). Larger orders with high levels of threat are the Gruiformes (rails, crakes, coots), Ciconiiformes (e.g. albatrosses, petrels, shearwaters, hawks, and falcons), and Psittaciformes (parrots, cockatoos, lories, macaws). These orders have also experienced high rates of recent extinction. The Passeriformes (perching birds) have relatively lower levels of threat than the other large orders (Figure 1.2).

Figure 1.2. The proportion of species threatened for different orders, considering only species that are restricted to oceanic islands. The numbers following the columns represent the total number of species in the order that are found on oceanic islands.



There are two families where all species are restricted to oceanic islands, and all species are threatened with extinction. These are Apterygidae (kiwis) and Rhynochetidae (kagu). In many other small families, the few oceanic island representatives are threatened, such as Fregatidae (frigatebirds), Spheniscidae (penguins), Eurostopodidae (nightjars), and Dendrocygnidae (whistling-duck) (Appendix 1.1). Larger families with a high percentage of threatened oceanic island species are: Rallidae (rails, crakes, coots) (81%), Phalacrocoracidae (cormorants) (80%), Procellariidae (petrels, shearwaters, albatrosses, and storm-petrels) (65%), and Psittacidae (parrots, cockatoos, lories, macaws) (50%) (Appendix 1.1). Relatively large families with low levels of threat are Trochilidae (hummingbirds) (7%), Nectariniidae (sunbirds and flowerpeckers) (11%), Vireonidae (vireos) (13%), Meliphagidae (honey-eaters) (15%) and Strigidae (starlings) (16%) (Appendix 1.1).

Threatened regions

The Pacific islands off the east coast of Australia and Papua New Guinea, but excluding islands c1000 km off the coast of the Americas, account for 395 of the 987 oceanic island species. Two hundred and forty nine species are found on islands off Southeast Asia including the islands of Malaysia and Indonesia. Islands just off the coast (within c1000 km) of the Americas and Africa account for 202 and 110 endemic species respectively. Thirty one species, such as petrels or albatrosses, are too broadly distributed to classify into any one region.

The endemic birds on islands off the coast of Africa have experienced the greatest proportion of recent bird extinctions (Table 1.1). Roughly one quarter of the endemic birds have become extinct in the past 500 years (Table 1.1). This is followed by birds of the Pacific islands where 13% of the endemic species have become extinct. Recent extinctions have been considerably rarer for endemic birds on islands off the Americas and on islands of Southeast Asia including Indonesia and Malaysia (Table 1.1). It is unlikely that the greater extinction rates on islands off the coast of Africa or in the Pacific are driven by a regional bias in the documentation of extinctions as there is no reason to believe that documentation in these regions would be any better than in the Americas or on islands off the coast of Southeast Asia. The main bias in the extinction data is likely an under representation of the proportion of recent extinctions that have occurred in the four regions (see Pimm *et al.* 1994; Bibby 1995).

Table 1.1. Endemic oceanic island birds are divided into four regions, and the total number of species, number of threatened species, percentage of species threatened, number of extinctions over the past 500 years, and percentage of the region's avifauna that have become extinct are listed.

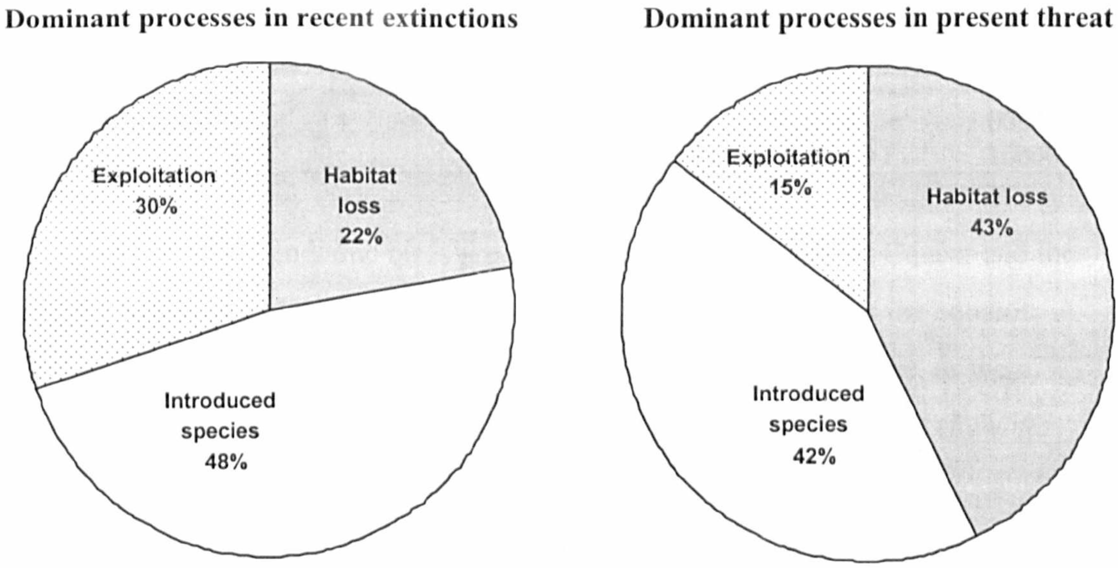
Island regions	**Number of species**	**Species threatened**	**Percent threatened**	**Species Extinct**	**Percent extinct**
Pacific	395	168	43%	61	13%
Southeast Asia	249	50	20%	4	2%
Americas	202	70	35%	12	6%
Africa	110	46	42%	35	24%

Threat levels follow a similar pattern where the highest proportion of island endemic threatened birds are found on islands off the coast of Africa and on the islands of the Pacific. The risk of extinction is lower for the birds on the islands off the coast of Southeast Asia and on islands off the coast of the Americas.

Processes of extinction

The putative cause of extinction was recorded for 68 species that went extinct in the past 500 years using Greenway (1967), Prestwich (1976), Collar and Stuart (1985), Fuller (1987), Mountfort (1988), Brouwer (1989), Day (1989), Johnson and Stattersfield (1990), Clements (1991), Gill and Martinson (1991), Jenkins (1992), Collar *et al.* (1994) BirdLife International (2000). Few extinctions have been well documented and so the identification of dominant extinction processes in the literature is often heavily reliant on conjecture. The processes of extinction associated with increased extinction risk are based on assessments of each species by BirdLife International (2000). Extinction processes have been divided into three general categories: introduced species, exploitation, and habitat loss. If a species became extinct or is presently threatened by only one extinction process, then the extinction process for that species is scored with a one. If there are two extinction processes, each process is assigned .5 and if three, each process assigned .33. The most dominant cause of recent extinctions appears to have been introduced species, followed by exploitation and finally habitat loss (Figure 1.3) ((see also Johnson and Stattersfield (1990)). However, the relative importance of each process appears to have changed when causes of past extinction are compared to causes of present threat. Habitat loss and introduced species are now the dominant processes followed by exploitation (Figure 1.3).

Figure 1.3. The causes of recent extinction are compared to the processes in present threat. Recent extinctions include 68 birds that have gone extinct over the past 500 years. The analyses for threatened birds include 346 species.



On the mainland the dominant processes of extinction appear to be very different from those on islands. Here only 4% of the birds are threatened by introduced species, 18% are threatened by exploitation, and 78% are threatened by habitat loss. Restricted-range species are defined as birds with a breeding distribution of less than 50,000 km^2 (Stattersfield *et al.* 1998). Mainland restricted-range birds may be expected to be subjected to similar processes of extinction as island species as they both have very small distributions. However, this subset of mainland birds provides an even greater contrast when island and mainland threat processes are compared. Only 2% of restricted-range mainland birds are threatened by introduced species, 12% are threatened by exploitation, and 86% are threatened by habitat destruction.

Distribution, distance from the mainland, latitude, and first human colonisation

The island bird distributions range from species such as the Seychelles brush-warbler *Bebrornis sechellensis* and Seychelles fody *Foudia sechellarum*, restricted to islands with a total distribution of less than 3 km^2, to species such as the plain pigeon (*Columba inornata*) or scaly-naped pigeon (*Columba squamosa*) found on many large islands throughout the Caribbean. The median size of the total island distribution for all oceanic island birds is 9104 km^2, which is about the size of Puerto Rico (Table 1.2).

Table 1.2. Each terrestrial oceanic island species in the data set has been assigned a total distribution, average latitude, minimum distance from the mainland, and date when humans first arrived within their range. The minimum value, 25th quartile, median, 75th quartile, and maximum value for each of these variables is given.

	N	Minimum	25th quartile	Median	75th quartile	Maximum
Distribution	901	2	1164.75	9104	38401.55	272346
Latitude	901	.16	4.01	10.4	18.58	54.48
Distance	901	14	300	680	1250	6064
First colonisation	855	0	2000	7000	33000	100000

The majority of island endemic birds are found between the Tropic of Cancer and the Tropic of Capricorn and roughly half of them are found within 10 ° of the equator. A notable exception is the relatively large number of endemic birds that are, or were, found on New Zealand located at roughly 42°S. The Auckland Island rail (*Lewinia meulleri*) found at 50.74°S or the South Georgia pipit (*Anthus antarcticus),* located at 50°S are examples of island endemic species found further from the equator. Endemic birds with the closest distributions to the mainland are those found on Cozumel, located 14 km from the coast of the Yucatán Peninsula. However, the median distance is about 700 km. Réunion, off the coast of east Africa, or Okinawa, off the east-coast of China, are examples of islands that are located at roughly this distance from the mainland. The most remote species inhabit islands in the central Pacific such as Tahiti in the Society Islands or Makatea in the Tuamotu Archipelago, both roughly 6000 km from the mainland. The Hood mockingbird *Nesomimus macdonaldi*, restricted to Hood Island in the Galápagos archipelago, is an example of a species whose island distribution has never been formally colonised by humans. A relatively large number of islands with endemic birds have only been colonised over the past millennium such as Auckland, Lord Howe, New Zealand, Isabela (Galápagos) and Norfolk (in the Pacific), Aldabra, Cocos, Mauritius and Reunion (in the Indian ocean), and Fernando de Noronha, Inaccessible, Cape Verde, and Gough (in the Atlantic). However, most large island groups have been colonised by humans for over 1000 years, and a few such as the Andaman Islands, Nicobar, and Timor (Southeast Asia), may have been colonised for as long as 100,000 years.

The phylogeny constructed from Sibley and Ahlquist (1990) and Sibley and Monroe (1990, 1993) is available on the CD included within this thesis. The Island bird data set will be available at www.bio.ic.ac.uk/evolve once the chapters from this thesis have been published.

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Appendix 1.1. The total number of birds in each family, the number and percentage of species endemic to oceanic islands, and the number and percentage of oceanic island endemic and non-oceanic island endemics that are threatened with extinction.

Family	Total number of species	Number of species endemic to oceanic islands	Percentage of species endemic to oceanic islands	The number of threatened species not endemic to oceanic islands	Threat rate for species not endemic to oceanic islands	Number of threatened oceanic island endemics	Percentage of oceanic island birds threatened
Acanthisittidae	2	2	100%	0	0%	0	0%
Apterygidae	3	3	100%	0	0%	3	100%
Callaeatidae	2	2	100%	0	0%	1	50%
Rhynochetidae	1	1	100%	0	0%	1	100%
Todidae	5	5	100%	0	0%	0	0%
Zosteropidae	94	59	63%	2	6%	15	25%
Chionidae	2	1	50%	0	0%	0	0%
Procellariidae	114	52	46%	10	16%	34	65%
Tytonidae	17	7	41%	2	20%	2	29%
Fregatidae	5	2	40%	0	0%	2	100%
Coccyzidae	18	7	39%	0	0%	2	29%
Megapodiidae	19	7	37%	3	25%	5	71%
Spheniscidae	17	6	35%	4	36%	6	100%
Halcyonidae	61	21	34%	2	5%	6	29%
Phaethontidae	3	1	33%	0	0%	0	0%
Columbidae	306	94	31%	26	12%	33	35%
Phalacrocoracidae	36	10	28%	2	8%	8	80%
Meliphagidae	177	48	27%	2	2%	7	15%
Centropidae	30	8	27%	4	18%	0	0%
Aegothelidae	8	2	25%	0	0%	1	50%
Sturnidae	143	35	24%	4	4%	10	29%
Corvidae	648	132	20%	30	6%	29	22%
Psittacidae	350	66	19%	57	20%	33	50%
Regulidae	6	1	17%	0	0%	0	0%
Alcedinidae	25	4	16%	3	14%	1	25%
Rallidae	132	21	16%	13	12%	17	81%
Vireonidae	52	8	15%	1	2%	1	13%
Eurostopodidae	7	1	14%	0	0%	1	100%
Apodidae	99	13	13%	2	2%	3	23%
Bombycillidae	8	1	13%	0	0%	0	0%
Strigidae	155	19	12%	11	8%	3	16%
Dendrocygnidae	9	1	11%	0	0%	1	100%
Sulidae	9	1	11%	1	13%	1	100%
Nectariniidae	170	18	11%	6	4%	2	11%
Pittidae	31	3	10%	7	25%	2	67%
Accipitridae	238	23	10%	24	11%	8	35%
Muscicapidae	449	42	9%	35	9%	12	29%
Fringillidae	983	83	8%	69	8%	37	45%
Coraciidae	12	1	8%	0	0%	1	100%
Pardalotidae	67	5	7%	3	5%	1	20%
Bucerotidae	54	4	7%	7	14%	2	50%
Laridae	127	9	7%	11	9%	2	22%
Petroicidae	44	3	7%	0	0%	1	33%
Sylviidae	558	37	7%	42	8%	13	35%
Caprimulgidae	79	5	6%	3	4%	2	40%
Turnicidae	17	1	6%	2	13%	1	100%
Charadriidae	87	5	6%	4	5%	5	100%

Scolopacidae	87	5	6%	7	9%	3	60%
Passeridae	388	22	6%	23	6%	6	27%
Cuculidae	78	4	5%	1	1%	0	0%
Trogonidae	39	2	5%	0	0%	0	0%
Picidae	216	11	5%	8	4%	2	18%
Podicipedidae	20	1	5%	3	16%	1	100%
Trochilidae	321	15	5%	26	9%	1	7%
Certhiidae	97	4	4%	2	2%	2	50%
Anatidae	146	6	4%	17	12%	6	100%
Sittidae	25	1	4%	4	17%	0	0%
Meropidae	26	1	4%	0	0%	0	0%
Pycnonotidae	138	5	4%	11	8%	1	20%
Hirundinidae	89	3	3%	3	3%	2	67%
Laniidae	30	1	3%	0	0%	1	100%
Tyrannidae	540	18	3%	37	7%	3	17%
Falconidae	62	2	3%	2	3%	2	100%
Cisticolidae	120	3	3%	6	5%	1	33%
Ardeidae	64	1	2%	8	13%	0	0%
Alaudidae	91	1	1%	7	8%	1	100%
Furnariidae	279	1	0%	22	8%	1	100%
Aegithalidae	8	0	0%	0	0%	0	
Anhimidae	3	0	0%	0	0%	0	
Anhingidae	4	0	0%	0	0%	0	
Anseranatidae	1	0	0%	0	0%	0	
Aramidae	1	0	0%	0	0%	0	
Batrachostomidae	11	0	0%	0	0%	0	
Brachypteraciidae	5	0	0%	3	60%	0	
Bucconidae	33	0	0%	0	0%	0	
Bucorvidae	2	0	0%	0	0%	0	
Burhinidae	9	0	0%	0	0%	0	
Cariamidae	2	0	0%	0	0%	0	
Casuariidae	4	0	0%	2	50%	0	
Cerylidae	9	0	0%	0	0%	0	
Ciconiidae	26	0	0%	6	23%	0	
Cinclidae	5	0	0%	1	20%	0	
Climacteridae	7	0	0%	0	0%	0	
Coliidae	6	0	0%	0	0%	0	
Conopophagidae	8	0	0%	0	0%	0	
Cracidae	50	0	0%	15	30%	0	
Crotophagidae	4	0	0%	0	0%	0	
Eurylaimidae	14	0	0%	2	14%	0	
Eurypygidae	1	0	0%	0	0%	0	
Formicariidae	60	0	0%	9	15%	0	
Galbulidae	18	0	0%	2	11%	0	
Gaviidae	5	0	0%	0	0%	0	
Glareolidae	18	0	0%	1	6%	0	
Gruidae	15	0	0%	9	60%	0	
Heliornithidae	3	0	0%	1	33%	0	
Hemiprocnidae	4	0	0%	0	0%	0	
Hypocoliidae	1	0	0%	0	0%	0	
Indicatoridae	17	0	0%	0	0%	0	
Irenidae	10	0	0%	1	10%	0	
Jacanidae	8	0	0%	0	0%	0	
Leptosomidae	1	0	0%	0	0%	0	
Lybiidae	42	0	0%	0	0%	0	
Maluridae	26	0	0%	2	8%	0	
Megalaimidae	26	0	0%	0	0%	0	
Melanocharitidae	10	0	0%	0	0%	0	

Menuridae	4	0	0%	2	50%	0	
Mesitornithidae	3	0	0%	3	100%	0	
Momotidae	9	0	0%	1	11%	0	
Musophagidae	23	0	0%	2	9%	0	
Neomorphidae	11	0	0%	1	9%	0	
Numididae	6	0	0%	1	17%	0	
Nyctibiidae	7	0	0%	0	0%	0	
Odontophoridae	31	0	0%	5	16%	0	
Opisthocomidae	1	0	0%	0	0%	0	
Orthonychidae	2	0	0%	0	0%	0	
Otididae	25	0	0%	4	16%	0	
Paramythiidae	2	0	0%	0	0%	0	
Paridae	65	0	0%	1	2%	0	
Pedionomidae	1	0	0%	1	100%	0	
Pelecanidae	9	0	0%	1	11%	0	
Phasianidae	175	0	0%	42	24%	0	
Philepittidae	4	0	0%	1	25%	0	
Phoenicopteridae	5	0	0%	1	20%	0	
Phoeniculidae	5	0	0%	0	0%	0	
Picathartidae	4	0	0%	2	50%	0	
Pluvianellidae	1	0	0%	0	0%	0	
Podargidae	3	0	0%	0	0%	0	
Pomatostomidae	5	0	0%	0	0%	0	
Psophiidae	3	0	0%	0	0%	0	
Pteroclidae	16	0	0%	0	0%	0	
Ptilonorhynchidae	20	0	0%	1	5%	0	
Ramphastidae	55	0	0%	2	4%	0	
Rheidae	2	0	0%	0	0%	0	
Rhinocryptidae	29	0	0%	3	10%	0	
Rhinopomastidae	3	0	0%	0	0%	0	
Rostratulidae	2	0	0%	0	0%	0	
Sagittariidae	1	0	0%	0	0%	0	
Scopidae	1	0	0%	0	0%	0	
Steatornithidae	1	0	0%	0	0%	0	
Struthionidae	1	0	0%	0	0%	0	
Thamnophilidae	190	0	0%	22	12%	0	
Thinocoridae	4	0	0%	0	0%	0	
Threskiornithidae	33	0	0%	6	18%	0	
Tinamidae	47	0	0%	6	13%	0	
Upupidae	2	0	0%	0	0%	0	
Grand Total	**9623**	**987**	**10%**	**741**	**9%**	**348**	**35%**

CHAPTER 2

LIFE HISTORY AND MORPHOLOGICAL TRENDS ON ISLANDS

Abstract

Many morphological and life history traits have been observed to change when species colonise and become endemic on oceanic islands. Despite extensive island/mainland comparisons, the generality of many of these island trends remains unclear. Few consistent patterns have been demonstrated, and large-scale comparative analyses controlling for confounding factors, such as phylogenetic relatedness and latitude, are lacking. Identifying convergent life history and morphological trends on islands is essential for providing insight into the unique processes that can occur in an isolated restricted environment, and may help to highlight the traits of island endemic birds that are associated with elevated extinction risk. I conduct comparative analyses of island and mainland birds, controlling for phylogeny, to test for convergent trends in clutch size, body length and sexual body size dimorphism. I then examine how these traits vary among island endemics in relation to the distance of a species' distribution from the mainland, a species total distribution, and the average latitude of its range. The analyses indicate that clutch size decreases in both passerines and non-passerines on islands, and that within islands, species with smaller total distributions tend to have smaller clutches. The commonly cited effect of clutch size increasing with latitude was supported for passerines, but not non-passerines. Small birds tend to become larger on islands and there is a trend for large birds to become smaller although the latter is not statistically significant. For island avifauna, I also found little support for Bergmann's rule that species' body size increases with latitude. Finally, sexual body size dimorphism tends to increase on islands, irrespective of which sex is larger on the mainland. These findings provide strong evidence that common processes are taking place within restricted and remote environments leading to the unique traits characteristic of island birds.

Introduction

Island endemic birds are often suggested to be particularly prone to extinction (King 1985; Johnson and Stattersfield 1990; Stattersfield *et al.* 1998). Much of this elevated extinction risk may be associated with their restricted distribution (Manne *et al.* 1999; Simberloff 2000). However, island birds may have traits that render them at increased risk of extinction to specific threats (Williamson 1981; Atkinson 1989; Vermeij 1991; Paulay 1994). To investigate the traits specific to island birds that are associated with elevated extinction risk, we must first establish consistent differences between island and mainland species. Many life history, morphological, behavioural, and ecological traits have been associated with insular or island endemic birds, examples of which are listed in Table 2.1.

Table 2.1. Avian life history, morphological, behavioural, and ecological trends that have been suggested to occur on oceanic islands.

Hypothesised island trends	
Change in body size	Amadon (1953), Grant (1968), Lack (1970), Williamson (1981), McNab (1994b); Clegg and Owens (submitted)
Bill and tarsal length changes	Murphy (1938), Grant (1965a)
Increased morphological variation	Van Valen (1965)
Reduced or no morphological variation	MacArthur *et al.* (1972), Keast (1996), Clegg and (Owens submitted)
Paedomorphic allometry	Herremans (1990)
Reduced Clutch size	Cody (1966), Lack (1970), Crowell and Rothstein (1981), Blondel (1991), Martin (1992), Grant and Grant (1998)
Delayed breeding	Lambrechts and Dias (1993), Wiggins *et al.* (1998), Blondel (2000)
Prolonged infantile behaviour	Blondel (2000)
Increased survivorship	Stamps and Buechner (1985)
More sedentary	Diamond (1985), McNab (1994), Blondel (1991, 2000)
Reduced genetic diversity	Frankham (1998)
Increase in bill dimorphism	Selander (1966)
Decreased dichromatism	Mayr (1942), Amadon (1953), Sibley (1957), Grant (1965b), Herremans (1990), but see Clegg and Owens submitted)
Immature plumage	Mayr (1942) Amadon (1953) Herremans (1990)
Feminisation of male characteristics	Lack (1970)
Reduction in complexity of song	Hamao and Ueda (2000)
Change in territorial defence	Stamps and Buechner (1985), Perret and Blondel (1993)
Increased fidelity	Griffith *et al.* (1999), Griffith (2000), Møller (2001)
Flightlessness	Diamond (1981), Roff (1994) McNab (1994a)
Island tameness	Atkinson (1985) Grant (1998)
Expansion of ecological niche	Diamond (1970), MacArthur (1972) Blondel (2000)
Density compensation	MacArthur *et al.* (1972), Blondel (1991)

Some of the observed trends on islands are conflicting and few have been rigorously tested on a large scale, controlling for the non-independence of closely-related species (see Grant 1998; Blondel 2000).

Island endemic birds are not a random subset of mainland species (McCall 1997) since there is a filter on the type of species capable of colonising islands (Diamond 1974, 1981) as well as on the type of species capable of long-term persistence in a restricted-range environment (Hamilton *et al.* 1964; Salomonsen 1974). While this may explain much of the variation observed between island and mainland communities, similar conditions associated with isolated oceanic islands, such as a reduction in competitors, a reduction in predators (Grant 1998) and a fixed restricted distribution, may result in conditions that promote convergent behavioural, ecological, and evolutionary traits (see MacArthur and Wilson 1967; Williamson 1981; Grant 1998; Blondel 2000).

Here I examine the influence of an isolated island environment on three life history or morphological traits: clutch size, body size and sexual size dimorphism. As these traits are correlated with many other aspects of a species life history, it may be possible to gain insight into many of the patterns and processes occurring on islands. While I outline and discuss hypotheses associated with the processes driving island/mainland differences and the variation within islands, the main objective here is to establish patterns of life history and morphological variation that appear robust in an insular environment.

Clutch size

Clutch size decreases in many island populations or species (Cody 1966; Crowell and Rothstein 1981; Blondel 1991; Martin 1992; Grant and Grant 1998). However, there are exceptions (George 1987), and the trend has not been tested using a broad-scale analysis controlling for the confounding effects of latitude (Grant 1998; Blondel 2000) and the non-independence of closely-related species. Very little work has been conducted on the relationship between island area, extent of isolation and clutch size. Wiggins *et al.* (1998) indicate that greater isolation may result in smaller clutch size, but larger egg size, as in island great tits *Parus major*. Environmental stability, multiple clutches, limited food supply, lack of predation, increased survivorship and reduced genetic diversity are all factors that have been suggested to be associated with the reduction of clutch size on islands (see Ashmole 1963, Cody 1966; Lack 1970; Snow

1970; Ricklefs 1980; Frankham 1998; Wiggins *et al.* 1998). Blondel (1991, 2000) and Grant (1998) also suggest that high densities, in the absence of predators and heterospecific competitors, may result in greater intraspecific competition thereby increasing selection for lower reproductive rates.

Body size

There is a general trend for large mammals to become smaller, and small mammals to become larger on islands (Van Valen 1973; Heaney 1978; Lomolino 1985; Brown *et al.* 1993; Damuth 1993). The mechanisms suggested to be driving these patterns are complex and involve interactions among food resources, competition, predation, and selection for physiological efficiency (Heaney 1978), aspects of a species mating system such as territoriality (Case 1978), and male-male competition (see Andersson 1994). A study based on 25 comparisons of mainland and oceanic island birds suggests that birds may follow a similar pattern as mammals, where small species get larger and large species get smaller on oceanic islands (Clegg and Owens submitted). However, in general, few consistent body size distribution patterns have been identified when comparing island and mainland bird species (Grant 1968; Case 1978; Blondel 2000). Regional studies have reported both increases and decreases in body size with no clear trend (see Mayr and Vaurie 1948; Amadon 1953; Bourne 1955; Benson 1960; Watson 1964; Grant 1968). The only taxonomic groups of birds that have been shown to consistently change in body size on islands are ducks (Anatidae) (Lack 1970; Williamson 1981; McNab 1994b) and perhaps crows (*Corvus*) (see McNab 1994b) where both tend to become smaller when they colonise islands.

Within islands there is evidence that a small island environment with limited resources may lead to selection for smaller body size. Body size has been shown to decrease with island area for many species of rail and duck (McNab 1994b). This relationship has also been documented in mammals. For example, the fruit-eating bats in the genus *Pteropus* on oceanic islands (McNab 1994b) and populations of the tri-colored squirrel (*Callosciurus prevosti*) on continental islands (Heaney 1978).

Sexual body size dimorphism

The mechanisms driving sexual body size dimorphism are varied and poorly understood (Andersson 1994). Niche partitioning of resources between sexes may play a significant role (Shine 1989). Morphological divergence between sexes may result in greater foraging efficiency in a biologically impoverished environment with reduced competition (Keast 1970). Sexual size dimorphism, primarily in bill morphology, has been observed in some island birds such as *Centurus* woodpeckers (Selander 1966) and the now extinct huia *Heteralocha acutirostris* (Gill 1991). Clegg and Owens (submitted) have demonstrated that non-passerines on islands have significantly greater sexual dimorphism in tarsus length. However, others have found no support for sexual size dimorphism as a general rule (Van Valen 1965; Keast 1970; 1996).

Many believe that sexual body size dimorphism is primarily driven by sexual selection (see Jehl and Murray 1986; Mueller 1990). In birds, males are generally the larger sex, a fact which can be attributed to male-male competition for territory or mates (Darwin 1871; Andersson 1994). Isolated island environments are commonly suggested to have higher population densities and therefore greater intraspecific competition (Grant 1998; Blondel 2000). In addition, island birds, unlike many other terrestrial vertebrates, remain territorial on islands, and territoriality is even believed to increase in some species (Stamps and Buechner 1985). Such conditions may intensify sexual male-male competition for territories and mates, leading to increased sexual size dimorphism.

Sexual body size dimorphism may also be influenced by relatively relaxed selection from female choice on islands. It is often suggested that island species have reduced levels of sexual selection, based on lower levels of extra pair paternity (Griffith *et al.* 1999; Griffith 2000; Møller 2001). This is supported by the observed trend for sexual colour dimorphism or dichromatism to decrease on islands (Amadon 1953; Grant 1965b but see Clegg and Owens submitted).

Here I compare these three traits between oceanic island and mainland species, controlling for phylogenetic relatedness. I test whether there is a trend for clutch size to decrease, sexual size dimorphism to increase, and body size to increase or decrease on oceanic islands. I then examine how these traits vary among species on islands in relation to a species distance from the mainland, average latitude, and total geographic distribution.

Methods

Refer to the island bird database (Chapter 1).

Life history and ecological data

Clutch size, body size, and sexual body size dimorphism data were from: Greenway (1967), Harris (1974), duPont (1975), Mayr (1976), Hannecart (1980), Watling (1982), Clunie (1984), Fuller (1987), Mountfort (1988), Day (1989), Gill and Martinson (1991), del Hoyo *et al.* (1992,1994,1996,1997), Bregulla (1992), Fry (1992), Jones (1995), Feare (1998), Rowlands (1998), Sinclair (1998), Clement (1999), Isler (1999), Madge (1999), and BirdLife International (2000). In addition, Dunning (1992) gives body mass and Bennett (1986) gives clutch sizes. Clutch size is defined as the mean number of eggs in a nest and was logarithmically transformed for analyses. Data were collected for 2259 species, 1915 of which are from the mainland, representing in all 880 genera. Body length is defined as the length in centimetres of a bird from the tip of its bill to the end of its longest tail feather. Data was collected for 684 species, 160 of which are mainland species. This includes 260 genera. Sexual body size dimorphism is measured as the difference between the larger and smaller sex, obtained by subtracting the natural logarithm of the larger sex from the natural logarithm of the smaller sex. Data were collected for 144 species, 84 of which are mainland species representing 91 genera. Male sexual size dimorphism is obtained by only including the species where the male is larger or there is no difference. Female body size dimorphism is obtained by only including the species where the female is larger or there is no difference.

Refer to the comparative approach (Chapter 1).

Island/mainland comparison

Where possible data were collected for the closest relatives within a genus or tribe for island and mainland species using Sibley and Monroe (1990, 1993). If data were only collected for one mainland representative of a genus or tribe, the mainland species with the closest geographical distribution to its island relatives was selected, providing data were available.

The BRUNCH algorithm in CAIC is used to analyse the contrasts (Comparative approach, page 29). Non-parametric statistics are only presented where the results are quantitatively different from the one sample t-test. Contrasts were examined for phylogenetic clustering and if clustering was evident between passerines and non-passerines, the analyses were also run separately for the two groups.

Island and mainland clutch size is first compared, controlling for latitude. Grant (1998) suggests that latitude is important to control for, as a general trend has been observed for clutch size to increase with latitude (Lack 1947). Not all mainland species for which there is information on clutch size are included in this first analysis as data were only collected on the average latitudinal distribution for a subset of mainland species. However, finding no significant difference when controlling for latitude, the larger data set, including all mainland species for which clutch size data exists is used to test whether there is a decrease in clutch size, among island endemics, for both passerines and non-passerines.

The average body length of closely-related island and mainland species is first compared, after controlling for the effect of latitude. Latitude has been controlled because body size may increase with latitude (reviewed by Gaston and Blackburn 2000). Finally, mainland genera were separated into two body size groups, less than and greater than 27 cm. When body length is regressed against body mass, 27 cm body length is about 100g body mass – a measure commonly used to distinguish small from large birds (e.g. Owens and Bennett 2000). The small and large mainland species are then compared to their closest island relatives to determine whether different processes are occurring for the different size classes.

I conduct three analyses to examine the relationship between sexual size dimorphism of island and mainland species. First I examine whether the difference in size between the larger and smaller sex of a species increases or decreases on islands. Second, I test for a change in male sexual size dimorphism, and third I test for a change in female sexual size dimorphism. For all three analyses the confounding effect of body mass is controlled for as larger species may be expected to have greater variation in body mass (Andersson 1994).

Variation among island species

The second set of analyses focuses on variation in clutch size, body length, and sexual size dimorphism within island species. Here, the variation of these three traits is examined with respect to a species' total geographic distribution, minimum distance from the mainland, and average latitude. Although the terms are all continuous variables, the BRUNCH option of CAIC is used (see comparative approach, page 29). The life history traits are treated as the dependent variable and total distribution, distance from the mainland, and latitude the independent variables. Regression was run through the origin and a stepwise multiple regression approach used to test for significance. However, if none of the independent variables are correlated with the dependent term, then the test statistic and the p-value are reported independently for each of the independent variables. As with the other analyses, if variation was observed between the passerines and non-passerines contrasts, the passerines and non-passerines contrasts were also run separately.

Results

Island/mainland comparison

The clutch size of oceanic island birds tends to be smaller than their mainland relatives without controlling for latitude (df=52, t=4.56, p<0.001). This relationship is maintained after controlling for latitude (Table 2.2). As latitude has little effect on this relationship it is possible to compare the larger database (including species where latitude is not known) to determine if the relationship is the same for passerines and non-passerines. The relationship is strong for both passerines and non-passerines (passerines, df=57, t=7.21, p<0.001; non-passerines, df=66, t=5.59, p<0.001).

When birds of all body lengths are compared to their mainland relatives there is no significant increase or decrease in body length (df=86, t=-0.28, 0.77); this non-significant result is maintained when controlling for latitude (Table 2.2). However, assessment of the large and small body size classes separately reveals that different processes may be acting on these two groups. After controlling for the effect of latitude, small species (<27cm) have island relatives that are significantly larger (Table 2.2) whereas large species (>=27cm) show a trend toward smaller body size on islands, although the latter relationship is not statistically significant (Table 2.2).

Sexual size dimorphism appears to be greater on oceanic islands than the mainland. This result is verging on significance after controlling for the effect of body size and using a one-sample t-test (Table 2.2), and is significant when the non-parametric Wilcoxon signed ranks test is employed (n=50, Z=-1.95, p=0.051). If only species where the male body mass is larger than the female body mass are considered, the sample size is much smaller, but the result is the same but stronger (Table 2.2). If the analysis is only conducted on the data where the female is larger, the trend still exists, but it is not significant using a one-sample t-test (Table 2.2). Using the non-parametric statistics, female body size tends to increase in relation to male body size on islands (n=14, Z=-1.97, p =0.048).

Table 2.2. The difference in clutch size, body length, and sexual size dimorphism of closely related island and mainland species. The effect of latitude on clutch size and body size, and the effect of body size on sexual size dimorphism have been controlled. One-sample t-test are used to analyse the standardised contrasts.

Variable	df	t	p-value
Clutch size	52	4.56	<0.001
Body length	86	-0.62	0.54
Body length >=27cm	44	1.49	0.15
Body length <27 cm	47	-1.98	0.053
Dimorphism LogBig-LogSmall (mass)	49	-1.93	0.058
Dimorphism Male (mass)	34	-2.51	0.017
Dimorphism Female (mass)	13	-1.72	0.11

Variation among island species

The analyses of clutch size indicate that island birds with a larger distribution tend to have a larger clutch size (Table 2.3; Figure 2.1).

Table 2.3. Clutch size as the dependent variable and distribution, distance, and latitude as the independent variables. Stepwise multiple regression, through the origin, across contrasts of oceanic island endemic birds.

Number of contrasts	R^2	F-Ratio	Independent variables	Slope	t	p-value
97	0.14	16.00				
			Distribution	0.047	4.00	<0.001
			Distance			NS
			Latitude			NS

When only passerines are analysed, species similarly tend to have a larger clutch size when their distribution is larger, but also when they are located at higher latitudes, and with a smaller clutch size with greater distance from the mainland (Table 2.4; Figure 2.2).

Table 2.4. Clutch size as the dependent variable and distribution, distance, and latitude as the independent variables. Stepwise multiple regression, through the origin, across contrasts of passerine oceanic island endemics.

Number of contrasts	R^2	F-Ratio	Independent variables	Slope	t	p-value
46	0.41	9.84				
			Distribution	0.044	2.39	0.021
			Distance	-0.052	-2.28	0.027
			Latitude	0.02	3.77	<0.001

In non-passerines also, larger distributions are associated with larger clutch sizes, but there is no relationship between clutch size and latitude or distance from the mainland (Table 2.5).

Table 2.5. Clutch size as the dependent variable and distribution, distance, and latitude as the independent variables. Stepwise multiple regression, through the origin, across contrasts of non-passerine oceanic island endemics.

Number of contrasts	R^2	F-Ratio	Independent variables	Slope	t	p-value
51	0.35	6.81				
			Distribution	0.058	2.61	0.012
			Distance			NS
			Latitude			NS

There is no general relationship between body length of oceanic island birds and a species total distribution, distance from the mainland, or average latitude (df=125, distribution, t=1.29, p=0.19, distance t=-1.23, p=0.21, latitude t=-1.59, p=0.11). However, large bodied birds tend to be associated with a greater total distribution (Table 2.6; Figure 2.3), but smaller bodied birds are not associated with large or small distributions (df=84, distribution, t=1.35, p=0.17, distance t=-1.51, p=0.13, latitude t=-0.75, p=0.45).

Table 2.6. Large body length as the dependent variable and distribution, distance, and latitude as the independent variables. Stepwise multiple regression, through the origin, across contrasts of oceanic island endemics >=27 cm in body length.

Number of contrasts	R^2	F-Ratio	Independent variables	Slope	T	p-value
54	.07	4.06				
			Distribution	0.016	2.01	0.049
			Distance			NS
			Latitude			NS

When sexual body size dimorphism is explored throughout oceanic islands after controlling for body size, there is no significant correlation (df=28, cofficient=-0.01, t=-1.52, p=0.19).

Figure 2.1. The total distribution contrasts in relation to the clutch size contrasts. Species that have smaller distributions are associated with smaller clutch size.

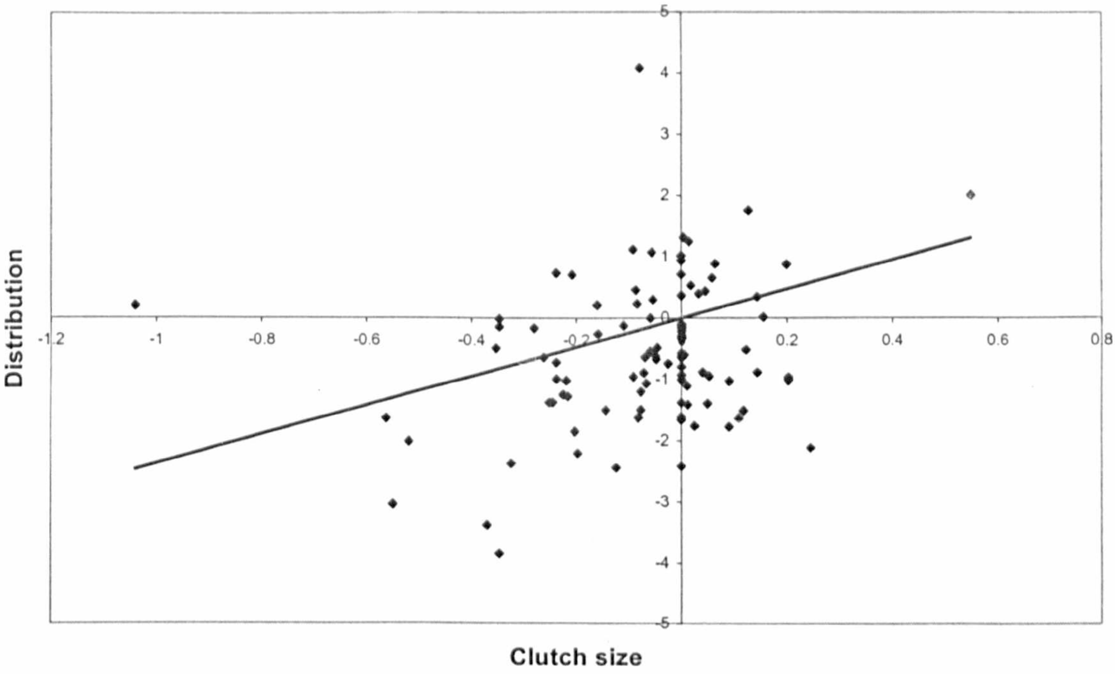


Figure 2.2. Oceanic island passerine birds. The average latitude contrasts in relation to the clutch size contrasts. Passerines closer to the equator tend to have a smaller clutch size.

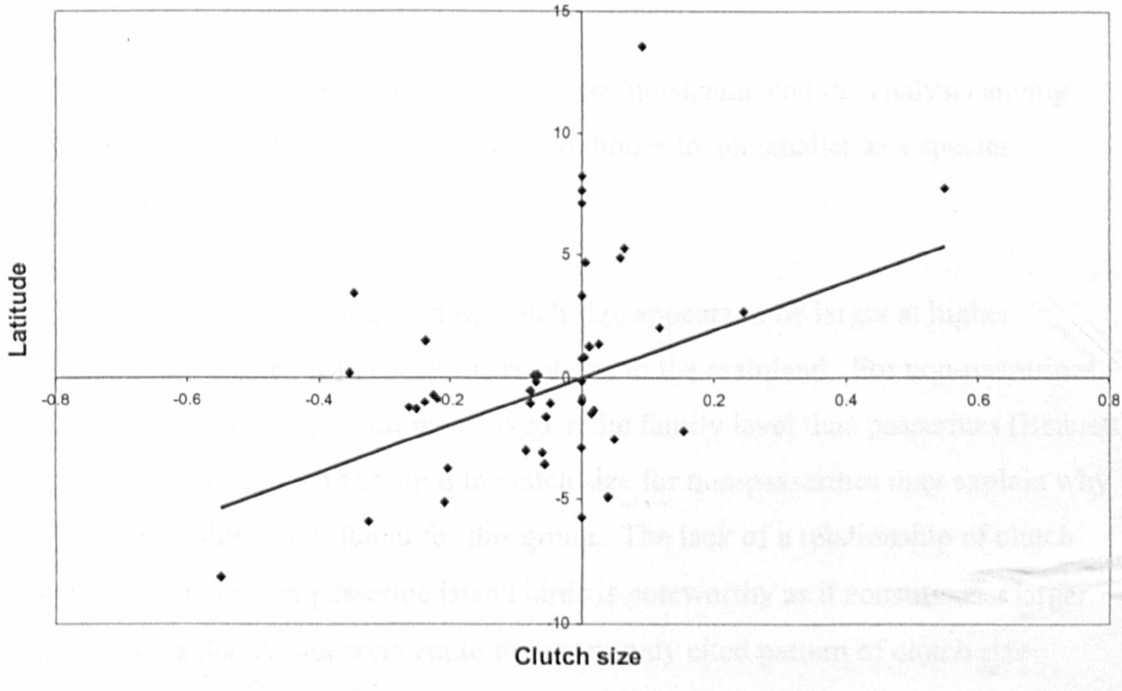
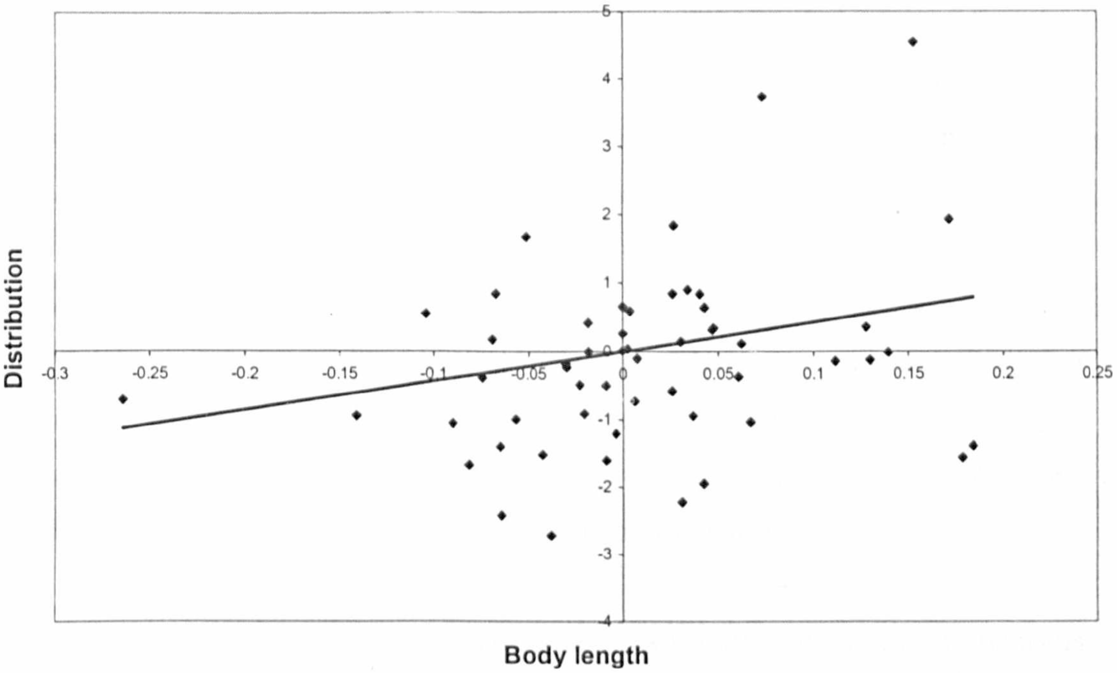


Figure 2.3. Oceanic island birds >=27cm. The total distribution contrasts in relation to body size contrasts. Larger bodied species are not associated with smaller geographic distributions.



Discussion

Clutch size

There is a strong trend for clutch size to decrease on islands, and the analysis among island species demonstrates that clutch size continues to get smaller as a species' distribution decreases.

For oceanic island endemic passerines, clutch size appears to be larger at higher latitudes, and for species with closer distributions to the mainland. For non-passerines, clutch size variation is in general more fixed at the family level than passerines (Bennett pers. comm.). The reduced variation in clutch size for non-passerines may explain why a similar relationship is not found for this group. The lack of a relationship of clutch size with latitude for non-passerine island birds is noteworthy as it constitutes a larger group of species that do not conform to the commonly cited pattern of clutch size increasing with latitude (see Lack 1947; Cody 1966; Ashmole 1963; Ricklefs 1980; Newton 1998).

It must first be considered that small clutch size on islands may simply be a result of the differential success of species with smaller clutch sizes colonising and becoming endemic on islands. However, this in not supported by McCall (1997) who found no evidence that families with smaller clutch size were more likely to produce island endemic species.

Another simple explanation would be that island birds have smaller clutches, but lay more clutches per year. This would be consistent with the theory that islands are more equitable, predictable or benign environments than the mainland (Cody 1966; Lack 1970; Abbott 1980; Blondel 1991). However, if multiple clutching were the main reason for the smaller number of eggs per nest, it is difficult to explain why birds with small total island distributions tend to have a smaller clutch size, as it is unlikely that species with smaller total island distribution have more clutches per year. While multiple clutching may play a role in the general trend for island birds to have a smaller clutch size, it would appear that other mechanisms are involved.

However, it is difficult to distinguish the evolutionary and/or ecological mechanisms behind reduced clutch size, as many of the proposed mechanisms are confounded with the size of a species total island distribution or the distance of a species distribution from the mainland. For example, species impoverishment is associated with smaller islands and greater distance from the mainland (Diamond 1974), and therefore density compensation (MacArthur *et al.* 1972) may be more common on small or distant islands, resulting in increased intraspecific competition and reduced fecundity (see Grant 1998; Blondel 2000). Mammalian predators were also traditionally less common on small and distant islands. Thus, adult survivorship may have increased in such environments, and increased survivorship is negatively correlated with clutch size (Bennett and Owens 2001). Food resources may be less abundant with distance (Salomonsen 1974) and area (McNab 1994b). Reduced resources may result in reduced clutch size (Lack 1970). Even the effects of low genetic diversity would be expected to follow this same pattern.

It is also possible that species with a smaller clutch size are associated with a smaller and more remote island distributions, simply because slowly reproducing species have been extirpated from much of their range. However, this does not explain why island species in general have smaller clutches, unless their slowly reproducing mainland relatives have already been driven to extinction.

One factor that deserves greater exploration is the effect of reduced dispersal on clutch size. The mainland relatives of species that colonise islands are believed to be abundant mobile generalists (Blondel 2000) associated with secondary growth and open habitat (Diamond 1970; Salomonsen 1974). Such species tend to have high reproductive rates and high dispersal. When these species colonise an island, the lack of competitors and predators may result in higher population densities. However, if strong selection for dispersal is maintained, then high population densities may not lead to a "slower" life history strategy. It is selection against dispersal and the subsequent shift from a high dispersal strategy to a sedentary strategy that may be the most important mechanism selecting for lower reproductive rates on islands.

Thus, there are many hypotheses that may explain the observed trends and further exploration into the mechanisms involved will likely identify multiple and synergistic processes involved in the reduction of clutch size. However, these will undoubtedly include greater intraspecific competition, reduced dispersal, increased survivorship, and reduced resource availability.

Body size

The island/mainland comparison of body length suggests that birds may follow a similar pattern to mammals in that large species may have a tendency to get smaller, and small species a tendency to get larger. This relationship is similar to that found by Clegg and Owens (submitted).

The exact mechanism driving the body size differences is difficult to distinguish. Small species may get larger due to lack of predators selectively targeting larger-bodied species, increased resource availability, selection for a 'slower' life history strategy, or sexual selection. Large species may get smaller due to energetic constraints or lack of predator selection for large body size. As suggested for mammals (Brown *et al.* 1993; Damuth 1993), there may be an optimal body size in birds that species evolve towards in the absence of predators and competitors. However, it is difficult to accept that taxa with such different ecologies would gravitate toward one central optimal mass or body length.

The weaker trend in birds may be a result of the mechanical constraints that flight places on body size. First the constraints of flight may reduce the extent of body size variation possible within any particular group. This is supported by the much broader range of body size variation found in flightless birds ranging from the Stephens Island wren *Traversia lyalli* to elephant birds (Aepyornithidae). Second, there may be even less variation in body size possible in species that require agility in flight. For example, species foraging for insects on the wing, such as swifts or swallows, may not be effective at a larger or smaller body size. If a lack of predators is driving body size shifts on islands, then species that have their mainland populations more heavily regulated by predators may experience a greater size shift when they reach predator free islands. This may explain why mammals experience greater size shifts than birds, as mammals may be more predator limited on the mainland. Finally, trends in bird body size may be less because adaptive shifts tend to be expressed in other morphological characteristics (Grant 1968; Case 1978). For example, shifts in bill size or tarsus length (Murphy 1938; Grant 1965a).

The results of analysing body length in relation to a species' distance from the mainland, total distribution, and average latitude, failed to support many previous hypotheses. First, oceanic island birds do not appear to follow Bergmann's rule, one of the oldest macroecological observations, (see Gaston and Blackburn 2000), whereby body size increases with latitude. Thus, although it may be that specific clades with larger body size are found at higher latitude, when closest relatives are compared there is no statistical difference. The inapplicability of Bergmann's rule may simply therefore be a result of controlling for phylogeny in conjunction with the similar conditions found on islands at different latitude. Another study examining Bergmann's rule using New World birds and controlling for phylogenetic relatedness only found weak support for the hypothesis (Blackburn and Gaston 1996). However, it is also possible that Bergmann's rule does not apply on islands because of the other body size shifts occurring in an island environment. For example, if small species are becoming larger and large species are becoming smaller on islands then this may confound mainland – based results.

Second, it is interesting that distance from the mainland has no effect on the size of species found on an island, indicating that large and small species within a genus are equally likely to colonise or persist on distant islands. This result is supported by McCall (1997) who found that body size was not associated with the tendency of families to evolve island endemics.

Large-bodied birds (>=27 cm) are less likely to have smaller total island distributions. It is possible that energetic constraints on small islands have resulted in selection for smaller body size (McNab 1994b). However, it is more likely that the relationship is due to a filter on some large-bodied species incapable of long-term persistence within a restricted distribution. This filter may be associated with larger bodied birds generally having a higher trophic position (Lawton 1994), greater energetic requirements (McNab 1994b), larger home range (Jenkins 1981), and lower abundance (Gregory and Blackburn 1995, but see Gaston and Blackburn 1995, 2000). These traits may both inhibit large species from colonising small islands and increase their risk of extinction in such an environment.

Sexual size dimorphism

The trend for sexual size dimorphism to increase on islands may be explained by resources being partitioned in a resource-limited environment with few or no competitors, increased male-male competition, or increased female choice for larger body size. These processes are interrelated and more than one mechanism may be acting at a time. If sexual body size dimorphism is primarily driven by niche partitioning, then one would expect both male and female divergence, whether bigger or smaller, to be of similar importance. However, when species comparisons where females are larger than males are removed from the analyses, the statistical relationship is considerably strengthened. This indicates that increased male-male competition for territories or mates may be a significant mechanism in the increase in body size dimorphism. However, using non-parametric statistics, female body size dimorphism also significantly increases on islands. This trend for both male and female body size dimorphism to increase provides support for competitive release and niche partitioning between the sexes as the dominant processes. However, we cannot reject the possibility that sexual selection pressures may intensify in an insular environment.

If sexual selection plays an important role in the increase in sexual size dimorphism then it is strange that sexual selection is often cited as decreasing on islands due to lower levels of extra-pair paternity (Griffith *et al.* 1999; Griffith 2000; Møller 2001). Although extra-pair paternity has been shown to be associated with dichromatism (Møller and Birkhead 1994), and dichromatism is associated with female choice (Møller 2001), the frequency of extra-bond offspring has not been demonstrated to correlate with body size dimorphism (Owens and Hartley 1998). Thus the reported decrease in extra-pair paternities on islands may have little influence on body size dimorphism. Alternatively, the trend for lower reproductive rates on islands may be the driving mechanism leading to lower levels of extra-pair paternity (Owens pers. comm.). The shift to a "slower" life history strategy on islands has been hypothesised to be driven by an increase in intraspecific competition on islands (Grant 1998), which may also lead to greater male-male competition for limited territories and resources. Therefore, extra-pair paternity may decline on islands, but the process of sexual selection through male-male competition may actually increase.

The consistent trends in clutch size, body size and sexual size dimorphism suggest that conditions on oceanic islands do select for certain convergent traits across bird taxa. The processes behind these trends are likely to be a combination of a filter on the type of species capable of colonising and persisting on a distant restricted-range island, and selection for specific traits within an island habitat. If the convergent traits have evolved in response to similar conditions on islands, such as reduced predation and competition, they may render a species more vulnerable to extinction, once humans introduce these selective pressures to islands. Thus, understanding the subtle convergent morphological and life history trends on islands may provide insight into traits that are associated with elevated extinction rates of island endemic birds.

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CHAPTER 3

HUMANS AS AN EXTINCTION FILTER ON OCEANIC ISLANDS AND THE CHANGING PROCESSES OF THREAT

Abstract

Early human colonists to oceanic islands have been implicated in extensive avian extinctions. If a large number of extinctions have occurred on islands due to human-related threats, then it should be possible to identify the effects of extinction filters. An extinction filter is a specific threat process that selectively removes a subset of species. Thus, island birds that have experienced a human-related extinction filter in the distant past may appear less susceptible to present threats because all the vulnerable species have already become extinct. It is possible to test for the role of humans as an extinction filter on oceanic islands by examining the relationship between the length of time that humans have been on an island, or archipelago, and the present level of avian endangerment. If the extinction filter effect has occurred, then islands colonised for a longer period of time should have fewer threatened species. I use a global database of all oceanic island birds to demonstrate that rates of recent extinction are lower on islands that have been colonised by humans for a longer period of time. This relationship is consistent for birds in the Pacific and non-Pacific. A similar trend exists for birds that are threatened with extinction, although the pattern is extremely weak. If threat types are analysed separately, there is a strong relationship for birds to be less threatened due to introduced species on islands that have been colonised for a long period of time, but not for species threatened by habitat loss or exploitation. The analyses indicate that humans have acted as an extinction filter on oceanic islands throughout the world. Past patterns of extinction have had a strong influence on which species have recently become extinct, but not which species are threatened with extinction. This indicates that the processes of extinction may be changing on islands.

Introduction

There are 987 endemic birds restricted to oceanic islands, 35% of which are threatened with extinction. This number is high compared to 9% of non-oceanic island birds classified as threatened (Chapter 1). Oceanic islands have also suffered a disproportionate number of recent bird extinctions. Of 128 extinctions recorded in historic times, 88% are oceanic island endemics (IUCN 2000; BirdLife International 2000). High levels of extinction and threat to island endemic birds are not recent phenomena. The first human colonists to oceanic islands have been implicated in many avian extinctions (Olson and James 1982; Diamond 1982, 1984, 1989; Cassels 1984; Olson 1989; Dye and Steadman 1990; Milberg and Tyrberg 1993; Pimm *et al.* 1994; Steadman 1990,1993, 1995, 1998). On the tropical Pacific islands, excavations of fossil and subfossil remains indicate that there may have been more than 2,000 birds that became extinct during the period of prehistoric human colonisation (Steadman 1991, 1995). The dominant extinction process in prehistoric times remains unknown (Milberg and Tyrberg 1993); however, exploitation, introduced species, and habitat loss have all been documented (see Diamond 1984; Atkinson 1985; Olson 1989; Kirch *et al.* 1992; Paulay 1994; Steadman 1995; Holdaway and Jacomb 2000). Johnson and Stattersfield (1990) assess recent extinctions and suggest that introduced species were the dominant cause, followed by hunting and habitat loss. Current assessments of the threats to island birds find habitat loss to be the most dominant process, followed by the introduction of exotic species and over-exploitation (Stattersfield *et al.* 1998; Chapter 1). Understanding the nature of extinction processes in the past is important because past processes may play an important role in determining the species that are now particularly vulnerable to extinction.

I examine the role of first human colonists as an extinction filter on oceanic islands on a global scale to understand both the extent of human-caused extinctions on islands and how the process of extinction has changed from prehistoric times to the present. An extinction filter occurs when a region's biota is faced with a novel threat that leads to the extinction of a susceptible subset of species. The traits that make some species more susceptible than others will depend on the specific threat. An extinction filter can be detected when the same threat or a similar threat recurs. If there has been an extinction filter, fewer species will become threatened or extinct in regions or islands that have previously experienced the threat than in other comparable areas. This is simply because all the particularly susceptible species have already perished (Pimm *et al.* 1994; Coope 1995; Balmford 1996). Areas that have experienced extinction filters can have both lower threat rates and lower diversity than comparable areas.

Pimm *et al.* (1994) observed that birds in the Pacific islands have lower levels of threat and extinction on islands that have been colonised by humans for a greater period of time. Here I extend this analysis to all oceanic island birds and control for potentially confounding variables such as the distance from the mainland, a species total distribution, and the effect of latitude. In addition, I control for the non-independence of closely related species and attempt to reduce the effects of spatial autocorrelation. I also examine the relationship between species that are susceptible to specific threats (introduced species, exploitation, and habitat loss) and the period of time that they have been exposed to humans. This enables the identification of threat processes that were significant in the distant past. If birds appear to be more resilient to a specific threat process on islands colonised more distantly in the past, it provides evidence that this extinction agent has played a significant role in prehistoric bird extinctions. These analyses also helps to identify threat processes where the probability of future persistence is not influenced by past resilience to human-related threats.

Methods

I explore the role of humans as an extinction filter on oceanic islands using a global data set of all oceanic island land birds, details of extinct and threatened species and the history of human colonisation in these areas. Two separate types of analyses have been employed to reduce the potentially confounding influence of spatial autocorrelation (Legendre 1993) and phylogenetic non-independence (Felsenstein 1985). The first approach uses general linear models to examine the relationship between the date of first human colonisation of an island, or group of islands, and the proportion of birds that are presently threatened or have recently become extinct. This reduces the effect of spatial autocorrelation as each island or island group is an independent data point. The second approach compares closely related species to determine if the data at which time humans arrived within a species island distribution affects its probability of being threatened or having recently become extinct. This approach reduces the effect of phylogenetic non-independence as each comparison between a pair of species is an independent data point.

Island based approach

Five different analyses are conducted. The first examines the relationship between the date of first human colonisation of an island or island group and the proportion of endemic birds that recently became extinct. The second examines the relationship between the date of first human colonisation of an island or island group and the proportion of endemics that are presently threatened. The other three models examine the relationship between the date of first colonisation and the proportion of extant birds that are recorded as threatened by specific threat processes (introduced species, exploitation and habitat loss).

The data on the island birds is based on BirdLife International's endemic bird areas (EBA's) of the world (Stattersfield, *et al.* 1998). This identifies 218 EBA's, defined as areas that encompass the entire breeding area of two or more endemic terrestrial bird species with breeding ranges of less than 50,000 km^2. I consider marine EBA's equal to or smaller than New Zealand giving a total of 63 individual islands or archipelagos (Appendix 3.1). Taxonomy is based on Sibley and Monroe (1990, 1993). For the recently extinct species the taxonomy follows IUCN (2000) and BirdLife International (2000).

In the first analysis the dependent variable is the proportion of bird species recorded as extinct in historic times on each of the 63 islands or island groups (E_X), where a historic extinction is one that occurred subsequent to 500 BP. If a species extinction occurred in more than one EBA, it was listed as extinct in both EBAs. For the second analysis the dependent variable is the proportion of endemic birds listed as threatened by BirdLife International (2000) (T_t). Species are not considered threatened if they have been listed simply because they have a small range. Recent extinctions provide the most reliable indication of islands or island groups that have particularly extinction-prone endemic birds. However, there is only weak and inferential evidence about the causes of extinction. In contrast, for extant threatened species, the dominant causes of threat have been identified by BirdLife International (2000) including over-exploitation, the introduction of exotic species or habitat loss (Appendix 3.1). I use these data to calculate the dependent variable for three of the analyses. The dependent variable in the third analysis is the proportion of endemic birds that are threatened by habitat loss or modification on each island or island group (T_h), for the fourth, the proportion that are threatened by the introduction of exotic species (T_i), and for the fifth, the proportion threatened by over-exploitation (T_e) such as hunting or the collection of eggs. If a species is threatened by more than one threat type (e.g. introduced species and habitat loss), it is included in all relevant analyses. Species are often threatened by more than one of these categories and there are synergistic relationships among threat types (Diamond 1984, 1989). However, here I am simply trying to determine the processes of threat that are playing a role on specific islands and such a division of threat types is therefore useful. For the five models the proportion of historic extinctions or threatened species on each island or island group are calculated. The proportions have been weighted by sample size (McCullagh and Nelder 1989) to minimise errors caused by islands that are represented by a lower number of endemic birds.

In addition to the date of first colonisation, six other independent variables are included in the analyses. These are the date of European discovery, the current human population density, the distance to the nearest mainland, the area of an island, maximum elevation, and latitude. The date of first colonisation refers to the time when human beings first arrived to an island. The date of European discovery is the date of the first record of an island or island group by Europeans BP. Estimates of the date of first colonisation and European discovery are obtained from Webster (1972), Olson and James (1982), Steadman *et al.*(1984), Munro (1988), Jones *et al.* (1992), Milberg and Tyrberg (1993), Pimm *et al.* (1994), Wragg (1995), Steadman (1995), Vianna (1997), Encyclopaedia Britannica (1998) Microsoft Encarta Encyclopaedia (1998) and Steadman *et al.* (1999) (Appendix 3.1). The date of European discovery is distinguished from the date of first colonisation because the recent arrival of Europeans, with exotic species and the technology to rapidly modify the landscape, may be the greatest factor responsible for shaping current patterns of threat and extinction.

Human population density is defined as the number of people per square kilometre. Population figures were taken between 1970 and 1995 (Encyclopaedia Britannica 1998;

Microsoft Encarta Encyclopaedia 1989). The distance of an island from the mainland is measured (in km) from the nearest point of the island or island group to a continental landmass (including Madagascar) (based on McCall 1997; with additions using Encarta World Atlas 1998). Island elevation was measured as the highest known point (in km). (Stattersfield *et al.* 1998). Latitude is based on Dahl (1991) and Encarta World Atlas (1998).

Island based approach analyses

Multivariate models were fitted to data from the islands or island groups. The seven variables above were used in each of five models to explain variation in the numbers of historic extinctions and species threatened due to habitat loss, the introduction of exotic species and human over-exploitation. All analyses were conducted using general linear models assuming a binomial error distribution and employing a logit link function (Crawley 1993).

First the data were explored to identify potentially significant interaction terms. The five oceanic island analyses were then fitted using the same full model:
Prop (dependent variable) = Region•first colonisation date + elevation + distance + area + latitude + European discovery + population density.

The dependent variables are E_x, T_t, T_i, T_h, and T_e. The dot symbol (•) indicates the interaction terms plus the main effects were considered in the model. Region was included as a factor to determine if there were significant differences between the processes acting in the Pacific and non-Pacific. The interaction term between region and the first colonisation date was included to investigate whether the effect of first human colonists had similar influences on current patterns of threat and extinction in the Pacific and non-Pacific.

The full model was fitted and terms were then dropped one by one starting with the least significant terms. If a term was found to contribute significantly to the overall model it was fitted back into the model. Once only significant terms remained in the model, each of the terms that had been removed from the model was re-entered to identify the minimum adequate model (Crawley 1993). Significant terms in the model were identified by the change in deviance, which is distributed approximately as χ^2 with degrees of freedom equal to those of the term that is added or removed. The χ^2 of terms with a significance value of $P<0.05$ are reported. Williams' correction for overdispersion was used (Collett, 1991). This keeps the scale parameter the same, but the weight directive is adjusted and the model is then reassessed. The standard errors are then increased to account for the overdispersion. This approach is recommended when the sample sizes are unequal, as here (Crawley 1993). The χ^2 for each of the terms in the final model were added and divided by the total deviance to determine the proportion of the deviance explained by the full model.

Species based approach

The questions addressed are similar to the previous analyses. However, this approach compares closely-related species to examine the relationship of threat and extinction with the time they have been exposed to human influences. The classification of threat and extinction, as well as the division of species by threat type (introduced species, exploitation, and habitat loss) all follow the method of the previous analyses.

Refer to the island bird database (Chapter 1).

Species based approach analyses

I first address whether island birds that have been exposed to human-related threats for a greater period of time are less likely to have recently become extinct. This analysis is then divided into birds found in the Pacific and those found on islands outside the Pacific to determine if patterns are similar for the two regions. Second, island birds are compared to determine if species are less likely to be threatened if they have been exposed to humans for a greater period of time. I also assess whether species that have been exposed to specific human-related threats (introduced species, exploitation, and habitat loss) are less likely to be threatened by these processes of extinction in the present.

The contrasts were calculated using the BRUNCH algorithm in CAIC (Comparative approach page 29). All contrasts were tested for normality and a one-sample t-test was used to determine significance. The results were similar when the analyse were repeated using Wilcoxon's test. The effect of the total area of a species' distribution and minimum distance from the mainland and latitude were controlled for independently as these terms are cross-correlated with date of first human colonisation and may be associated with extinction risk. The results from the biogeographic controls are only given if they alter the significance of the relationship between human presence and levels of threat or recent extinction. The above analyses were also run with date of first human colonisation divided into 10 categories (0, 250, 1000, 2000, 4000, 8000, 16000, 32000, 64000, >64,000 years ago). This was done because exact dates of colonisation are often poorly known and precision decreases with greater time. However, dividing the date of first human colonisation into 10 categories did not significantly alter the results.

Results

Island based approach

There were several significant variables reflecting both geography and human colonisation history in the final minimum adequate models (Table 3.1). Region was consistently non-significant across all the models indicating that there is no difference in the relationships of threat and recent extinction with first colonisation date between birds on Pacific and non-Pacific islands.

Extinction model

Fewer recent extinctions (i.e. extinctions within the last 500 years) have occurred on islands that were colonised by humans in the distant past (Figure 3.1). In contrast, recent extinctions have been more common on islands that have high human population densities or islands that are located at greater distance from the mainland. Finally, species on islands with higher latitude have experienced a greater proportion of recent extinctions (Table 3.1).

Threat models

Similar to the extinction model, birds are less threatened on islands that have been colonised for a great period of time (Table 3.1), a relationship solely driven by island birds being less threatened by introduced species on islands that have been colonised for a greater period of time (Figure 3.2). No relationship is found between the date of first human colonisation and the proportion of birds that are threatened by exploitation or habitat loss. Islands with high human population densities are more likely to have a higher proportion of threatened birds, a relationship driven by species that are vulnerable to habitat loss and to a lesser extent to introduced species. Finally, birds on more distant islands tend to be more threatened. This is consistent for the three threat types, indicating that birds on distant islands are particularly susceptible to exploitation, habitat loss and especially introduced species.

Table 3.1. The regression coefficient for the significant explanatory variables (P<0.05) in the five minimal adequate models. A plus or minus sign indicates whether the significant coefficient is positive or negative. χ^2 values and associated probabilities are listed. * represents a probability of ≤ .05 and > .025, ** ≤.025 and > .001, *** ≤ .001. The deviance explained by each model is listed directly below the model.

Explanatory variable	HISTORIC EXTINCTION	THREATENED	THREATENED BY HABITAT LOSS	THREATENED BY INTRODUCED SPECIES	THREATENED BY OVER-EXPLOITATION
First colonisation	- 28.8***	- 5.7**		- 12.3***	
European discovery					
Population density	+ 12.8***	+ 3.9*	+ 13.9***	+ 5.2**	
Area					
Distance	+ 14.8***	+ 10.8**	+ 8.7**	+ 22.5***	+ 5.3**
Elevation					
Latitude	+ 12.6***				
Region					
Region*first col. date					
Deviance explained	39.5	23.4	27.5	38.6	8.2

Figure 3.1. The relationship between the proportion of endemic birds that have become extinct on an island or island group in historic times and the date of first human colonisation.

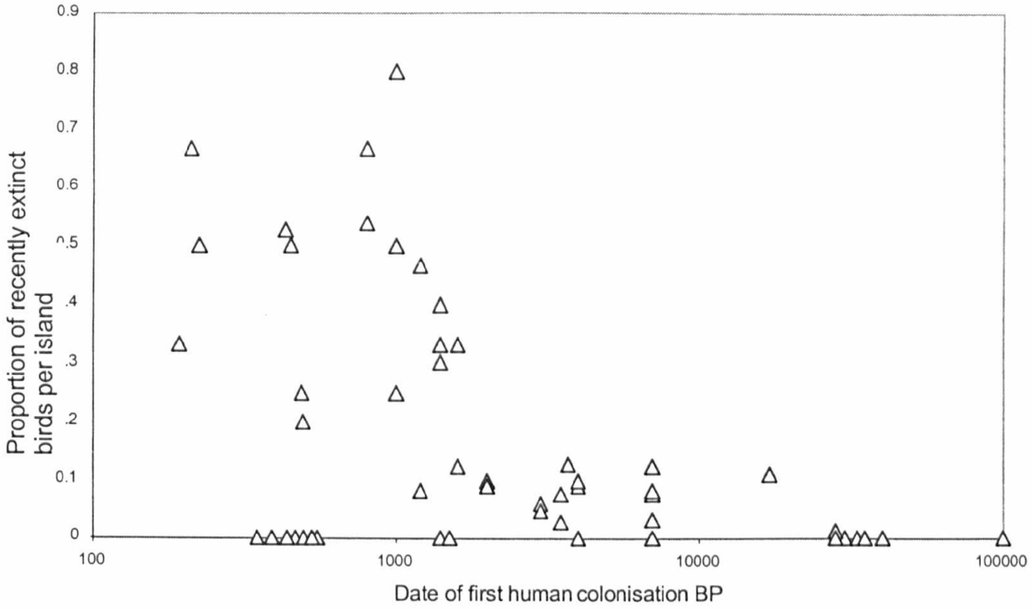
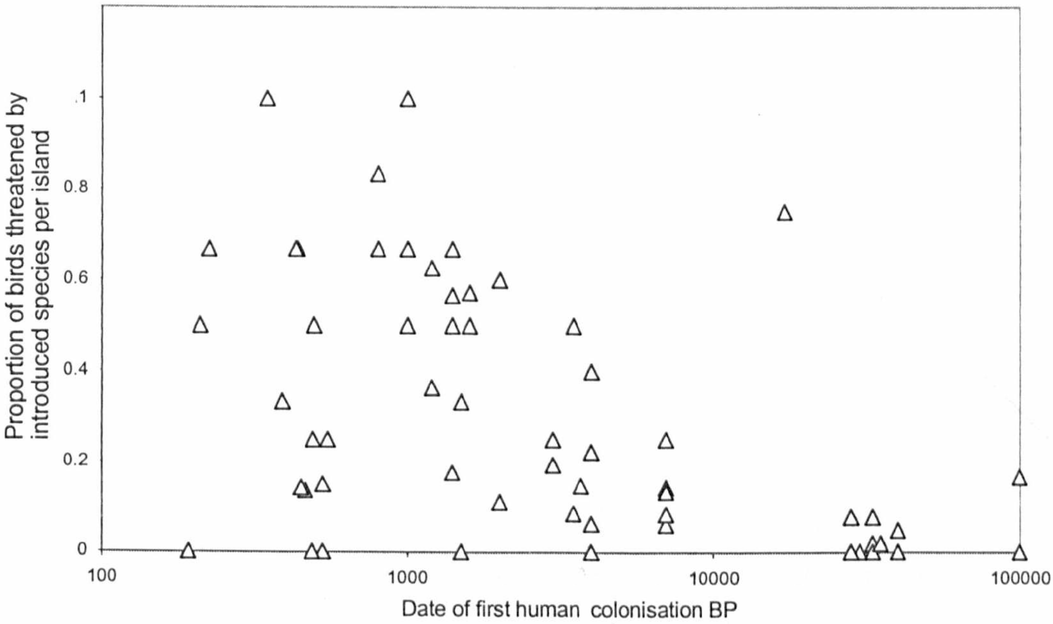


Figure 3.2. The relationship between the proportion of endemic birds threatened by introduced species on an island or island group and the date of first human colonisation.



Species based approach threat and extinction models

The results from the species based approach are consistent with the island based approach. Birds are less likely to have recently become extinct if they have been exposed to human-related threats for a greater period of time (Table 3.2). This relationship is true for both island birds in the Pacific and non-Pacific. Island birds are also less threatened if they have been exposed to humans for a greater period of time. However, when I control for the total distribution of a species, this falls just below significance (Table 3.2). Island birds are less likely to be threatened by introduced species if they have had long term exposure to humans. A similar weak relationship is found with habitat loss, but becomes non-significant if I control for either a species total distribution or minimum distance from the mainland. Finally, there is no relationship between long term exposure to humans and a species vulnerability to exploitation.

Table 3.2. The relationship between first human colonisation date within a species distribution and recent extinction, recent extinction in the Pacific, recent extinction in the non-Pacific, threatened species, threatened by habitat loss, threatened by introduced species, threatened by exploitation. Species' total island distributions, distance from the mainland, and average latitude have been controlled for independently. One sample t-tests are used to analyse the standardised contrasts.

Analyses	Number of contrasts	t	p-value	Controls		
				Total island distribution	Distance from the mainland	Average latitude
Extinct	49	-5.54	<0.001	No effect	No effect	No effect
Extinct Pacific	28	-3.76	<0.001	No effect	No effect	No effect
Extinct non-Pacific	23	-3.18	0.004	No effect	No effect	No effect
Threatened	102	-2.87	0.005	T=-1.85, P=0.067	No effect	No effect
Habitat loss	92	-2.12	0.037	T=-1.12, p=0.27	T=-1.80, p=0.075	No effect
Introduced species	76	-5.09	<0.001	No effect	No effect	No effect
Exploitation	33	-0.28	0.78	No effect	No effect	No effect

Discussion

The results of the island-based approach and the species-based approach are very similar. They demonstrate that recent extinctions have been less common in regions where humans have been present for a long period of time. In both analyses this relationship holds for birds in the Pacific and non-Pacific. Both approaches also demonstrate a similar, but much weaker trend for species to be less threatened in regions where humans have been present for a long period of time. This trend is particularly strong for birds threatened by introduced species, but less so for species threatened by habitat loss or exploitation. This provides strong evidence that humans have acted as an extinction filter on oceanic islands throughout the world selectively removing species particularly susceptible to human related threats.

In the multivariate analyses the interaction term between region and date of first colonisation was not significant in any of the models supporting the contention that the extinction filter effect has been similar in the Pacific and non-Pacific. This is also supported by the species based approach that demonstrate a similar extinction-filter effect for recently extinct species in both the Pacific and non-Pacific. The uniform extinction filter effect is likely a result of the similar biogeographic constraints and selection pressures on oceanic islands throughout the world. First, island birds tend to have restricted ranges that may make them more susceptible to most threats (Simberloff 2000). Secondly, similar conditions on islands such as lower species diversity and a reduction of competitors and predators (Grant 1998; Blondel 2000; Chapter 2) may lead to selection of convergent life history, ecological, behavioural, and morphological traits that result in similar susceptibility to specific human-related threats – e.g. flightlessness, ground nesting, or tameness.

A strong extinction filter effect indicates that there is a relationship between persistence to past human-related threats and resilience to present extinction processes. Conversely, the lack of an extinction filter effect implies that resilience to past human-related threats has little influence on a species' probability of surviving given present extinction processes. The latter scenario may occur if the process of extinction changes or intensifies over time.

The absence of the extinction filter effect can be observed by comparing the analysis on recently extinct birds, where the filter effect is strong, with the analysis of threatened species where the filter effect is weak. Either we are not very good at identifying species that are prone to extinction, or the process of extinction is changing and/or intensifying. Attempts to identify causes of recent extinction (Johnson and Stattersfield 1990; King 1985; Chapter 1) and present threat (Collar *et al* 1994; Stattersfield *et al.* 1998; BirdLife 2000; Chapter 1) support the latter. Introduced species and exploitation have been identified as the dominant cause of recent extinctions, and habitat loss is now by far the greatest threat on islands.

An examination of the relationship between past exposure and present susceptibility to specific types of threat helps to illuminate processes of extinction that were significant in the distant past. In addition, it enables the identification of threat processes where the probability of future persistence is not influenced by past resilience to human-related threats. There is a strong filtration effect evident for birds threatened by introduced species, but not those threatened by habitat loss or exploitation. Thus, introduced species were likely a dominant threat during the period of prehistoric human colonisation. These data suggest that species susceptible to this specific threat have been selectively filtered from islands colonised by humans for a long time period. Thus, the remaining birds on these islands now appear to be more resilient, on average, to introduced species than those birds on other islands that have not had similar exposure.

The lack of an extinction filter effect for species threatened by exploitation is interesting because there is strong support for exploitation as a dominant human-related extinction process by early colonists to islands (Diamond 1982; Olson and James 1982; Olson 1989; Dye and Steadman 1990; Milberg and Tyrberg 1993; Steadman 1995; Holdaway and Jacomb 2000). An extinction filter effect may be difficult to detect if the extinction process is very rapid and thus has run its course. For example, if virtually all large flightless birds have been selectively removed from islands, then no variation will be detected when islands colonised recently are compared with islands colonised in the distant past. An extinction filter will also be difficult to detect if the target species changes over time. Traditionally, exploitation would have been based on subsistence hunting. Species now threatened by exploitation are often harvested for the pet trade (e.g. Beissinger 2000). For many of these species intense exploitation is a novel threat.

Extensive habitat destruction by early human colonists has been documented on a few islands (e.g. Olson and James 1982; Diamond 1984; Flenley and King 1984; Kirch *et al.* 1991; Kirch *et al.* 1992; Paulay 1994). However, the extent to which habitat destruction or modification by early colonists has caused past extinctions remains a mystery. The lack of a filtration effect with species threatened by habitat loss may indicate that there is little relationship between the extent or rate of habitat destruction and the date of human colonisation. Thus, it may have been the dominant process of extinction but has not been identified as an extinction filter. However, if habitat loss was a dominant threat for past extinctions but does not function as an extinction filter, we would not expect such a strong relationship between the date of first human colonisation and the proportion of species that have recently gone extinct on islands. The fact that the filtration effect is much weaker for species that are at present threatened is strong support that the process of extinction has changed or intensified. Estimates of the cause of historic extinctions and present threat support the conclusion that habitat destruction has only recently become the dominant extinction process on oceanic islands (Johnson and Stattersfield 1990; Stattersfield *et al.* 1998; Chapter 1) and continues to intensify (Simberloff 2000).

The distance term was added to the multivariate analyses to control for the potentially confounding relationships among the date of first human colonisation, the distance of a species from the mainland and extinction risk. However, the strong effect of distance in all the multivariate models is of interest as it provides strong support that species at greater distance from the mainland are at greater risk of extinction. This relationship is particularly strong for the models examining species that have recently become extinct or birds that are threatened due to introduced species. This increased susceptibility at greater distance from the mainland is likely a result of isolated endemic birds evolving in a species-poor environment with few predators or competitors (Williamson 1981).

This study supports the hypothesis that humans have acted as an extinction filter on oceanic islands throughout the world. Birds on islands that have experienced such extinction filters have been less prone to recent extinctions. However, now that the process of extinction is changing on islands, species that have survived past extinction filters may be no more resilient to future threat processes. This is because different threat processes target different species. As habitat destruction continues to intensify on islands, past human-caused extinctions will continue to play a smaller role in shaping overall patterns of threat and extinction. This analysis has demonstrated that extinction is a dynamic process where both the threats and intrinsic characteristics associated with increased extinction risk change over time. If we are to effectively identify extinction-prone species in the future, we must examine species in the context of historical versus present extinction processes.

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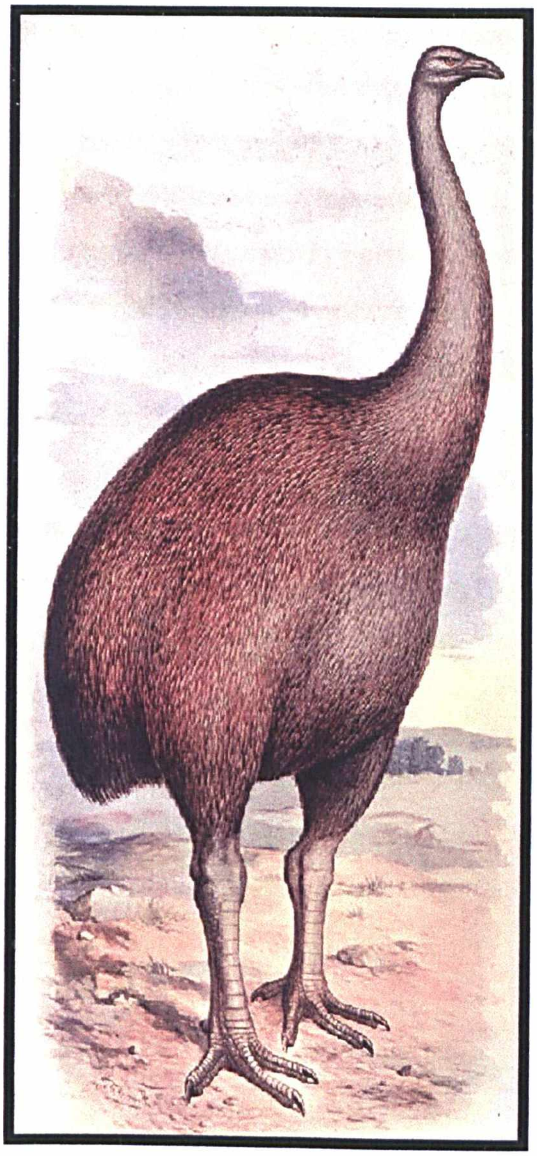
Appendix 3.1. The number of restricted-range birds, historic extinctions, restricted-range threatened birds, and birds threatened due to habitat loss, introduced species, and over-exploitation on each of the 63 islands or island groups considered in the analyses. The data on birds is from Stattersfield *et al.* (1998), but using Sibley and Monroe taxonomy (1990,1993). Estimated dates of first human colonisation are given as before present (BP).

Islands or island groups	Extant	Extinct	Threatened by			Date of first human colonisation BP.	European discovery
	Restricted range birds	Historical extinctions	All threats	Introduced species	Habitat loss	Exploitation		
Admiralty	13	0	1	1	0	0	33000	1616
Aldabra	3	1	0	0	0	0	490	1511
Andaman	12	0	2	2	2	1	100000	1789
Annobon	2	0	0	0	0	0	530	1471
Auckland	2	1	0	0	0	0	195	1806
Bahamas	7	1	1	1	1	0	7000	1492
Banda Sea	41	0	0	0	0	0	4000	1512
Banggai and Sula	16	0	3	0	3	1	4000	1511
Buru	28	0	4	0	4	1	4000	1511
Cape Verde	4	0	2	1	0	0	551	1450
Central Hawaiian Islands	23	10	13	13	12	1	1400	1778
Chatham	4	4	2	2	2	0	1000	1791
Christmas	2	0	2	2	2	1	351	1650
Cocos	3	0	1	1	0	0	392	1609
Comoros	17	0	4	3	4	0	1400	1506
Cook Southern	7	1	5	4	4	0	1600	1520
Cozumel	3	0	1	0	1	0	30000	1518
Cuba	12	1	5	3	4	1	7000	1492
Fernando de Noronha	2	0	1	1	1	0	498	1503
Fiji	35	1	8	3	8	3	3500	1774
Galapagos	22	0	3	3	1	1	466	1535
Halmahera and Obi an	42	0	9	2	9	3	40000	1511
Hawai'i	15	10	10	10	9	3	1400	1778
Henderson	4	0	0	0	0	0	1500	1767
Hispaniola	33	0	9	2	9	5	7000	1492
Izu	3	0	2	1	1	0	1500	1643
Jamaica	33	3	6	2	6	2	7000	1494
Juan Fernandez	3	0	2	2	1	0	438	1563
Laysan	2	1	1	1	0	1	1400	1778
Lesser Antilles	34	5	12	5	10	5	3700	1493
Lord Howe	2	4	1	1	0	1	213	1788
Madeira and Canarys	9	1	1	1	1	1	2000	1334
Marianas	12	1	6	6	5	2	3500	1521
Marquesas	10	1	6	6	2	1	2000	1595
Mauritius	9	10	6	6	6	0	433	1568
Nansei Shoto	10	1	5	4	5	0	4000	1853
New Britain and New Ireland	54	0	6	1	6	2	35000	1700
New Caledonia	31	2	6	6	4	0	3000	1774

New Zealand North Is	3	6	2	2	1	0	800	1642
New Zealand South Is	6	7	5	5	2	1	800	1642
Norfolk	3	3	2	2	2	0	227	1774
Palau	16	0	1	1	0	1	4000	1543
Principe	11	0	1	0	1	0	531	1470
Puerto Rico and Virgin Islands	24	0	6	2	5	2	7000	1493
Rennell and Bellona	12	0	0	0	0	0	28000	1568
Reunion	7	7	1	1	1	1	451	1550
Rimatara	2	1	1	1	0	1	1600	1520
Rodriguez	2	8	2	2	2	0	1000	1520
Samoa	20	1	5	5	5	3	3000	1722
Sao Thome	20	0	8	3	8	1	531	1470
Seram	30	0	4	0	4	2	40000	1521
Seychelles	11	1	4	4	4	1	1200	1502
Society	8	7	6	5	2	1	1200	1767
Socorro	3	1	2	2	0	0	1000	1550
Solomon	78	1	15	6	14	6	28000	1568
St Matthias	8	0	0	0	0	0	33000	1767
Sulawesi	54	0	7	1	7	3	33000	1512
Timor and Wetar	35	0	5	0	5	5	100000	1520
Tristan da Cunha	4	1	1	1	0	0	495	1506
Truk, Pohnpei and Kosrae	18	2	4	4	4	2	4000	1580
Tuamotu	8	1	6	6	3	2	17000	1606
Vanuatu and Temotu	30	1	8	4	7	4	7000	1768
Yap	7	0	0	0	0	0	4000	1791

CHAPTER 4

HUMANS AS A SELECTIVE FORCE: FILTRATION OF AVIAN LIFE HISTORY AND ECOLOGICAL TRAITS ON ISLANDS



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Abstract

There is strong evidence that a wave of avian extinction occurred on oceanic islands throughout the world following the arrival of humans. Endemic island birds have experienced fewer extinctions on islands that have been colonised by humans for a long period of time than on islands colonised recently. This indicates that the susceptible species had already been removed from the island avifauna before extinctions began to be recorded. I therefore hypothesise that those life history or ecological traits that predispose species to extinction may have been largely eliminated from such islands. Here I test five ecological and life history traits that are believed to result in species being at greater risk to human-related threats, and therefore might have been selectively removed from the island avifauna. I test this by comparing the ecological and life history traits of birds on islands that have been inhabited for a long period of time with birds on islands that have more recently or never been colonised by humans. I demonstrate that non-forest specialists, ground nesters, and flightless birds have likely been filtered from islands by human colonists. I do not find any relationship between body size or clutch size and time of first human colonisation. This study indicates that humans have created a new selective regime and are presently in the process of shaping avian ecological and life history traits on oceanic islands. It also suggests that traits associated with past extinctions may be very different from extinction-prone traits of presently threatened species. This implies that species may be at risk even in landscapes with a long history of human disturbance.

Introduction

The first human colonists to oceanic islands are believed to have caused extensive bird extinctions (Milberg and Tyrberg 1993; Steadman 1995). In the Pacific such colonists are estimated to have been responsible for the extinction of roughly half the species on each island group (Pimm *et al.* 1994). Support for extensive prehistoric extinctions is provided by patterns in the geographical distribution of recent extinctions and extant threatened birds, because extinctions over the past 500 years and present levels of threat are lower on islands that have been colonised by humans for greater periods of time (Pimm et al 1994; Chapter 3). This implies an extinction filter effect (Coope 1995; Balmford 1996), whereby species that were particularly prone to anthropogenic threats have gone extinct on islands, leaving only the less susceptible species. If this is true, it begs the obvious question of which specific traits are related to extinction proneness, and so have been filtered from the island avifaunas.

Species that evolve or adapt in an isolated, species-poor environment with few or no predators may have life history or ecological traits that make them especially vulnerable to the arrival of humans (Williamson 1981). Alternatively, traits not specifically associated with islands may render species particularly susceptible to human disturbance in a restricted-range environment. Whatever the reason for their susceptibility, extinction-prone species may be quickly exterminated from an oceanic island's avifauna once humans and their commensal species arrive (e.g. Holdaway & Jacomb 2000). If this process has occurred it should be possible to identify specific life history or ecological traits associated with this extinction by comparing birds on islands that have been colonised in the distant past with species on islands that have only recently or have never been colonised by humans. If specific traits have been directly or indirectly targeted by humans these traits should be rare or absent on islands that have been colonised for a long period of time, but still present in faunas on islands more recently or never colonised. Here, I examine five ecological or life history traits that may have been selectively removed by human colonisation causing extinctions. The traits I investigate are forest specialism, poor flight ability or flightlessness, ground nesting, large or small body size, and small clutch size.

Forest endemics or forest specialists are presently the most threatened subset of oceanic island land birds (Stattersfield *et al.* 1998). The extinction prone nature of forest specialists is predicted by the theory of the taxon cycle, where species colonise an archipelago as generalists, but evolve to become poor dispersers and increasingly specialised, and often experience a shift in habitat distribution from open grassland and shrubland to mature forest (Ricklefs and Cox 1972, 1978). Species at later stages of the taxon cycle are believed to be at greater risk of extinction due to reduced competitive ability produced by counter-adaptation (Ricklefs and Cox 1972). If species at later stages of the taxon cycle tend to be both restricted to the forest habitat and associated with elevated extinction risk, then they may be among the first to go extinct on islands subsequent to human colonisation. Alternatively, the threat to forest specialists may only appear to be greater, because more susceptible open area and non-forest specialists may have already gone extinct. The habitat preferred by these latter species tends to be the first to be colonised when humans arrive. Either way, the distribution pattern of forest specialists and generalists across islands ought to be related to the date of first human colonisation.

The evolution of flightlessness has occurred on many oceanic islands throughout the world. It is thought to be associated with lower rates of predation, and the potential benefits of energy conservation from reduction in muscle mass required for flight (McNab 1994). Of the 116 that have gone extinct, or extinct in the wild, on oceanic islands over the past 500 years, at least 23 are known to have been flightless or poorly flighted (see BirdLife International 2000). On the basis of subfossil remains, Steadman (1995) has estimated that prehistoric human colonisation preceded the extinction of at least 2000 Pacific island birds, most of which were flightless rails (see also Olson and Jouventin 1996; Rando *et al.* 1999; Steadman *et al.* 1999). Flightless species have been identified as particularly susceptible to exploitation by humans (Diamond 1984; Bibby 1995; Paulay 1994) and the introduction of predators (Willis 1974; Newton 1998; but see Duncan & Blackburn submitted).

Ground nesting may be more common on islands where historically there have been fewer mammalian predators. Ground or near-ground nesters have been identified as having elevated extinction risk (Duncan & Blackburn submitted) as they are particularly susceptible to introduced mammals such as *Rattus norvegicus* and *Rattus exulans* (Diamond 1984; Atkinson 1985; Moors *et al.* 1992). In addition, they are particularly vulnerable to human exploitation. Thus, rapid extinction of ground nesters may occur shortly after humans and their commensals reach islands.

Large-scale comparative analyses have identified larger-bodied birds as being at greater risk of extinction (Gaston and Blackburn 1995; Bennett and Owens 1997). Larger birds on islands would be obvious targets for hunters (Holdaway 1999, 2000). Large body size is also associated with lower population densities and lower rates of reproduction (Gaston and Blackburn 2000), which may lead to an elevated extinction risk in a restricted-range environment (Pimm *et al.* 1988) especially when mortality increases due to processes such as exploitation (Beissinger 2000) and introduced species. In the New Zealand avifauna, Duncan and Blackburn (submitted) found that a disproportionate number of large bodied birds went extinct subsequent to human colonisation. Many of the well known extinctions on islands have been large-bodied species such as the moas (Dinornithidae) (Holdaway 2000), rails in the genus *Porphyrio* (Daugherty *et al.* 1993), elephant birds (Aepyornithidae) (Diamond 1984), the giant eagle (*Harpagornis moorei*) (Newton 1998), the great auk (*Pinguinus impennis*), and the dodo (Raphidae) (Fuller 1987). However, many of the large-bodied birds that have gone extinct were also flightless.

The extermination of small-bodied birds by early human colonists has also been documented on many islands (Diamond 1984; Duncan and Blackburn submitted). On New Zealand, Duncan and Blackburn (submitted) identified egg predation by introduced mammalian predators as a likely cause of the extinction of many small birds. In addition to introduced predators, Diamond (1984) identified habitat destruction as a cause of small bird extinction. Many island birds have extremely restricted distributions and therefore relatively small overall populations. Under these conditions smaller species, which tend to have higher birth and death rates, may be more susceptible to stochastic demographic extinction (Pimm 1988; 1991), especially if their already small populations are reduced by human-related threats.

Bennett and Owens (1997) demonstrated that in general mainland birds with smaller clutch sizes are at greater risk of extinction. Reduced clutch size of island birds has been reported in many species (Crowell and Rothstein 1981; Blondel 1991; Grant and Grant 1998), a trend that is robust when potentially confounding effects of phylogenetic relatedness and latitude are controlled (Chapter 2). Thus, there may be strong selection for lower reproductive rates on islands which represent isolated species-poor environments with few or no predators. This life history strategy may then be particularly susceptible to human-related threats such as exploitation and introduced species that greatly increase mortality. It is possible that species with low reproductive rates may be among the first to be exterminated following the arrival of humans.

Here I test for the presence or absence of these five traits in association with the date of first human colonisation. I control for the phylogenetic relatedness of species, as well as for biogeographic features that may be associated with variation in life history or ecological traits.

Methods

Refer to the Island bird database (Chapter 1).

Life history and ecological traits

Data were collected on nest site (ground versus tree), body length, and clutch size for each species using the following sources: Greenway (1967) Harris (1974), duPont (1975), Mayr (1976), Hannecart (1980), Watling (1982), Clunie (1984), Bennett (1986), Diamond (1987), Fuller (1987), Mountfort (1988), Day (1989), Gill and Martinson (1991), del Hoyo *et al.* (1992,1994,1996,1997), Bregulla (1992), Fry (1992), Jones (1995), Feare (1998), Rowlands (1998), Sinclair (1998), Clement (1999), Isler (1999), Madge (1999), and BirdLife International (2000). In addition to these sources, Roff (1994) and Trewick (1997) were used to assess flight ability. Sibley and Monroe (1990,1993), Stattersfield *et al.* (1998), and Collar *et al.* (1994) were used to identify forest specialists. These are birds that are restricted to the forest habitat, versus non-forest specialists that are found in forest and/or open habitat.

Poorly-flighted birds include all flightless birds and birds that are virtually flightless, but capable of flying very short distances. Data on flight ability were collected for all oceanic island birds. Ground nesters are defined as birds that have open ground nests. This includes nesters in grass but does not include ground hole nesters. Tree nesters are birds that nest in tree holes or on tree limbs, but does not include shrubs. Data were collected for 309 ground nesters and tree nesters (165 genera). Body length is defined as the length of the bird from the tip of the beak to the end of the longest tail feather, and was collected for 529 species (226 genera). Body length data were used instead of body mass as the latter has not been measured for many island birds. The data were also divided into large and small-bodied birds. Species body mass between 50 and 150g were regressed against body length to identify the body length of species that would be on average larger or smaller than 100g. The 100g cut-off point is used because it has been identified as an important threshold in relation to different processes of extinction (Owens and Bennett 2000). One hundred grams is roughly equal to a body length of 27cm. Species >=27cm were therefore considered large and species <27 cm were considered small. Clutch size is the mean number of eggs per nest. Mean annual fecundity would have been a preferable measure, but these data are not available for most island birds. Clutch size is believed to be an appropriate surrogate to provide an indication of fecundity (see Bennett and Owens 1997). Data were collected for 348 species (181 genera).

Refer to comparative approach (Chapter 1)

Analyses with categorical variables

First I address whether there are significantly fewer (1) forest specialists (2) ground nesters, and (3) poorly flighted or flightless birds on islands colonised more distantly in the past. Independent contrasts were calculated using the BRUNCH algorithm in CAIC (Comparative approach, page 29). All contrasts were tested for normality and a one-sample t-test was used to determine significance. The results were similar when the analyse were repeated using Wilcoxon's test. The effect of the total distribution of a species and it's minimum distance from the mainland were controlled for independently, as these terms are cross-correlated with date of first human colonisation and may be associated with the traits in question. For example, there is a relationship between the distance of a species distribution from the mainland and the likelihood that a bird is flightless. Most flightless birds are also ground nesters, and so the ground nesting analysis was run both with and without the flightless species.

Analyses with continuous variables

Second I tested whether species with a (1) greater body length (2) body length >=27cm or body length <27 and (3) smaller clutch size are less common on islands colonised by humans more distantly in the past. The natural logarithm was used to transform the continuous variables, and independent contrasts were calculated using BRUNCH (Comparative approach, page 29). As the variables were continuous it was possible also to calculate contrasts to control for total distribution and distance from the mainland. I also controlled for latitude, as body size (reviewed by Gaston and Blackburn 2000) and clutch size (reviewed by Grant 1998) have both been shown to be correlated with latitude in birds. Linear regression through the origin was used to analyse the contrasts, with the life history trait as the dependent variable and date of first human colonisation, total distribution, distance from the mainland, and latitude as independent variables. Stepwise regression was employed to identify the minimum adequate model.

All the above analyses were also run with date of first human colonisation divided into 10 categories (0, 250, 1000, 2000, 4000, 8000, 16000, 32000, 64000, >64,000 years ago). This was done because exact dates of colonisation are often poorly known and certainty decreases over time. The division of the dates into ten categories did not alter the results.

Results

Analyses with categorical variables

All three dichotomous variables, forest-specialism, poor flight ability/flightlessness, and ground nesting, have a significant correlation with time of first human colonisation. There are more forest specialists on islands colonised more distantly in the past, or conversely, fewer non-forest specialists on islands colonised more distantly in the past (Table 4.1). Flightless birds and ground nesters are less common on islands colonised by humans more distantly in the past. This latter relationship holds if flightless birds are removed from the analyses (Table 4.1). The number of contrasts is similar for the two analyses because many of the flightless birds have close relatives that are ground nesters, but not flightless. When total distribution and minimum distance are controlled for, all three relationships remain significant (Table 4.2).

Table 4.1. The relationship between the date of first human colonisation and ground nesting, flightless or poorly flighted birds, and forest specialists. One sample t-tests are used to analyse the standardised contrasts. The minus value in the test statistic dose not indicate the direction of the relationship.

Dependent variable	df	t	p-value
Ground nesters	15	-3.51	0.003
Ground nesters (excluding flightless birds)	13	-3.76	0.002
Flightless birds	10	-2.91	0.015
Forest specialists	121	-4.10	<0.001

Table 4.2. The relationship between the date of first human colonisation and ground nesting, flightless or poorly flighted birds, and forest specialists while controlling for a species total distribution and distance from the mainland. One sample t-tests are used to analyse the standardised contrasts. The minus value in the test statistic dose not indicate the direction of the relationship.

Dependent variable	Controls	df	t	p-value
Ground nesters	Distribution	15	-2.84	0.012
Ground nesters	Distance	15	-3.53	0.003
Ground nesters (no flightless birds)	Distribution	13	-3.03	0.01
Ground nesters (no flightless birds)	Distance	13	-3.88	0.002
Flightless birds	Distribution	10	-2.50	0.032
Flightless birds	Distance	10	-2.71	0.022
Forest specialist	Distribution	121	-4.90	<0.001
Forest specialist	Distance	121	-4.61	<0.001

Analyses with continuous variables

There is no relationship between body length and time of first human colonisation (n=106, t=0.99, p=0.32). Total distribution, distance and latitude are also not significantly correlated with body length and when controlled for have little effect on the relationship between body length and time of first colonisation (n=106, t=1.27, p=0.21). When the analysis is divided into large-bodied (>=27cm) birds and small-bodied (< 27cm) birds there is still no significant relationship (large bodied birds, n=50, t=-0.12, p=0.91, small bodied birds, n=66,t=-0.02, p=0.98). There is also no relationship between clutch size and date of first human colonisation (n=76, t=0.22, p=0.83). In the clutch size model, total distribution and latitude are significant indicating that birds with larger island distributions and living at higher latitudes have larger clutch sizes (Table 4.3).

Table 4.3. Clutch size as the dependent variable and first colonisation date, total distribution, distance, and latitude as the independent variables. Stepwise multiple regression, through the origin, across contrasts of oceanic island endemic birds.

Number of Contrasts	R^2	F-Ratio	Independent variable	Slope	t	p-value
76	0.20	9.14				
			First human colonisation			NS
			Total distribution	0.046	3.41	<.001
			Distance			NS
			Latitude	0.008	2.55	0.013

Discussion

The analysis indicates that if species have been exposed to humans for a long period of time they are more likely to be forest specialists than species that have more recently been exposed to humans. This indicates that there may be some feature of islands colonised more distantly in the past that results in species there being more likely to be a forest specialist. Islands colonised for a longer period of time tend to be slightly larger and closer to the mainland. Forest specialists may be poor colonisers (MacArthur *et al.*

1972) and therefore less likely to reach islands that are more distant from the mainland. Alternatively, forest specialists that reach distant biologically-impoverished islands may expand their ecological niche in the absence or reduction of competitors and predators (see Blondel 2000) and therefore would be less likely to be restricted to forest habitat. However, the relationship of forest specialism to colonisation date remains very strong even when both total distribution and distance from the mainland are controlled for (Table 4.2). This indicates that the correlation may not be a result of biogeographic patterns, but rather of human colonisation itself. Non-forest specialists may have become either restricted to forest habitat, or else driven to extinction where humans have been present for a long period of time because humans impact non-forest areas most intensely.

The impact of human colonisation on different oceanic island endemic avifaunas will differ in detail, but are similar in broad generalities. The first habitat types to be devastated are usually the most accessible and desirable for humans (Paulay 1994). They often include areas that can easily be modified using techniques such as burning (Diamond 1984). This opportunistic pattern of habitat destruction can easily be observed on oceanic islands or island groups throughout the world such as Guadalupe, Mauritius, Rodrigues, Seychelles, Hawaii, Society islands and Norfolk, where the open areas and lowland, often dryer, forest have experienced the greatest levels of destruction (see Crosby 1993; Pimm *et al.* 1994; Stattersfield *et al.*1998). As the open area and lowland regions are modified it is the species that use this habitat type that may experience the greatest extinction risk. This will include many of the open area and non-forest restricted endemics. The most susceptible non-forest specialists may become extinct or have their range restricted to the remaining native forest habitat, while a few may be able to persist in the transformed human landscape. The remaining forest acts as a refuge where species are less accessible and therefore less vulnerable to human exploitation, and there are often fewer introduced predators and competitors (Diamond and Veitch 1981; Chapter 6). As the process of deforestation continues the forest refuges then become the most threatened habitat type as the now restricted non-forest specialists and forest specialists are limited to an increasingly small distribution.

Islands that have been colonised for a greater period of time may be at a later stage in this process, and many of the non-forest specialists are now entirely restricted to forest habitat or else driven to extinction. The extent to which undocumented non-forest specialists have been removed from islands inhabited for a greater period of time awaits extensive studies of subfossil remains. The 'taxon cycle' predicts that highly endemic species become restricted to 'interior,' forest (Ricklefs and Cox 1972, 1978). The analyses here indicate that this may simply be an artefact of an extinction filter in open and accessible areas where human disturbance has been most intensive. Thus, highly endemic species may appear to be restricted to forest habitat simply because they have been extirpated or driven extinct by humans in open areas.

This study indicates that humans and their commensal species may be responsible for the selective removal of ground nesters and flightless or poorly flighted endemic birds on islands that have been occupied by humans for a long period of time. Ground nesters appear to be missing from islands colonised in the distant past even when flightless birds are removed from the analyses. The wave of ground nester extinction was likely primarily caused by nest predation from introduced mammalian predators. This process has been observed on islands where mammalian predators have only recently been introduced (e.g. the impact of pigs on Auckland Island or rats (*Rattus norvegicus*) on South Georgia Island: Atkinson 1985), and inferred from studies of longer term extinction patterns (e.g. Duncan and Blackburn submitted). Unfortunately, it is not possible to examine the effect of flightlessness independently of ground nesting as most flightless birds are also ground nesters. Therefore, it is possible that all flightless birds are missing from islands colonised by humans for a long period of time simply because they were ground nesters. Although there is evidence that humans have heavily exploited flightless birds on oceanic islands (Steadman 1995; Holdaway 1999), an analysis of extinction in the pre-human avifauna of New Zealand found no significant effect of flightlessness on extinction probability once ground nesting and body size had been controlled for (Duncan and Blackburn submitted). The difficulty of separating flightlessness from the characteristics with which it is typically correlated means that the susceptibility to extinction bestowed by flightlessness *per se* remains unclear. Nevertheless, whatever the reason, flightless birds have been extremely susceptible to extinction following human colonisation of islands and current human pressures may continue to selectively remove this trait.

The lack of a relationship between the time of human colonisation and body size indicates that prehistoric human-caused extinctions have occurred across the range of body sizes. This highlights the extremely complex relationship between body sizes and avian extinction risk (Terborgh and Winter 1980; Tracy and George 1992; Gaston and Blackburn 1995; Duncan and Blackburn submitted). Owens and Bennett (2000) have demonstrated that different threat types appear to affect species of different body size. Thus the broad spectrum of threats ranging from human exploitation to habitat destruction to introduced species and disease may be the reason why specific size classes have not been targeted. Even within threat types, there may be larger variation in the size of species that are susceptible. For example, Holdaway (1999) suggests that the body size of birds driven to extinction in New Zealand depended on the size and capabilities of the introduced predators and that a broad size range of introduced predators resulted in extinction of species right across the avian body size distribution. This suggestion is supported by a multivariate statistical analysis of Holdaway's data (Duncan and Blackburn submitted). It is possible that the extermination of a specific size class has not been identified in this analysis because that size class has been so efficiently removed on islands colonised distantly in the past, as well as more recently. If this process has occurred, there would be no variation detected when birds on islands inhabited for a long period of time were compared to birds on islands recently colonised. This may be the case with the very largest birds such as moa, elephant birds, large flightless megapodes, and Hawaiian giant waterfowl. At present, island birds with larger body size are more threatened (Chapter 5). If species with large bodies were not more susceptible to extinction in the past, then this may indicate a change in the selective nature of the extinction process on islands.

Species with lower reproductive rates do not appear to have been selectively removed from islands inhabited by humans for a longer period of time. This result is surprising as the arrival of humans has unquestionably increased mortality rates of many island birds, and those with lower reproductive rates would be expected to have experienced differentially higher extinction rates. Again this process of extinction may have run its course or specific traits such as ground nesting or flightlessness may be much more important in terms of susceptibility than whether a species has high or low reproductive rate – and therefore dominate the results here.

These analyses provide strong support that humans have selectively removed bird species with particular life history or ecological traits from oceanic islands. Humans have essentially imposed a new, strong selective regime on islands where specific traits are in the process of being filtered from the endemic avifauna. While many of these traits are now associated with an elevated extinction risk, species with such traits may have been well adapted to an island environment prior to human arrival. These findings have important implications for studies trying to identify traits that may be associated with elevated extinction risk in extant species. Extinction-prone traits are directly related to the dominant threat process in a region and the most vulnerable traits are likely to change as threat processes change or intensify (Holdaway 1999; Duncan and Blackburn submitted). Life history or ecological traits that appear to be vulnerable in the present are also strongly shaped by the history of past threats in a region. Therefore, a specific life history characteristic or ecological trait may not be identified as being associated with elevated extinction risk if the trait has already been largely selectively filtered. Therefore, if we hope to gain a true understanding of traits associated with elevated extinction risk we must examine the question in relation to specific threat types, and have a strong understanding of the impact of recent human-caused extinctions on a region's biota.

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CHAPTER 5

AVIAN EXTINCTION RISK ON OCEANIC ISLANDS

Abstract

Island birds are often claimed to be particularly susceptible to extinction. However, it is unclear whether island or mainland species, with similar geographical range size, are at present more threatened with extinction. I control for phylogenetic relatedness and compare island and mainland restricted-range birds to determine whether island birds are more or less extinction-prone, and I identify the extinction processes to which island birds are uniquely susceptible. Results show no significant difference in levels of threat between island and mainland restricted-range birds, but indicate that the processes of extinction are slightly different. Island and mainland birds are both threatened by habitat loss and exploitation, but island birds are more susceptible to introduced species. Although island birds with similarly-sized distributions to their mainland relatives are not at present at greater risk of extinction, there are a disproportionate number of island birds that are threatened because they tend to have small ranges. It is therefore, important to try to understand the traits associated with island birds that are particularly extinction-prone. Here the comparative method is used to test whether seven traits are associated with greater extinction risk. I demonstrate that flightless birds and habitat specialists are at greater risk of extinction than others. When I limit the analyses to birds that inhabit islands that have been colonised by humans for less than 1000 years, species with larger body size and ground nesting birds are also associated with greater extinction risk. As specific processes of extinction are likely to affect species with different life history, ecological or morphological traits, analyses were also conducted to determine if the seven life history, ecological, or morphological traits are associated with species that are particularly prone to introduced species, but no correlates of extinction from this source of threat were identified.

Introduction

Extensive prehistoric extinctions of oceanic island birds have been well documented (Olson and James 1982; Olson 1989; Dye and Steadman 1990; Milberg and Tyrberg 1993; Pimm *et al.* 1994; Steadman 1990, 1993, 1995, 1998). Most recent avian extinctions have occurred on oceanic islands and a disproportionate number of island birds are presently threatened (see Johnson and Stattersfield 1990; BirdLife International 2000; Chapter 1). Despite this, the processes of extinction on islands and the traits associated with increased extinction risk are poorly understood. In this Chapter I explore how island and mainland extinction processes differ. I examine how life history, ecological, or morphological traits are associated with elevated extinction risk in an island environment.

Island species are often hypothesised to be particularly vulnerable to introduced predators and competitors (Williamson 1981; Atkinson 1989; Vermeij 1991; Paulay 1994). However, the apparent vulnerability of island birds may largely be a result of their restricted range (Simberloff 1995, 2000). Species with a small range size are more susceptible to stochastic demographic and environmental effects (King 1985; Pimm *et al.* 1988), as well as being more vulnerable to almost any extinction process (Simberloff 1995), than broad range species. Manne *et al.* (1999) demonstrate that, after controlling for range size, passerines on islands off the coast of the Americas are no more threatened than their mainland relatives. Furthermore, when they limit their analysis to species with a range size of 1,000 to 100,000 km^2, they find that island birds are actually less threatened than their mainland lowland relatives. They postulate that these lower levels of extinction risk on islands may be a result of competitive release (see MacArthur *et al.* 1972) resulting in higher population densities. They also consider the role of extinction filters (see Pimm *et al.* 1994; Balmford 1996; Chapter 3; Chapter 4). Here I first test whether island birds are less prone to extinction by comparing all closely-related restricted-range oceanic-island and mainland species. I then test whether island birds are less threatened by specific processes of extinction, specifically, habitat loss, exploitation, and introduced species.

Irrespective of whether island birds are less threatened than their mainland restricted-range relatives, when controlling for their range, it is clear that a disproportionate number of island birds are threatened with extinction (Stattersfield *et al.* 1998; Chapter 1). For conservation purposes it is therefore important to understand why certain species are particularly extinction-prone in an island environment. Insight into life history, ecological, or morphological attributes associated with elevated extinction risk may help to identify traits that are less well adapted to a restricted-range environment. It may also highlight extinction-prone characteristics of island birds that make them susceptible to specific threat processes.

Previous large-scale comparative analyses of birds analysing traits associated with increased extinction risk have focused primarily on mainland species (Gaston and Blackburn 1995; Bennett and Owens 1997; Owens and Bennett 2000). Here the global data set (Chapter 1) of oceanic island birds is used to test seven traits that have been hypothesised to be associated with higher probabilities of extinction. These traits are flightlessness or poor flight ability, ground nesting, habitat specialisation, small clutch size, large body size, dichromatism, and sexual size dimorphism.

Flightless bird extinctions have been extensive in historic (BirdLife International 2000) and prehistoric (Steadman 1995; Milberg and Tyrberg 1993) times, and can largely be attributed to over-exploitation and introduced species (see Johnson and Stattersfield 1990; Trewick 1997; Duncan and Blackburn submitted). Ground nesters have been identified as especially susceptible to introduced predators such as pigs, dogs or rats (Atkinson 1998; Moors *et al.* 1992). Both ground nesting and flightless birds have been shown to be less common on islands that were colonised by humans in the distant past, indicating that many species with these potentially extinction prone traits may have already become extinct (Chapter 4).

Habitat specialists have been shown to have an elevated extinction risk in an analysis of 95 avian bird families (Owens and Bennett 2000). Forest specialists on islands have been identified as particularly threatened with extinction (Stattersfield *et al.* 1998). Island birds are often believed to become habitat generalists on islands (Diamond 1970; Keast 1996). However, this may be a result of an observational bias toward small islands where species are arrested in the initial stages of evolutionary diversification (Grant 1998). It is possible that island birds undergo a taxon cycle (see Wilson 1961; Ricklefs and Cox 1972; 1978; Schluter 2000; Blondel 2000) whereby endemic species become less competitive, increasingly specialised and ultimately extinct (Ricklefs and Cox 1972).

Small clutch size has been associated with elevated extinction risk for mainland species (Bennett and Owens 1997). This has been attributed to species with lower fecundity recovering more slowly from a reduction in population size (Pimm *et al.* 1988). Thus, species on islands with lower rates of fecundity may be particularly extinction prone when human-related threats result in a significant increase in mortality.

Large body size has been demonstrated to be associated with elevated extinction risk for birds (Gaston and Blackburn 1995; Bennett and Owens 1997). More specifically, large birds have been shown to be at great extinction risk due to persecution and introduced predators (Owens and Bennett 2000). Large birds tend to have slower reproductive rates and lower levels of abundance that may result in greater extinction risk. These traits may be particularly prone in a restricted-range environment. However, the general relationship between extinction risk and large body size remains under debate (reviewed by Gaston and Blackburn 2000).

There are a number of reasons why more intense sexual selection may result in increased risk of extinction. (1) The exaggeration of secondary sexual characteristics, reflected in both dichromatism and dimorphism between the sexes, may result in costs to individuals of the chosen sex, thus causing a reduction of the mean fitness of individuals of a population (McLain *et al.* 1995; Møller 2000). (2) Intensely sexually-selected species may be more inbred and therefore lower heterozygosity because of an extreme skew in male mating systems (Møller 2001). (3) Small populations with intense sexual selection may be more susceptible to demographic stochasticity as a result of strict female preference (Møller 2000). (4) Species that experience strong sexual selection may be more likely to speciate (Barraclough *et al.* 1995; Møller and Cuervo 1998; Owens *et al.* 1999) and therefore become restricted to small, potentially vulnerable distributions (Møller 2000). There is support for the hypothesis that sexual selection may be associated with increased extinction risk in small populations in studies that have demonstrated that dichromatic species introduced to oceanic islands are less likely to persist than monochromatic species (McLain *et al.* 1995; Sorci *et al.* 1998; McLain *et al.* 1999). There is at present no evidence that size dimorphism is associated with greater risk of extinction in birds. However, a study of beetles on islands demonstrated that more dimorphic species are less likely to occur within a smaller distribution, and are less likely to persist within smaller distributions from one year to the next (McLain and Vives 1998).

One of the problems with testing correlates of extinction in an environment where humans may have caused extensive selective extinctions is that many of the species with particularly vulnerable traits may have already become extinct (Chapter 4). Thus, it may be difficult to identify species with traits that are associated with an increased risk of extinction. To identify whether extinction-filters influence the traits that are associated with elevated extinction risk, an analysis was conducted for the subset of birds that are restricted to islands that have been colonised by humans for less than 1000 years. It is assumed that species with vulnerable traits are less likely to have already been filtered from these islands.

Finally, Owens and Bennett (2000) demonstrate that different extinction processes may target species with different traits. As island birds are often cited as being especially vulnerable to introduced species (Williamson 1981; Vermeij 1991; Paulay 1994), the data have also been analysed to determine if specific traits are associated with birds susceptible to introductions. This may help to highlight especially vulnerable traits of island endemic birds.

Methods

Different data sets have been used for the island versus mainland comparisons and the analysis of life history, ecological, or morphological traits that are correlated with greater extinction risk. There are however many similarities. Species are defined following the taxonomy of Sibley and Monroe (1990, 1993) for extant birds, and BirdLife International (2000) for recent extinctions. In addition, both data sets define an oceanic island endemic bird as a species with a breeding distribution restricted to islands that were not attached to a mainland during the last period of glaciation. Only islands smaller than or equal to New Zealand are considered.

The IUCN categories of threat are also used in both analyses to assess extinction risk (IUCN 1994; BirdLife International 2000). Species have been scored on a scale from species that are not threatened to species that have recently become extinct. The categories of threat consist of: data deficient (DD); lower risk, least concern (LRlc); lower risk, near threatened (LRnt); lower risk, conservation dependent (LRcd);

vulnerable (VU); endangered (EN); critically endangered (CR); extinct in the wild (EW); or extinct (EX). Only extinctions that have occurred over the past 500 years are considered and species that are extinct in the wild are classified as extinct. The few species that are listed as conservation dependent by BirdLife International I categorised as near threatened, and species classified as data deficient are not included in the analyses. For some analyses, recent extinctions are excluded, and near threatened and lower risk species are merged into one category. The explanation for this is given in each of the specific analyses. BirdLife International (2000) identifies the major processes of extinction associated with every species classified as threatened. Therefore, it is possible to create an extinction risk index for specific threat types. Here, species threatened by introductions, exploitation, and habitat loss have been divided into three different groups. Each species threatened by a specific extinction process is listed with its conservation status ranging from zero to three (lower risk=0, vulnerable=1, endangered=2, and critically endangered=3). Recent extinctions cannot be included, as we are uncertain of their causes of extinction.

Island mainland database

The database consists of 2130 mainland and oceanic island species (including representatives of 797 genera) that are considered to be restricted-range birds by BirdLife International (Stattersfield *et. al* 1998). Restricted-range species are defined as birds with a breeding range of less than 50,000 km^2. Mainland birds are defined as species with any part of their breeding distribution on a mainland. Species restricted to islands that were attached to the mainland during the last period of glaciation (continental island species) are not included in the data set. Sea birds have also been excluded, as they are generally not limited to the resources of their restricted breeding distribution.

Refer to the island bird database (Chapter 1).

Life history, ecological, and morphological traits

Data were collected for nest site (ground versus tree), dichromatism, flight ability, clutch size, body length, and sexual size dimorphism using the following sources: Greenway (1967) Harris (1974), duPont (1975), Mayr (1976), Hannecart (1980), Watling (1982), Clunie (1984), Fuller (1987), Mountfort (1988), Day (1989), Gill and Martinson (1991), del Hoyo *et al.* (1992,1994,1996,1997), Bregulla (1992), Fry (1992), Jones (1995), Feare (1998), Rowlands (1998), Sinclair (1998), Clement (1999), Isler (1999), Madge (1999), and BirdLife International (2000). In addition to these sources, Roff (1994) and Trewick (1997) were used to specifically assess flight ability, Bennett (1986) for mainland birds clutch size, and Dunning (1992) for body weights. Sibley and Monroe (1990,1993), Stattersfield *et al.* (1998), and Collar *et al.* (1994) were used to identify the type and number of habitats in which oceanic island birds are found.

Ground nesters are defined as birds that have open-ground nests. This includes nesters in grass, but does not include ground-hole nesters. Tree nesters are birds that nest in tree holes or on tree limbs, but does not include species that nest in shrubs. Data were collected for 309 ground nesters and tree nesters (165 genera). Dichromatic birds are defined as birds where the male and female differ in colour or markings. Data were collected on 513 species including 214 genera. Poorly-flighted birds include all flightless birds and species that are capable of flying only very short distances. Data on flight ability were collected for all oceanic island birds. Clutch size refers to the mean number of eggs per nest. Data were collected for 348 species (181 genera). Body length is defined as the length of the bird from the tip of the beak to the end of the longest tail feather, and was collected for 529 species (226 genera). The data were also divided into sets for large (>=27 cm) and small-bodied (27 cm) birds (see Chapter 4). Sexual body size dimorphism is measured as the difference between the larger and smaller sex, obtained by subtracting the natural logarithm of the larger sex from the natural logarithm of the smaller sex. Here 85 species have been collected with weights for both males and females (64 genera). Island birds are classified by the number of habitat types in which they are located. The habitat classification system is based on Collar *et al.* (1994) and includes 12 habitat codes such as, scrub, savannah, grassland, wetlands or forest. Data were collected for all oceanic island birds.

Refer to the comparative approach (Chapter 1).

Island/mainland analyses

The first set of analyses address whether oceanic-island restricted-range birds are less threatened than mainland species with similar restricted-range distributions. Restricted-rage birds are used as a surrogate to control for a species distribution as exact distributions were not collected for mainland species. Oceanic-island restricted-range birds and mainland restricted-range birds are then compared to determine if they are susceptible to specific processes of extinction. These are: introduced species, exploitation, and habitat loss. Extinction risk is scored on a four point scale (lower risk=0, vulnerable =1, endangered=2, critically endangered=3). Species classified as lower risk/near threatened and lower risk/least concern have been merged. This has been done because causes of threat have not been attributed to near-threatened species. In addition the analyses have also been conducted excluding oceanic island birds with range sizes below 10,000 km^2 (roughly the size of the Hawaiian Islands). This is because few mainland restricted-range-species have distributions smaller than 10,000 km^2 (see Stattersfield *et al.* 1998). Removing oceanic island birds with smaller distributions helps to determine whether the range size bias between island and mainland restricted-range birds significantly influences the results from the restricted-range island-mainland comparison.

The island/mainland bird comparisons have also been run separately for passerines and non-passerines to determine if the differences between oceanic island and mainland birds are consistent for these two groups. It is particularly important to analyse the passerines separately as this is the group that Manne *et al.* (1999) have demonstrated to be less threatened on islands than on the lowland mainland, when they control for the effect of range size. Independent contrasts were calculated using the BRUNCH algorithm in CAIC (Comparative approach, page 29). All contrasts are analysed using Wilcoxon's test which assumes neither normality nor homogeneity of variance (Siegel and Castellan 1988).

Correlates of extinction analyses

The second group of analyses examines characteristics of birds restricted to oceanic islands that may be associated with elevated extinction risk. These analyses have been conducted separately for traits that have been recorded as dichotomous and traits that are continuous. I first test if (1) ground nesting, (2) dichromatic, (3) poor-flight ability or flightlessness is associated with increased extinction risk. Here the extinction risk scale runs from zero to five (lower risk=0, near threatened=1, vulnerable=2, endangered=3, critically endangered=4, and extinct or extinct in the wild=5). The effect of a species' total distribution and minimum distance from the mainland are controlled for independently in each of the analyses. Results are presented where they influence the overall significance of the association between the term of interest and extinction risk. As with the previous analyses, independent contrasts are calculated using the

BRUNCH algorithm from CAIC (Comparative approach, page 29) and contrasts are compared using Wilcoxon's test.

I then test whether species with (1) smaller clutches, (2) larger body length, (3) increased sexual size dimorphism, and (4) habitat specialism are associated with increased extinction risk. Again the extinction risk scale runs from zero to five. Independent contrasts are calculated using BRUNCH (Comparative approach, page 29). Linear regression through the origin is used to analyse the contrasts, with threatened status as the dependent variable and the specific trait in question as the independent variable. As the variables were continuous it is possible also to calculate contrasts to control for total distribution and distance from the mainland. I also control for latitude since body size (reviewed by Gaston and Blackburn 2000) and clutch size (reviewed by Grant 1998) have both been shown to be correlated with latitude. In addition, latitude may have an influence on the number of habitat types that are available for an island bird. These results are given where there is a significant relationship between the term in question and extinction risk. Stepwise regression was employed to identify the minimum adequate model.

The past 1000 years

All analyses examining life history, ecological, or morphological traits associated with elevated extinction risk were also run for a subset of birds whose total range is restricted to oceanic islands that were colonised by humans within the last 1000 years. This has been done to identify whether extinction filters influence the traits that are identified as associated with greater extinction risk.

Introduced species

Finally, to identify birds with traits that may be particularly susceptible to introduced species the analyses are also run considering only species threatened by introductions. The extinction risk scale runs from 0-3 (0=lower risk, 1=vulnerable, 2=endangered, and 3=critically endangered). All seven life history, ecological, or morphological characteristics are considered in these analyses.

Results

Island/mainland

There appears to be no significant difference between the extinction risk of island and mainland restricted-range species (Table 5.1). There is however, a non-significant trend for oceanic-island restricted-range birds to be more threatened. The analyses further indicate that oceanic-island restricted-range birds are not significantly more threatened by exploitation or habitat loss, but are significantly threatened by introduced species. If the analyses are run separately for passerines and non-passerines the results are similar for both groups (Table 5.2; Table 5.3).

Table 5.1. Restricted-range oceanic-island endemic birds are compared with mainland restricted-range birds to determine if general threats or threat due to habitat loss, exploitation, and introduced species are stronger or weaker for oceanic island birds. The Wilcoxon sign rank test is used to test the contrasts for significance. n=131contrasts.

Oceanic island VS mainland	Z	p-value
Threatened	-1.66	0.097
Habitat loss	-0.56	0.58
Exploitation	-0.83	0.40
Introduced species	-6.75	<0.001

Table 5.2. Restricted-range oceanic-island endemic non-passerines are compared with mainland restricted-range non-passerines to determine if general threats or threat due to habitat loss, exploitation, and introduced species are stronger or weaker for oceanic island birds. The Wilcoxon sign rank test is used to test the contrasts for significance. n=39 contrasts.

Oceanic island VS mainland	Z	p-value
Threatened	-1.56	0.118
Habitat loss	-1.05	0.30
Exploitation	-1.16	0.24
Introduced species	-4.32	<0.001

Table 5.3. Restricted-range oceanic-island endemic passerines are compared with mainland restricted-range passerines to determine if general threats or threat due to habitat loss, exploitation, and introduced species are stronger or weaker for oceanic island birds. The Wilcoxon sign rank test is used to test the contrasts for significance. n=92 contrasts.

Oceanic island VS mainland	Z	p-value
Threatened	-1.01	0.31
Habitat loss	-0.01	0.99
Exploitation	-0.31	0.76
Introduced species	-5.21	<0.001

When only oceanic-island restricted-range birds with distributions greater than 10,000 km^2 are compared to restricted-range mainland birds, there is no significant difference between extinction risk for island or mainland birds (n=91, Z=0.21, p=0.21). As with the analysis including all restricted-range species, there is no significant difference between island and mainland restricted-range species in relation to the threat of habitat loss or exploitation. In this analysis island species also remain disproportionately threatened by introduced species (n=91, Z=-3.42, p<0.001).

Correlates of extinction

Within oceanic islands, flightless or nearly flightless birds are at greater risk of extinction than birds capable of flight (Table 5.4). There is a near-significant trend for ground nesters to be more threatened than tree nesters. This trend becomes weaker however, when I control for a species' distribution (Table 5.4). There is no significant relationship between a species' risk of extinction and dichromatism.

Table 5.4. The relationship between extinction risk and ground nesting, dichromatism, and flightlessness. Wilcoxon sign rank test is used to test the contrasts for significance.

Independent variable	Number of contrasts	Z	p-value	Controls	
				Total island distribution	Distance from the mainland
Ground nesting	17	-1.91	0.06	Z=-1.49, p=0.14	No effect
Dichromatism	63	-1.34	0.18	No effect	No effect
Flightlessness	11	-2.09	0.04	No effect	No effect

Clutch size is not correlated with extinction risk (Table 5.5). Body size is also not correlated with extinction risk (Table 5.5), even when large (>=27 cm) or small (<27 cm) species are analysed separately (large, n=54, t=0.67, p=0.51; small, n=83, t=0.91, p=0.36). Species where there is an increased difference in body size between the sexes are not at greater risk of extinction than species that are less sexually size dimorphic (Table 5.5). Finally, habitat specialists are at greater risk of extinction than habitat generalists (Table 5.5; Figure 5.1). This relationship is maintained if I control for species' total distribution, minimum distance from the mainland, and average latitude (Table 5.6).

Table 5.5. The relationship between extinction risk and clutch size, body length, sexual size dimorphism, and habitat specialisation. Regressions, through the origin, are used to analyse the standardised contrasts.

Number of contrasts	R^2	F-Ratio	Independent variable	Slope	t	p-value
97	0.02	1.82	Clutch size	-0.49	-1.35	0.18
125	0.00	0.00	Body length	-0.02	-0.03	0.98
30	0.06	1.90	Sexual size dimorphism	-2.29	-1.38	0.18
184	0.12	21.87	Habitat specialists	-0.66	-4.68	<.001

Table 5.6. The relationship between extinction risk and habitat specialisation, controlling for a species distribution, minimum distance from the mainland and latitude. Stepwise multiple regressions of contrasts, through the origin.

Number of contrasts	R^2	F-Ratio	Independent variable	Slope	t	p-value
184	0.25	19.77				
			Number of habitats	-0.67	-5.11	<0.001
			Distribution	-0.19	-4.89	<0.001
			Distance	NS	NS	NS
			Latitude	0.03	2.71	0.007

The analyses examining correlates of threat for oceanic-island birds are also analysed excluding birds that occupy islands that have been colonised for more than 1000 years. Three of the results were different from the analyses including birds from islands that were colonised more than 1000 years ago. The correlation between ground nesting and extinction risk becomes significant (n=10, Z=-2.67, p=0.008) and this correlation remains significant when one controls for a species' distribution and distance from the mainland (ground nesting controlling for distribution, n=10, Z=-2.80, p=0.005; controlling for distance, n=10, Z=-2.70, p=0.007). The relationship between flightless birds being at greater risk of extinction falls below significance, although a non-significant trend remains (n=9, Z=-1.40, p=0.16).

Large bodied birds are associated with greater risk of extinction (n=34, R^2=0.17, coefficient=2.64, t=2.61, p=0.013) (Figure 5.2) and this remains significant if I control for species total distribution, minimum distance from the mainland, and average latitude (Table 5.7). Traits that are associated with birds that are at greater risk of extinction are listed in Table 5.8.

Table 5.7. Birds on islands colonised by humans for less than 1000 years. The relationship between extinction risk and body length, controlling for a species distribution, minimum distance from the mainland and average latitude. Stepwise multiple regression, through the origin, are used to analyse the contrasts.

Number of contrasts	R^2	F-Ratio	Independent variable	Slope	t	p-value
33	0.27	6.04				
			Body length	3.01	3.09	0.004
			Total distribution	-0.20	-2.12	0.04
			Distance	NS	NS	NS
			Latitude	NS	NS	NS

As oceanic island birds have been shown to be particularly vulnerable to introduced species, the analyses are also run only including threatened species from introductions. The significant results from the analyses considering all threat types become non-significant and none of the other traits show any relationship with species particularly susceptible to introduced species.

Table 5.8. Traits significantly associated with greater extinction risk are assigned a check (✓) and those not associated with greater extinction risk are assigned an (✗).

Independent variable	Birds on all oceanic islands	Birds on islands that have been colonised by humans for less than 1000 years
Ground nesters	✗	✓
Dichromatic species	✗	✗
Flightless or poorly-flighted	✓	✗
Small clutch size	✗	✗
Large body length	✗	✓
Sexual size dimorphism	✗	✗
Habitat specialists	✓	✓

Figure 5.1. The habitat specialist contrasts in relation to the threatened status contrasts. Habitat specialists tend to be at greater risk of extinction than non-habitat specialists.

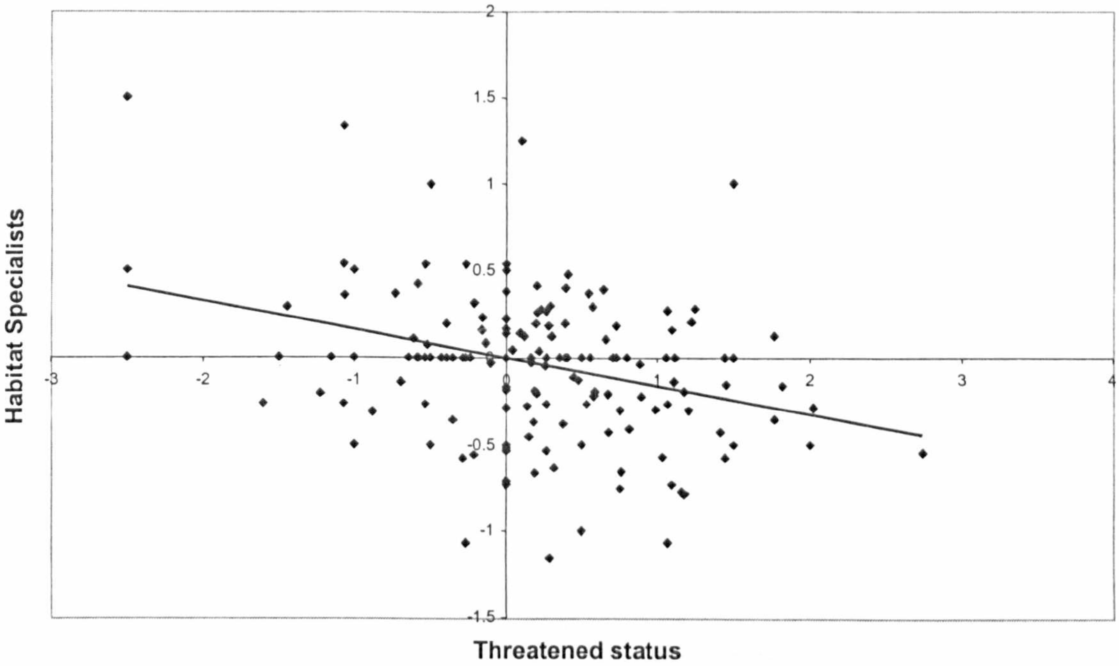
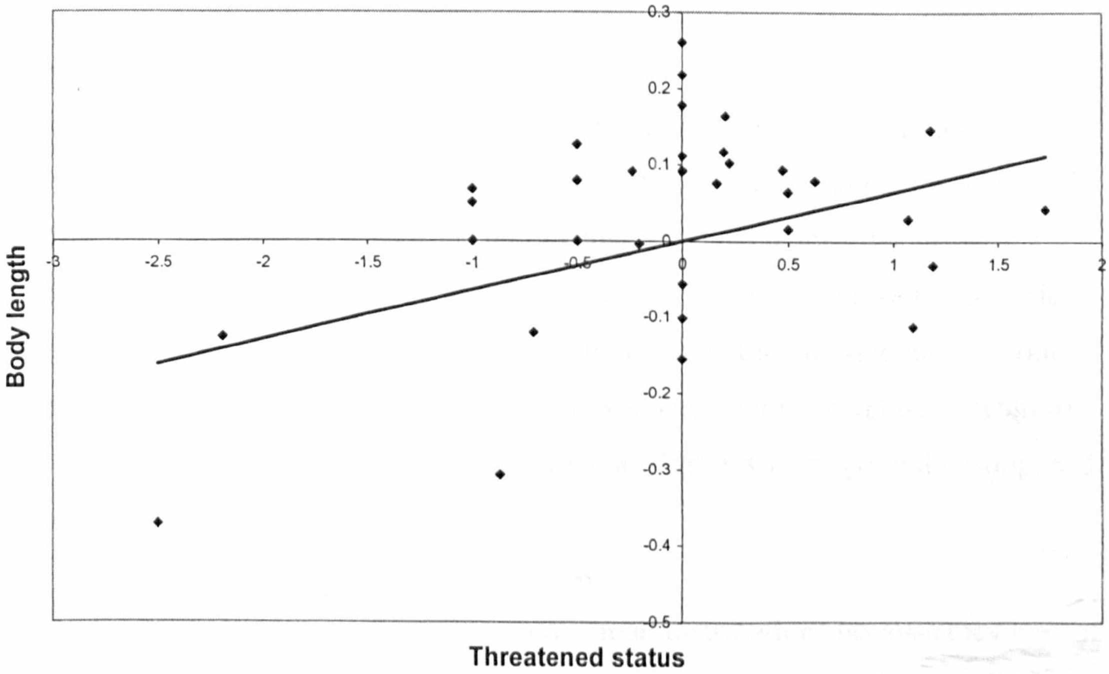


Figure 5.2. Birds exposed to humans for less than 1000 years. The body size contrasts in relation to the threatened status contrasts. Large bodied birds tend to be at greater risk of extinction.



Discussion

Island/mainland comparison

The island/mainland comparison of restricted-range species indicates that the risk of extinction for the two groups is similar, but that the processes of extinction are slightly different. These results are similar for passerines and non-passerines and robust to the removal of island species with ranges smaller than 10,000 km^2. Island and mainland restricted-range birds are similar in their vulnerability to habitat loss and exploitation, but oceanic island birds are much more threatened due to introduced species.

Island restricted-range birds differ from mainland restricted-range species in a number of aspects that may either increase or decrease their susceptibility to specific extinction processes. First, there is a filter on the type of species that get to islands and are able to persist for long enough to become endemic (Salomonsen 1974). Thus, birds that are found on islands have demonstrated an ability to adapt to a novel environment and persist within a restricted distribution for a long period of time. The restricted range of island birds is not necessarily a reflection of their inability to compete or a result of habitat specialisation; they are restricted by a fixed geographic barrier. Density compensation may be common on islands since there are fewer competitors and predators (MacArthur *et al.* 1972). High population densities may be particularly important for reducing extinction risk in a restricted-range environment (Manne *et al.* 1999; Chapter 7). However, evolutionary or ecological adaptations that occur in a species-poor environment with few competitors and predators may result in oceanic island birds being more threatened than mainland birds by the introduction of exotic species (Williamson 1981). Many of the traits associated with island birds becoming more prone to extinction are discussed here such as flightlessness, ground nesting, and reduced reproductive rates.

Mainland restricted-range species tend to have small distributions because they are not able to compete or they are dependent on a specific habitat type or resource. Their distributions have either always been small or their range size has decreased over time, the latter will make them particularly vulnerable. The abundance of species with restricted distributions tends to be lower than broadly-distributed species (Gaston *et al.* 1997; Gaston and Lawton 1990). This relationship is unlikely to hold if island and mainland species are compared as island species often express density compensation (see Blackburn *et al.* 1997). However, among islands, the general trend may exist. The low abundance levels associated with restricted-range mainland species may result in an elevated risk of extinction for this group of species. However, mainland birds have had evolutionary history with a broad range of predators and competitors and this may make them less susceptible than island species to introductions and human exploitation.

Humans have introduced species throughout the world (Vermeij 1991) and the extremely high vulnerability of island birds to this specific extinction process indicates an intrinsic susceptibility. Although the introduction of exotic species is still a significant threat, it is possible that most of the extinctions due to this process have now taken place (King 1985). This view is supported by the fact that fewer birds are threatened due to introduced species on islands that have been colonised by humans for a greater period of time (Chapter 3) than on more recently colonised islands. Assuming that extensive extinctions have already occurred as a result of introduced species, then island restricted-range birds were likely to be much more extinction prone than mainland restricted-range birds in the recent past, even after controlling for the effect of distribution. Extremely high prehistoric extinction rates among island birds is supported by the subfossil records of extinct birds (Pimm *et al.* 1994; Steadman 1995; James 1995). Past estimates of bird extinctions on islands are as high as one fifth of all birds extant during the Holocene (Milberg and Tyrberg 1993).

However, exploitation, and to a lesser extent habitat destruction, have also been implicated in this wave of island bird extinctions (Diamond 1984, Paulay 1994; Steadman 1995; Holdaway and Jacomb 2000). Although there is, at present, no significant difference between island and mainland restricted-range birds in relation to exploitation, it would appear that traits such as flightlessness or tameness may make island birds especially susceptible to this process of extinction. It is possible that species particularly susceptible to exploitation such as the extinct moas (Holdaway 1999) and as many as 2000 flightless rails (Steadman 1995) may have already been exterminated from islands in part due to human exploitation. With these vulnerable species now gone, threat rates due to exploitation between island and mainland birds would be similar. The extinction filter effect (Chapter 3, 4) and the subfossil record, including extinct species from larger islands (Duncan and Blackburn submitted) indicates that similar threat rates of island and mainland restricted-range-birds is a relatively new phenomenon.

Correlates of extinction

Habitat specialists and birds that are flightless or poorly-flighted are associated with a greater risk of extinction on oceanic islands. If birds that inhabit islands that have been colonised by humans for more than 1000 years are excluded, then ground nesters and large bodied birds are also associated with elevated extinction risk. For this second analysis the relationship between flightless or poorly flighted birds and extinction risk falls just below significance, but the sample size is very small and the trend remains. The non-significant relationship of ground-nesting species and large-bodied birds with extinction risk, in the analyses including all island birds, may indicate that the particularly vulnerable birds with these traits have already been filtered from islands colonised for a long period of time. Thus, the subset of ground nesters and flightless birds that remain on islands colonised in the distant past may be resilient to human-related threats. This filtration effect bias makes it difficult to identify ground nesting and large body size as an extinction prone trait. This demonstrates the difficulties that may arise when the relationships between life history or ecological traits and extinction risk are explored without making a distinction between regions where an extinction filter has occurred and regions where an extinction filter is in progress. It also illustrates that life history or ecological traits shown to be associated with increased extinction risk for species in one region may not always applicable to another.

There is strong support for the result that ground nesters and flightless or poorly-flighted birds have historically been at greater risk of extinction (Diamond 1984; Steadman 1995) than flighted and non-ground nesting birds. This is also supported by the finding that flightless or poorly-flighted birds and ground nesters are less prevalent on islands that have been colonised by humans for a long period of time (Chapter 4). While it is difficult to know whether the species are threatened due to being flightless or being ground nesters (see Duncan and Blackburn submitted), both traits are likely to be associated with elevated extinction risk from exploitation and introduced species, resulting in a double jeopardy for flightless birds.

Species that have been classified as habitat specialists represent a gradient of birds ranging from species that are highly adapted to a specific habitat type to those that have been recently restricted in range due to exploitation, predation, disease, or competition. In general, habitat specialists may be more threatened because they are less able to adapt to a human-modified environment. They may also be restricted to small areas within islands, making them susceptible to habitat destruction, as well as other threat processes. Forest specialists are by far the most common habitat specialists on islands (Stattersfield *et al.* 1998) and are particularly threatened because the last remaining refuges are now being deforested (Simberloff 2000) on most islands. However, levels of threat may be particularly high for forest specialists because more forest endemics and species now restricted to forest habitats have escaped past extinction filters. This view is supported by the fact that there appear to be fewer non-forest restricted specialists on islands that have been colonised for a long period of time (Chapter 4). Thus, when forest specialists are compared to other island endemic birds they may appear to be disproportionately threatened simply because the extinction process has been much slower for species that have been able to persist in refuges of native or near-native forest habitat.

Although this analysis demonstrates that there is an association between habitat specialists and extinction risk, it does not necessarily support the theory of the taxon cycle. The taxon cycle predicts that during the process of becoming more endemic, species become increasingly restricted in distribution because they are not able to compete with new generalist colonisers (Rickleffs and Cox 1972). This is supported by the observation that highly endemic species are often restricted to 'interior' forest habitat (Wilson 1961; Rickleffs and Cox 1972; Ricklefs and Bermingham 1999). However, these observations rely on patterns that have occurred subsequent to humans completely modifying island environments. The distribution and relative threatened status of highly endemic species was most likely very different in the past. Thus, even if highly endemic species are at present restricted to few habitat types and are at great risk of extinction, it is not necessarily true that a natural cycle exists, where generalists to arrive on islands, become increasingly specialised and ultimately extinct.

The greater extinction risk associated with birds of longer body length on islands supports the general trend for large species to be at greater extinction risk (e.g. Gaston and Blackburn 1995; Bennett and Owens 1997). In general, large body size may make species susceptible to human exploitation (Diamond 1984; Owens and Bennett 2000). Large body size is associated with low rates of intrinsic increase and low abundance. These traits combined with a restricted range, which limits total population size, may make large-bodied species particularly susceptible to human-related threat processes. As previously discussed, large-bodied species that are prone to extinction may have already been removed from many of the islands colonised for more than 1000 years. However, it is interesting to note that there is no significant difference in the body size of endemic birds found on islands recently colonised by humans and those colonised in the distant past (Chapter 4).

The relationship between clutch size and extinction risk on islands is not significant. This is contrary to the general trend for mainland birds to be more threatened if they have a smaller clutch size (Bennett and Owens 1997). It is interesting to note that clutch size decreases with a species' range size on islands (Chapter 2). If this is also the case on the mainland, then clutch size may be acting as a surrogate for small range size, which is known to be associated with a high extinction probability (Caughley 1994; Simberloff 1998). If one controls for range size, there may also be no relationship between fecundity and extinction risk on the mainland.

Similarly, there does not appear to be any relationship between sexual size dimorphism or dichromatism and extinction risk on islands. This implies that there is no relationship between extinction risk and intense sexual selection. There are however, mechanisms other than sexual selection that may play a role in the expression of dichromatism (Mayr 1942, Amadon 1953; Herremans 1990) and sexual body size dimorphism (Selander 1966; Chapter 2). As discussed in the Introduction, there may be costs associated with sexual body size dimorphism and dichromatism. However, there may also be benefits associated with these traits in a restricted-range island environment. For example, a relationship has been demonstrated between sexual body size dimorphism and high levels of social polygamy, as well as large differences in parental care (Owens and Hartley 1998). In a restricted-range environment, where species are more prone to demographic stochasticity, a polygamous breeding strategy may be advantageous (see Legendre *et al.* 1999). If sexual body size dimorphism is strongly influenced by niche partitioning between the sexes on islands (Selander 1966; Keast 1996) this adaptation may enable species to live at higher population densities and therefore reduce their exposure to extinction. There is a commonly observed trend for island birds to become less dichromatic (Mayr 1942, Amadon 1953; Sibley 1957; Grant 1965; Herremans 1990). If the change from dichromatism to monochromatism is associated with highly endemic species, then species classified as dichromatic may have a slightly lower extinction risk as more endemic species have been shown to be at greater risk of extinction (see McDowall 1969; Duncan and Blackburn submitted). Thus, while there may be costs to sexually selected traits, these may be balanced with benefits associated with dichromatism and sexual size dimorphism.

No correlations were found between species threat by the introduction of exotics and any of the life history, ecological, or morphological traits tested. This is possibly due to the fact that species classified as threatened by introductions include a broad range of processes. For example, a species threatened by introductions may be susceptible to competitors, predators and habitat modifiers, all of which probably target species with slightly different traits. If the analyses were run with these processes more clearly divided then those traits correlated with elevated extinction risk might emerge. However, it is very interesting that flightlessness or ground nesting are not particularly vulnerable traits in this subset of species. Perhaps this has to do with the difficulty in distinguishing proximate from ultimate processes of extinction, and disentangling synergistic threat processes.

Island and mainland threat processes may now be similar with the exception of introduced species. Many of the island species that are particularly susceptible to introductions have most likely already gone extinct. As the process of extinction by introduced species runs its course and habitat loss intensifies, there will be even greater similarities between the processes of extinction on islands and the mainland. There are specific traits of island birds that are associated with a heightened risk of extinction. However, these appear to vary depending on whether or not a region has long experienced human-related threats. The presence or absence of extinction filters has major implications for studies that try to identify traits that make species extinction prone so they can be used to make predictions about which species may be at greatest risk of extinction. First, it may be difficult to identify traits associated with extinction prone birds if data is collected from areas where a specific extinction filter has occurred, as well as areas where the extinction filter is occurring. Second, if traits are identified in a region where a specific extinction filter is occurring, those findings may not be applicable to regions where that extinction filter has already run its course or a different extinction filter is in progress. This highlights the temporal nature of susceptible traits and the importance of understanding historic threat processes in any attempt to identify which species are likely to be at the greatest risk of extinction.

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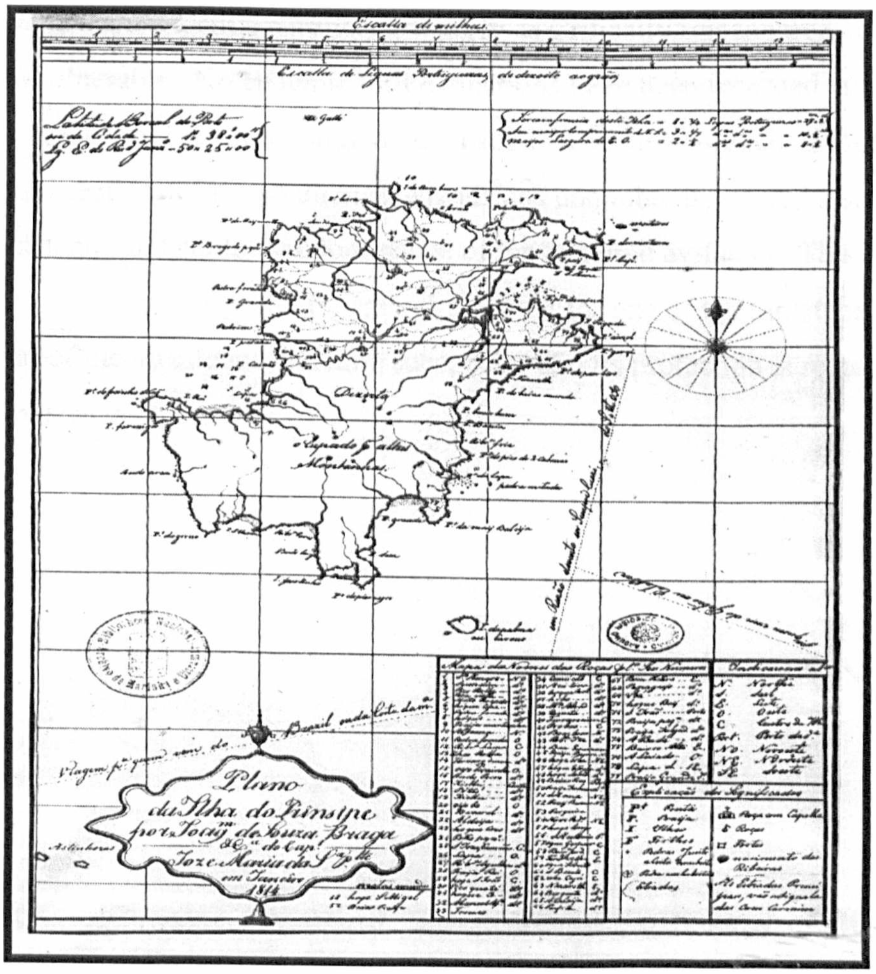
CHAPTER 6

CONSERVATION STATUS OF THE ENDEMIC BIRDS OF PRÍNCIPE: INSIGHT INTO PAST RESILIENCE AND FUTURE PERSISTENCE



Abstract

Research was carried out in August of 1999 to determine the distribution and status of the poorly-known endemic birds of the island of Príncipe, Gulf of Guinea, in the mountain and southern lowland forest. The results from this study have been combined with past research in order to assess trends in abundance, to determine the overall conservation status of the birds and to identify essential habitats for the threatened species and subspecies. This research is particularly important as the government has been considering large-scale economic development plans for the island of Príncipe, and has recently signed an oil exploration agreement with Nigeria that may lead to rapid development. Based on this research, two of the seven endemic birds qualify as Vulnerable to extinction under the IUCN Categories and Criteria, due to their restricted range. Two of the eight endemic subspecies qualify as Critically Endangered, and another one as Vulnerable. No endemic bird extinctions have been recorded, and endemics remain the most common birds on the island. The maintenance of forest in the mountain and sections of the southern lowlands has undoubtedly played a strong role in the persistence and continued dominance of the endemic avifauna. This native and late-successional forest is presently essential habitat for one of the threatened species and four of the threatened endemic subspecies and its protection is required for their future persistence.

Introduction

Príncipe is a small island in the Gulf of Guinea with unusually high numbers of single island endemic birds given the small size of the island (Jones 1994) and its relative proximity to the mainland. However, little is known about the distribution and status of the island's unique avifauna (Christy 1996). This is of particular concern as the government recently considered a proposal to designate 36% of the island as a free-trade zone (WADCO 1999). At present it does not look like the free-trade zone will be implemented. However, the government has just agreed to set up a joint oil exploration zone with Nigeria (Irin 2000) which will potentially lead to rapid development of the island. If such development were to occur, there would be very little baseline data from which declines could be determined, or information to determine which sections of the island are particularly important for the persistence of specific endemic birds.

Up until this study, we have been dependent on reports from Keulemans (1866), Dohrn (1866), Boyd Alexander (1909) (see Bannerman 1914), and Correia (1929) for information on the status and distribution of the endemic birds for large sections of the island. The high central mountains had not been explored since the time of Correia (1929) and some of the higher peaks of the island, such as the Pico do Príncipe, had never been visited by ornithologists (Christy and Clarke 1998). Since the time of Correia (1929) only small sections of the southern lowland forest have been explored (see Christy and Clarke 1998). Studies subsequent to Correia have focused primarily on the easily-accessible northern section of the island (Snow 1950; Frade 1958; de Naurois 1973, 1975, 1980, 1983, 1988, 1994; Jones and Tye 1988; Harrison and Steel 1989; Sargent 1994; Atkinson *et al.* 1991; Christy and Clarke 1998) (for a review of ornithological study on Príncipe see Jones and Tye 1988; Jones and Tye 2001).

The focus of this study is the least-known section of the island, the mountain forest in the central to southern section of the island down to the southern lowland forest. With an understanding of the status of the species that live in the mountain forest and southern lowland forest, it is possible to comment on the conservation status of all the endemic species and subspecies of Príncipe and identify essential habitat for threatened endemics. Understanding their distribution and conservation status will help to identify whether this community of species has been truly resilient to human-related threats, and if so, may provide insight into the conditions necessary for the long term persistence of island endemic species.

Background to Príncipe

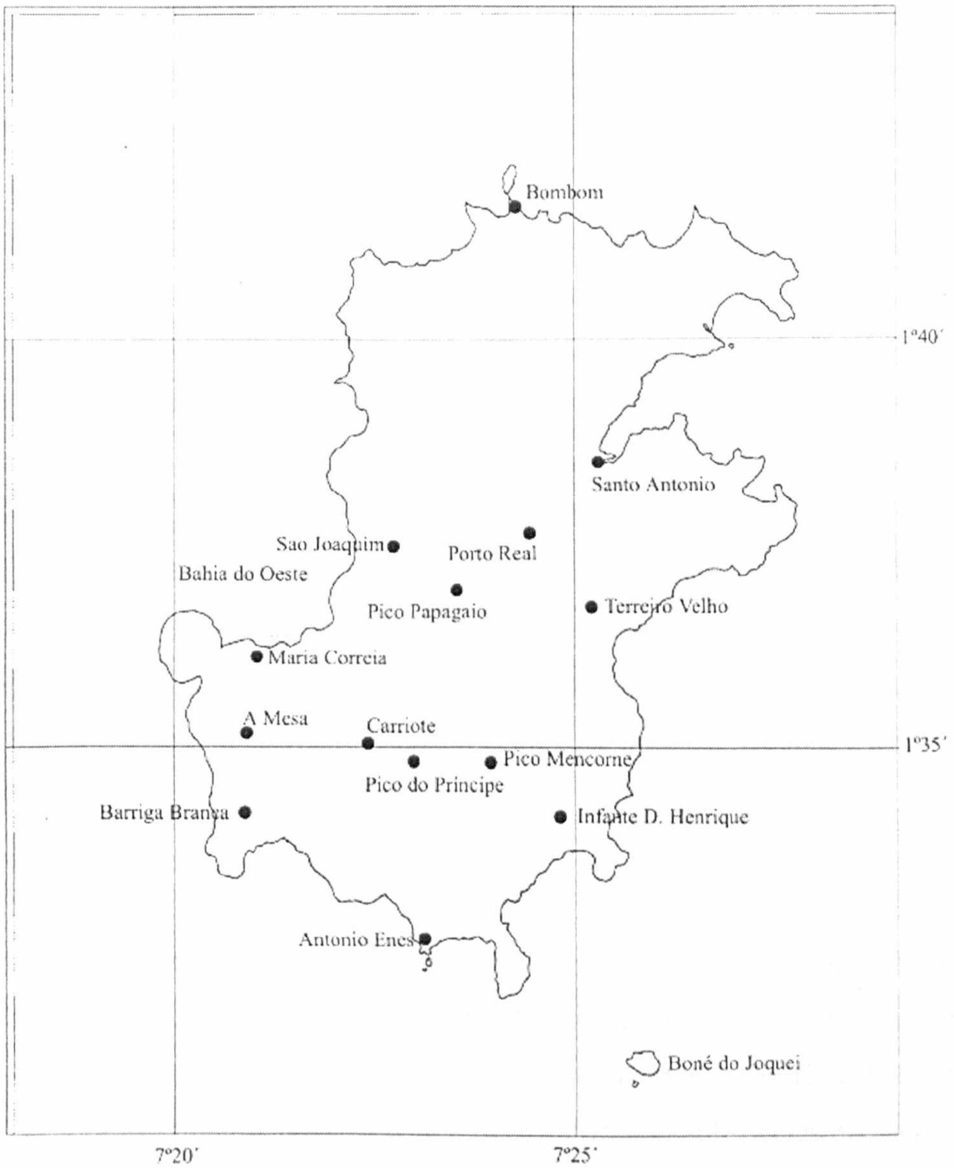
Geography and Climate

Príncipe is 220 km from the African mainland in the Gulf of Guinea (Juste and Fa 1994) with a total area of 139 km^2 and a maximum elevation of 945 m. In conjunction with São Tomé, the islands form the Democratic Republic of São Tomé e Príncipe. Both São Tomé and Príncipe were formed by volcanic eruptions (Lee *et al* 1994) and have never been connected to the mainland or each other (Exell 1944; Amadon 1953). The topography of the island is relatively flat in the north but becomes increasingly hilly towards the central and southern regions with numerous deep valleys that taper off into the rocky lowland forest in the south-west section of the island. The climate is equatorial with rainfall in the north averaging 1,000 mm and up to 5,000 mm in the south (Johnson 1988), and monthly temperatures range between 25 and 31 °C (Bredero *et al.* 1977). Each year there are two dry seasons and two wet seasons. The driest months are July to August, and the end of December to the beginning of January. The wettest months are October, November, March and April.

Land use history

In 1471 the Portuguese discovered the completely forested and uninhabited island of Príncipe (Hodges and Newitt 1988). Settlers arrived in the early 1500s and engaged in sugar cane production (largely restricted to the north), the slave trade and subsistence farming. By 1580 the sugar cane industry went into decline and was not replaced by another significant commercial crop until the beginning of the 19th century with the introduction of coffee and cocoa (Bredero *et al.* 1977). Large plantations only began in the late 19th century and were largely devoted to cocoa. Between 1893 and 1900 three large estates were formed in the southern and central uninhabited section of the island (Baillie and Gascoigne in preparation). At the end of the 1800s most of the north had been cultivated (Bannerman 1914) and large sections of the southern lowlands cleared or modified. However, the central mountains and sections of the southwest remained as primary forest (Jones *et al.* 1991; Baillie and Gascoigne in preparation).

Figure 6.1. Map of Príncipe in the Gulf of Guinea.



Cocoa production reached its peak on Príncipe in 1913 (Vasconcellos 1918). From 1920 onward agricultural production declined sharply as a result of poor soil, disease, and labour shortages. As a result, plantations were abandoned in the southwest in the early 20th century. Plantations such as Infante D. Henrique along the southeast coast and Maria Correia in the south/central eastern region (Figure 6.1) were abandoned shortly after independence in 1975. Now the section of the island south of pico do Príncipe is completely abandoned. Agricultural production has continued in the northern section of the island to the present, although it is now mostly subsistence level farming.

Exploitation and Introduced species

During the colonial period much of the island was accessible due to extensive cultivation (Bannerman 1914), and exploitation was likely to have been a significant threat for some species. Keulemans (1866) noted that the endemic pigeons and doves were heavily hunted around towns and that other birds such as olive ibis *Bostrychia olivacea rothschildi* and Príncipe glossy starling *Lamprotornis ornatus* were hunted for food. The following mammals have been introduced to Príncipe over the past 500 years: ship rat (*Rattus rattus*), Norway rat (*Rattus norvegicus*), house mouse (*Mus musculus*), mona monkey (*Cercopithecus mona*), domestic cats, dogs, goats, pigs, sheep, cattle, donkeys, horses (Dutton 1994), and civet (*Civettictis civetta*) (Bruto da Costa *et al.* 1916). Thus, most mammalian culprits of island bird extinctions have been documented on Príncipe, with the exception of weasels and mongoose, and habitat modifiers such as rabbits and deer. Birds known to have been introduced to the island, and which may be competitors with native species or vectors of disease, are laughing dove (*Streptopelia senegalensis*) (Snow 1950), feral pigeons (*Columba livia*) and chickens.

Avifauna

There are approximately 33 breeding land birds on Príncipe (Jones and Tye 2001), of which seven are restricted to Príncipe, one of these seven, *Horizorhinus*, being a monospecific genus. A further five are restricted to both São Tomé (150 km to the south-west) and Príncipe, three of which have a different subspecies on each island (Peet and Atkinson 1994). A further four subspecies are endemic to Príncipe and two more subspecies are restricted to the Gulf of Guinea.

In Threatened Birds of the World (2000) none of the endemic birds of Príncipe were listed as threatened at the species level, however, the endemic Príncipe drongo *Dicrurus modestus* and speirops *speirops leucophaeus* were classified as Near Threatened. Príncipe white-eye *Zosterops ficedulinus* was listed as Vulnerable and Gulf of Guinea thrush *Turdus olivaceofus xanthorhynchus*as as Near Threatened, both of which have a subspecies on Príncipe and São Tomé, and in both cases the subspecies is rarer on Príncipe. I am only aware of the thrush being recorded three times since its discovery in 1901 (see Jones and Tye 2001) and Príncipe white-eye being sighted twice since de

Naurois in 1972 or 1973 (de Naurois 1983). Past documentation of the islands subspecies indicated that, in addition to Príncipe white-eye and Gulf of Guinea thrush, other endemic subspecies may be threatened or extremely rare such as Príncipe seedeater *Poliospiza rufobrunnea rufobrunnea*, olive Ibis, and the postulated endemic owl (Atkinson *et al.* 1991). There have been various reports on the status of Príncipe seedeater on Príncipe ranging from virtually extinct in accessible areas (Atkinson *et al.* 1991) to common (Keulemans 1866; Snow 1950). The status of olive ibis is even less well known as there have only been three reported sightings over the past 100 years (see de Naurois 1973, Sargent 1994; Jones and Tye 2001). The owl is a still greater enigma. De Naurois noted hearing an owl call near the airport (de Naurois 1975) and postulated that it may be an endemic species. Many of the above species and subspecies were reported to inhabit the mountain forest and southern lowland forest at the beginning of last century, but their current status in the south of the island has been uncertain. The mountain forest and southern lowland forest combined account for more than 30% of the island's landmass. The presence or absence and relative abundance of these species in the mountain forest and southern lowlands has major implications for their overall conservation status.

Methods

This study is the result of field research conducted from the 30th of August to 7th of October, 1999. Data on the distribution and abundance of the island's birds were collected while spending 16 days in the mountain forest and eight days in the southern lowland forest. The mountain forest is defined as the area above 250 meters south of Sao Joaquim (c20 km^2) and the southern lowland forest is below 250 m south of the peak of A Mesa, Pico do Príncipe and Pico Mencorne (c25 km^2) (Figure 6.1). This study focuses on the endemic species and subspecies restricted to Príncipe. However, species restricted to Príncipe and the other islands in the Gulf of Guinea, and the African grey parrot *Psittacus erithacus*, are also included as they are restricted-range species or populations of conservation concern. The scientific names of the endemic birds follow Peet and Atkinson (1994) with the exclusion of olive sunbird *Nectarinia olivacea cephaelis*, that is no longer believed to be an endemic subspecies (Jones and Tye 2001). The common names follow Christy and Clarke (1998) and the sequence of species follows Jones and Tye (1988). Relative and absolute abundance were estimated in the central mountain and southern lowland forest. For relative abundance, species were categorised by the number of sightings per day (see Table 6.1). This method is consistent with earlier methods used for estimating relative abundance (Atkinson *et al* 1991).

For estimates of absolute abundance, distance sampling with point counts on line transects was employed (see Buckland *et al* 1993). Ninety eight point counts were carried out in the mountain forest and seventy in the southern lowland forest. At each point two minutes were spent waiting for the birds to settle. Numbers of birds and their distance were then estimated for the following five minutes. In the southern lowland forest stratified random sampling was used (see Bibby *et al* 1998). Following an old road that runs along the south end of the island, transect lines were paced out at 200 m intervals from Barriga Branca to Antonio Enes (Figure 6.1). In total there were 25 transect lines. These transect lines were divided into groups of five of which one group of five was randomly selected each day. The transect line within the group of five and the starting point (top, middle, bottom) was then randomly selected. If the middle selection was chosen a coin was tossed to select the direction. Once one of the five groups of transects had been selected it was not considered for subsequent selections. If the selected transect line was completed, (above 250 m) or it was impossible to continue, a coin would be tossed to determine whether to continue on the transect line to the right or the left. All transects were walked along a 60° north-east axis. All point counts were taken between 6:30 and 11:00 am. During this time the forest was almost always covered in cloud and the temperature remained relatively constant ranging from 25.6 to 27 °C. Ninety-four percent of the point counts were based on call only.

Due to the topography, stratified-random sampling was not possible in the mountain forest. In this region, transects followed navigable routes and point counts were conducted at 200 m intervals on alternate sides of the line at a perpendicular distance of 50 m (see Jones *et al* 1995). The mountain region was first explored to identify accessible routes. Transects were carried out on Pico Mesa, Pico do Príncipe, Carriote, and Pico Mencorne above 250 m (Figure 6.1). In the mountain rainforest point counts were conducted whenever the rain permitted during daylight hours. Point counts would not be resumed until 20 minutes after a rain shower. The mountains were covered in cloud throughout the study and the temperature ranged from 18 to 24 °C. Again, 94% of the point counts were based on calls.

These data were analysed using Distance Software 3.5 (Thomas *et al* 1998). Various distance bands were applied using post stratification (between 4 to 8 bands). The most distant band was set so that approximately 5% of the most distant estimates would be removed from the analysis. The encounter rate variance was estimated empirically (Buckland *et al* 1993) to provide an abundance estimate with 95% confidence intervals (Table 6.1). For some of the extremely rare species the detection function of other ecologically similar Príncipe species were used to enable a rough estimate of abundance. These have been conducted to provide a density estimate of the most rare species, but should be treated with caution.

This study, in conjunction with other past and recent research, has been used to provide an estimate of the distribution and conservation status of the endemic species and subspecies of Príncipe. Their conservation status has been assessed using the IUCN categories and criteria (1994). The IUCN Categories and Criteria have been applied to subspecies to highlight the extinction risk faced by these unique populations. This is particularly important in situations such as on Príncipe where some of the subspecies are not well studied and further investigation could result in their elevation to full species status. The IUCN Categories and Criteria are not applied to the Gulf of Guinea endemic species with distributions greater than Príncipe as their distribution and status outside of Príncipe is beyond the scope of this study. However, the African grey parrot has been assessed as it may be a geographically isolated population and is presently of conservation concern due to harvesting.

Results

See tabel 6.1.

Table 6.1. Relative and absolute abundance and maximum and minimum elevation of endemic species and subspecies of bird in the mountain forest and the southern lowland forest. The African grey parrot and birds endemic to Príncipe as well as the Gulf of Guinea are also included. Absolute abundance estimates in bold should be interpreted with caution as their detection function is based on a more common species. The initials are given of the scientific name of species used as the detection function for a rare species. For example, (PE) indicates that *Psittacus erithacus*, the African grey parrot, has been used for detection function.

Species and Subspecies restricted to Príncipe	**Mountain Forest (above 250m)**		**Southern Lowland Forest**		**Minimum & Maximum Elevation**
	Relative abundance	Absolute abundance per km^2, 95 % C.I.	Relative abundance	Absolute abundance per km^2, 95 % C.I.	
Olive ibis *Bostrychia olivacea rothschildi*	-	-	-	-	-
Green pigeon (PE) *Treron calva virescens*	-	-	*	4.9 (0.3 - 9.4)	0-300
Lemon dove (HD) *Aplopelia larvata principalis*	***	8.6 (2.2 - 15.0)	***	7.9 (1.0 - 14.8)	0-750
White-bellied kingfisher (NH) *Alcedo nais*	**	9.8 (1.9 - 17.6)	***	21.0 (8.0 - 33.8)	0-700
Blue-breasted kingfisher *Halcyon malimbicus dryas*	****	9.1 (3.6 - 14.52)	****	29.8 (16.4 - 43.2)	0-900
Príncipe drongo (HMD) *Dicrurus modestus*	-	-	**	8.3 (2.3 - 14.3)	0-380
Príncipe glossy starling *Lamprotornis ornatus*	****	16.1 (4.92 - 27.3)	****	239.2 (106.2 - 372.2)	0-750
Gulf of Guinea thrush (HMD) *Turdus olivaceofuscus xanthorhynchus*	***	4.3 (.30 - 8.28)	*	1.6 (.11 - 3.0)	0-800
Dohrn's thrush-babbler *Horizorhinus dohrni*	*****	167.2 (136.7 - 197.7)	*****	361.0 (292.5 - 429.5)	0-945
Príncipe sunbird *Nectarinia hartlaubii*	****	210.6 (105.1 - 316.0)	****	35.6 (17.1- 54.1)	0-945
Príncipe white-eye *Zosterops ficedulinus ficedulinus*	-	-	*	-	0-350
Príncipe speirops (HD) *Speirops leucophaeus*	***	20.9 (8.9 - 32.8)	***	14.5 (4.5 - 24.5)	0-800
Príncipe seedeater (Príncipe) *Poliospiza rufobrunnea rufobrunnea*	*****	117.3 (79.8 - 155.7)	*****	338.7 (209.4 - 468.0)	0-945
Príncipe golden weaver *Ploceus princeps*	*	18.0 (5.8 - 30.2)	**	55.7 (10.9 - 44.8)	0-600
Species and subspecies restricted to islands in the Gulf of Guinea					
Gulf of Guinea bronze-naped pigeon *Columba malherbii*	*	-	*	-	0-750
Emerald cuckoo *Chrysococcyx cupreus insularum*	*	-	*	-	0-750
Little swift *Apus affinis bannermani*	-	-	*	-	0-250
São Tomé spinetail *Chaetura thomensis*	-	-	*	-	0-250
Special conservation concern					
African grey parrot *Psittacus erithacus*	****	17.7 (9.1 - 26.3)	****	184.7 (140.8 - 264.6)	0-800

Abundant:	*****	50+ seen or heard per day in a specific habitat
Very Common:	****	10-50 seen or heard in a day.
Common:	***	1-10 seen or heard in a day.
Frequent:	**	Seen or heard on more than one occasion in a habitat but not on a daily basis.
Rare:	*	Special record on very few occasions in a certain habitat despite specific attempts to locate them.
Not present:	-	Not recorded in a specific region.

Conservation status and distribution

Olive ibis *Bostrychia olivacea rothschildi*

Endemic subspecies to Príncipe. Other subspecies are found on the African mainland.

Status and Distribution

After extensive searches in the mountain and southern lowland forest it was not seen or heard. The olive ibis is believed to have always been rare in the south of the island. Dohrn (1866) found it in the almost inaccessible rocky and forested localities in the south, seeing them daily for two weeks and hearing them crowing like ravens. Keulemans (1866) found them only in forest of the south and west. Fea collected one more specimen in 1901 (Salvadori 1903). De Naurois (1994) reports a sighting in 1973, the last published documentation until Sargeant reported a sighting in August 1991 (Sargeant 1994). Christy and Clarke (1998) believe that the ibis still exists in the south and central primary forest with a restricted distribution of 40 km^2, citing disturbance at the nest by mona monkeys as a possible explanation of its rarity. Keulemans (1866) stated that it was also hunted for food. If this subspecies is not extinct its total distribution is extremely restricted.

Threatened Status: Critically Endangered D.

Green pigeon *Treron calva virescens*

Endemic subspecies to Príncipe and the islet of Boné do Joquei. Other subspecies are found on Bioko and the African mainland.

Status and Distribution

Frequent in the southern lowland forest up to 300 m, but not observed in the mountain forest (Table 6.1). Dohrn (1866) documented it as very common throughout the island. Keulemans (1866) described it as the most common dove on the island, referring to parties of 30 to 50 birds feeding in tall fruiting trees. It was recorded as common to abundant by de Naurois (1983) as well as by Jones and Tye (1988); who found it along forest edge and re-growth. Atkinson *et al.* (1991) only saw it twice during their four-day stay. Christy and Clarke (1998) found it common in cocoa plantation and forest-edge habitat. This species was historically hunted (Keulemans 1866) and continues to be hunted (Jones and Tye 1988) on a small scale (pers. obs.). The total present estimated distribution and status is frequent to common in plantations, secondary forest, and edge habitat at lower elevations in the north, rare in the southern lowland forest and rare to absent in the mountain forest.

Threatened Status: Near Threatened

Lemon dove *Aplopelia larvata principalis*

Endemic subspecies to Príncipe. Other subspecies are found on São Tomé, Annobon, Bioko and mainland Africa.

Status and Distribution

Common in the southern lowland and mountain forest up to 750m. It is the only dove found to be common in the primary forest (Table 6.1). Keulemans (1866) found it to be more common than the Gulf of Guinea bronze-naped pigeon and occurring throughout the island. Boyd Alexander in 1909 documented it as common in the plantations (Bannerman 1914) as did Snow (1950) who also found them common in the hill forest. Jones and Tye (1988) documented it as common to abundant in heavily shaded cocoa plantations and dense secondary forest. Atkinson *et al.* (1991) only saw one lemon dove during their four-day visit. Christy and Clarke (1998) recorded it as common from the coast to high-altitude forest. The total present estimated distribution and status is frequent to common in plantations, secondary forest, edge habitat along roads and paths as well as in primary forest up to 750m.

Threatened status: Lower Risk lc.

Gulf of Guinea bronze-naped pigeon *Columba malherbii*

Endemic species to Príncipe, São Tomé and Annobon.

Status and Distribution

Frequent in the southern lowland forest and rare in the mountain forest with a maximum observed elevation of 750 m (Table 6.1). However, locals claim that it is more common in the mountain forest during the dry season. Keulemans (1866) recorded it as most common in the higher parts of Príncipe. Dohrn (1866) found it to be very rare, having only seen it a few times during his six month stay. Jones and Tye (1988) found it frequently in forests and plantations with tall trees and Atkinson *et al.* (1991) reported flocks of up to 30 individuals seen in the north, but classified it as frequent to common. Christy and Clarke (1998) found it in all habitat types but less common in the south-west forest. Keulemans (1866) cites hunting as the cause of rarity in the inhabited zones at lower elevation. Its total present estimated distribution and status is frequent to common in plantations and secondary lowland forest throughout the island and rare in the mountain forest.

African grey parrot *Psittacus erithacus*

Afrotropical including Príncipe, Bioko and São Tomé.

Taxonomy

Debate remains over its subspecific status on Príncipe. Boyd Alexander suggested it should be considered as a separate species from the African grey parrot (in Bannerman 1914) and recommended the name *Psittacus princeps*. Bannerman (1914) treated it as a subspecies *Psittacus erithacus princeps*. Amadon (1953), de Naurois (1983) and Christy and Clarke (1998) stated the subspecies is no longer valid. However, the matter is still under investigation (Martim de Melo, unpublished).

Status and Distribution

Very common in the southern lowland forest and the mountain forest up to 700 m at which point the trees begin to become smaller (Table 6.1). Dohrn (1866) and Keulemans (1866) found grey parrots very common. Boyd Alexander in 1909 wrote that they were still fairly numerous, but had no doubt declined due to deforestation (Bannerman 1914). Snow (1950) De Naurois (1983), Jones and Tye (1988), Christy and Clarke (1998) all found them common throughout the island. Apparently there are two major roosting sites, one around the Pico Papagaio and the other nearby Pico Negro (Snow 1950), but this warrants further investigation (Harrison and Steele 1989) as they are abundant throughout the south-west forest in the evening in August and September (pers. obs.). In the past they were hunted for food (Keulemans 1866, Bannerman 1914) and are now harvested for the pet trade (Melo 1998). Their present estimated status and distribution is very common throughout the island up to 700 m and most abundant where large trees are found.

***Threatened Status*:** Near Threatened

Emerald cuckoo *Chrysococcyx cupreus insularum*

Endemic subspecies to Príncipe, São Tomé and Annobon. The other subspecies is on the mainland and Bioko.

Status and Distribution

Rare in the southern lowland forest and not heard or seen in the mountain forest above 250 m. However, locals claim that it can be found up to 750 m in the dry season (Table 6.1). This corresponds with the observations of Dohrn (1866) and Keulemans (1866) who stated that the cuckoo lives in the southern mountain section of the island during the dry season, and the lower forest during the wet season. It was heard but not seen by Snow (1950) and Jones and Tye in 1988 (Jones and Tye 2001). Harrison and Steele

(1989) considered it common and Atkinson *et al.* (1994) recorded it as frequent around Bom Bom in the north. Christy and Clarke (1998) document it as present in all forested habitats, particularly shaded plantations and primary forest but noted that it is less abundant than its counterpart on São Tomé. The total present estimated distribution and status is restricted primarily to, and is frequent in, dense lowland forest and shaded plantations and rare in the mountain forest.

Scops owl *Otus* sp?

Heard on Príncipe by de Naurois near the airport in 1974 (de Naurois 1975). Despite searches in the evenings and the use of playbacks of *Otus hartlaubi* (from São Tomé), the species reported by de Naurois was not heard or seen during the month spent in the forest of Príncipe. The existence of this species is very questionable. A forest guide who lives next to the airport, where de Naurois heard an owl calling, has never heard a bird calling at night. Another guide, who lives and works in the forest, stated that he has only seen one in his life in 1993. He saw it huddled in a tree at Pico Zau in the south-west, but never heard it call. It is possible that a species of owl periodically lands on Príncipe, but based on the lack of sightings and the lack of calls, it is unlikely that the island maintains a viable population. However, species such as the Scops owls have been known to persist at very low population densities and to escape observation for decades (Safford 1993) and Annobon, a much smaller island in the Gulf of Guinea, has its own endemic subspecies. If this owl truly exists and it is endemic, it is restricted to an extremely small area.

Threatened Status: Critically Endangered D.

Little swift *Apus affinis bannermani*

Endemic subspecies to Príncipe and São Tomé. The other subspecies is from mainland Africa.

Status and Distribution

Frequent in the very southern section of Príncipe and absent above 250m in elevation. Keulemans (1866) observed it throughout the island including the forest of the uninhabited parts. Dohrn documented it as common near the town (Bannerman 1914). Jones and Tye (1988) found it abundant over clearings, in plantations and in secondary forest in the north. Atkinson *et al.* (1991) reported it as common in the north. Christy and Clarke (1998) stated they are found throughout the island particularly along the Rio Papagaio. Its present estimated distribution and status is common in the northern section of the island around the larger plantations, in both open areas and secondary forest. It is also common near the town of Santo Antonio, and along the coast where large inlets are present. However, it is not common in the south and rare to absent above 250 m.

São Tomé spinetail ***Chaetura thomensis***

Endemic species to Príncipe and São Tomé.

Status and Distribution

It is rarely seen in the south-west section of the island, as there is very little open habitat and was not observed above 250 m (Table 6.1). However, it is common in the south-east and south-west/central regions along the coast and in open areas often at the site of abandoned plantations. Jones and Tye (1988) found it frequently in the east and north-west over plantations, forest clearings and valleys. Atkinson *et al* (1991) observed it in similar habitat and documented it as common. Christy and Clarke (1998) found it in all open habitats, plantations and forest edges, and the valley of the Rio Papagaio. Its total present estimated distribution and status is common in open and edge habitat below 250 m, with the exception of the south-west where it is rare.

White-bellied kingfisher ***Alcedo nais***

Endemic species to Príncipe.

Taxonomy

Fry and de Naurois (1984) treated it as a race of *Alcedo leucogaster.* Similarly, Christy and Clark (1998) treat it as a subspecies, *Alcedo leucogaster nais* and Jones and Tye (2001) as *Corythornis leucogaster nais.* Here I follow Sibley and Monroe (1990), Peet and Atkinson (1994), and Stattersfield *et al.* (1998) and treat the Príncipe White-bellied kingfisher as a full species, *Alcedo nais.*

Status and Distribution

Common along the coast and forested regions along rivers up to 250 m and frequent in the dense forested regions in the southern lowland forest. Frequent along rivers up to about 700 m, but absent from the dense rainforest (Table 6.1). Keulemans (1866) documented it as being found throughout the island and relatively common at lower elevations. Dohrn (1866) stated that it was common on the shore, but that single specimens were also seen flying around the interior of the island. Snow (1950), Jones and Tye (1988), Atkinson *et al.* (1991), Sargeant (1994) all had similar observations to Dohrn (1866) finding it common along watercourses, but also away from rivers including in plantations, gardens, and native forest (Jones and Tye 2001). Christy and

Clarke (1998) stated that it is spread throughout the island. Its total estimated distribution and status is common along the coast and lowland forest near rivers, and frequent in lowland forest and plantations away from river systems. It is rare in the mountain forest, and primarily restricted to waterways.

Threatened Status: Lower Risk lc.

Blue-breasted kingfisher *Halcyon malimbicus dryas*

Endemic subspecies to Príncipe and the islet of Boné do Joquei. Formerly recorded on São Tomé, although these records appear to be erroneous (de Naurois 1980; Jones and Tye 2001). The other subspecies is found on the African mainland.

Status and Distribution

Very common in all forested habitats throughout the southern lowland forest and up to 750 m. Keulemans (1866) and Dohrn (1866) document it as most common in thick dense forest near rivers. Snow (1950) found it to be common in all plantations visited. Jones and Tye (1988) found it to be common in plantations and around Santo Antonio. Christy and Clarke (1998) noted it as found in most habitats. Its total estimated distribution and status is very common in all forest habitats throughout the island and up to 750 m.

Threatened Status: Lower Risk lc.

Príncipe drongo *Dicrurus modestus*

Endemic species to Príncipe.

Taxonomy

The Príncipe drongo is treated as a subspecies of *D. adsimilis* by Sibley and Monroe (1990). Here I follow Peet and Atkinson (1994), Christy and Clark (1998), Jones and Tye (2001) and treat the Príncipe drongo as an endemic species.

Status and Distribution

Rare to frequent in the southern lowland forest up to 350 m and absent from the mountain forest (Table 6.1). Keulemans (1866) found it fairly common throughout the island including the forest and uninhabited areas. Snow (1950) found them most common on plantations. Jones and Tye (1988) and Atkinson *et al.* (1991) found it frequent to common in open habitat with scattered trees such as in the town of Santo Antonio, in plantations and along roads. Christy and Clarke (1998) stated that they prefer open or low-density areas of the north and central regions, and that their distribution in the southern lowland forest and mountainous areas is not well known.

This species may have experienced a significant decline in the early 1970s, probably due to pesticide use (de Naurois and Castro Antunes 1973; Jones and Tye 2001). The total estimated distribution and status is frequent to common in open or edge habitat, including Santo Antonio in the north of the island, rare to frequent in the southern forest and absent from the mountain forest.

Threatened Status: Vulnerable D2.

Príncipe glossy starling *Lamprotornis ornatus*

Endemic species to Príncipe.

Status and Distribution

Very common to abundant in the southern lowland forests and common to very common in the mountainous forest with a maximum recorded elevation of 750 m (Table 6.1). The closely related splendid glossy starling *Lamprotornis splendidus* from the mainland also inhabits the island, although it was not observed. Dohrn (1866) and Keulemans (1866) document the Príncipe glossy starling as common in the higher parts of the interior. Snow (1950), Jones and Tye (1988), Atkinson *et al.* (1991), and Christy and Clarke (1998) recorded it as abundant to very abundant in plantations and secondary forest, although Snow (1950) found it to be less common in the southern plantations. It was hunted in the past for food (Keulemans 1866) and children continue to capture and sell them (pers. obs.). The total estimated distribution, and abundance is very common to abundant in lowland forests and plantations and common to very common in the mountainous forest.

Threatened Status: Lower Risk lc.

Gulf of Guinea thrush *Turdus olivaceofus xanthorhynchus*

Endemic subspecies to Príncipe, the other subspecies is on São Tomé.

Taxonomy

With different morphology, behaviour, song and habitat requirements, it is probable that the Príncipe subspecies is a separate species altogether. As noted by Amadon (1953) the bill is much more yellow than the São Tomé subspecies Turdus olivaceofus olivaceofus, the tarsi tends to be more yellow, ventral markings are more blackish and the entire body is smaller (Figure 6.2). It also appears to be more restricted in its distribution than its relative on São Tomé. The São Tomé subspecies has been documented as common in all forest types including plantations and found at highest densities in the lowland primary forest and lowland shade forest (Atkinson et al. 1991).

The Príncipe subspecies is also much tamer allowing approach within a few meters. Finally the song of the two subspecies is distinct (Sasha d'Assis Lima in litt. to Peter Jones, 1998; Pers. obs.).

Figure 6.2 Gulf of Guinea thrush *Turdus olivaceofus xanthorhynchus*

Status and Distribution

Rare in the southern lowland forest. However, it appears to be relatively common at lower elevations in the region of A Mesa. Frequent to common above 250 m in the late successional and primary forests with highest observed numbers between 500 to 700 m on Pico do Príncipe and Pico Mencorne. Maximum observed elevation of 800 m (Table 6.1). This accounts for the species' entire distribution. Príncipe thrush was discovered in 1901 by Fea (Salvadori 1901), who noted that it was not common and appeared to be restricted to the western coast of the island (Bannerman 1914). In 1909 Boyd Alexander searched for the thrush, but it was never observed. Correia collected four specimens (Amadon 1953) in the hill forest of the south (Jones and Tye 2001) and stated that they were found only on the highest peaks (Correia 1929). De Naurois (1984), like Boyd Alexander, searched for it to no avail. In 1996 possible thrush anvils were discovered in the primary forest along Rio Papagaio and a month later at Oque Pipi (Christy and Gascoigne 1996). Shortly after the thrush was observed twice on A Mesa (see Jones and Tye 2001). Thus, until this study the thrush had only been observed three times since the time of its discovery. The total estimated distribution and status is rare in the lower elevation primary and late successional secondary forest starting from Pico Papagaio south to the southern lowland forest with the exception of A Mesa where it is common. Frequent to common in the mountain forest.

Threatened Status: Vulnerable D

Dohrn's thrush-babbler *Horizorhinus dohrni*

Endemic species to Príncipe.

Status and Distribution

Abundant in the southern lowland and mountain forest up to 945 m (Table 6.1). Keulemans (1866) made similar observations in 1865. Snow (1950) documented Dohrn's thrush-babbler as second only to the Príncipe weaver in abundance. Later expeditions have documented it as abundant in cocoa plantations and forest regrowth (Jones and Tye 1988; Atkinson *et al.* 1991). The total estimated distribution and status is abundant in all forest habitats on the island and very common in brush habitat, plantations, and gardens. It is undoubtedly the most common species when the entire island is considered.

Threatened Status: Lower Risk lc.

Príncipe sunbird *Nectarinia hartlaubi*

Endemic species to Príncipe.

Status and Distribution

Very common in the southern lowland forest and mountain forest up to the summit of Pico do Príncipe (Table 6.1). This corresponds with the observations of Keulemans (1866). Dohrn (1866) described it as not uncommon. Snow (1950) found it in most habitats explored, but did not observe it in the hill forest. Atkinson *et al.* (1991) found it common to abundant in plantations, primary and secondary forest and present but less common in gardens and cultivated areas. The total estimated distribution and status is very common in the plantations and forested areas from sea level to 945 m and common in gardens and heavily cultivated regions in the north.

Threatened status: Lower Risk lc.

Príncipe white-eye *Zosterops ficedulinus ficedulinus*.

Endemic subspecies to Príncipe. The other subspecies is endemic to São Tomé.

Status and Distribution

Groups of this subspecies were only observed on one day of the study near Infante D. Henrique at mid altitude in the south-east of the island (figure 6.1). Local people claimed that it is more common at lower elevations in October and November. These observations are at odds with earlier reports of them being fairly common in the higher parts (Keulemans 1866; Dohrn 1866; Bannerman 1914). Dohrn (1866) also stated that they did not occur much in the lower section of the island. Correia (1929) was only able to collect two specimens of this subspecies (Amadon 1953) indicating that it was relatively rare. It was not observed by Snow (1950) or Frade (1958). De Naurois (1983) observed one white-eye in the south-west forest in the early 1970s and noted that they had been rare for most of the century. It was not seen by any of the ICBP expeditions. Christy and Clarke (1998) stated that it is not common and lives in the central mountainous region and on the margins of that area. The total estimated distribution and status is extremely rare in the southern forest along forest edge at mid- to low altitude with a maximum elevation of 350 m. It is also possibly seasonally present in the north.

Threatened Status: Critically endangered B1 + 2e

Príncipe speirops *Speirops leucophaeus*

Endemic species to Príncipe.

Status and Distribution

Frequent to common in the south-west and mountain forest up to 800 m (Table 6.1). The abundance of this species is difficult to estimate because it tends to travel in groups of up to 30 individuals and while it is found throughout the island, its distribution appears to be relatively localised leading to sporadic observations of many individuals. Dohrn (1866) stated that they live in small flocks in restricted regions, however, Keulemans (1866) during the same time period found it very common throughout the island. Correia in 1928 collected many specimens (Amadon 1953). De Naurois (1983) described this species as abundant at all altitudes. Snow (1950) like Dohrn documented it as rather local. Jones and Tye (1988) found it frequent in small parties in plantations. Peter Jones and John Burlison observed them as quite common in noisy groups with Dohrn's thrush-babblers between Sao Joaquim and Maria Correia (*pers. comm.* Peter Jones). Jones and Tye (1988) state they are occasionally eaten for food and are vulnerable to pesticide use. The total estimate of its distribution and status is frequent to locally common in plantations, secondary and primary forest including the mountain region.

Threatened Status: Vulnerable D2.

Príncipe seedeater *Poliospiza rufobrunnea rufobrunnea*

Endemic subspecies to Príncipe. One of the other subspecies is endemic to São Tomé and the other to Boné do Joquei.

Status and Distribution

Abundant in the south of the island from sea level to 945 m and common on the east and west coast. It is the second most common bird in the southern lowland forest and the third most common in the mountain forest (Table 6.1). It was documented as common by most of the early collectors and ornithologists, for example Keulemans (1866), Correia (1929) and Snow (1950). However, Dohrn (1866) documented it as a rare bird, restricted to the Bahia do Oeste, where it lived in bushy uncultivated areas. De Naurois (1975) found the seedeater common in 1970 but uncommon in 1972-1973. Jones and Tye (1988) only saw two seedeaters in the north over five days and Atkinson *et al.* (1991) did not observe the subspecies during their four-day stay in the north. Christy and Clarke (1998) documented it as occurring throughout the island but relatively rare in the north and cultivated areas. The total estimated distribution and status of the Príncipe subspecies is abundant in the southern and mountain regions, and common on the east and west coast, but only rare in the north.

Threatened Status: Near Threatened.

Príncipe golden weaver *Ploceus princeps*

Endemic species to Príncipe and the islet of Boné do Joquei.

Status and Distribution

Common along the coast up to 200 m in the southern lowland forest, frequent from 200 m to 600 m. In the mountain forest it was not observed above 600 m. Keulemans (1866) believed it to be the most numerous bird on the island. Snow (1950) also found them abundant, but did not observe them in the hill forest. All recent records continue to document this species as abundant (Jones and Tye 1988; Atkinson *et al* 1991; Christy and Clarke 1998). Its total estimated distribution and status is abundant throughout the north with highest densities in plantations, the edge of secondary forest and along the coast. It is abundant along the east and west coast, but only common along the coast of the southern lowland forest. In the south it is frequent at mid- to low altitude forest and absent from the high mountain forest.

Threatened Status: Lower Risk lc.

Discussion

Threatened status

This study indicates that only two of the seven endemic birds at the species level qualify for the IUCN threat categories. These are Príncipe speirops and Príncipe drongo, both of which are listed only on the basis of their restricted range (Vulnerable D2). The University of East Anglia group (Atkinson *et al* 1991) noted that, based on Keulemans' comments on the drongo's distribution, it may be common in the primary forest. However, given the few sightings in the south-west and the absence of the drongo in high mountain forest it is clear that this species has a lower overall density than was previously estimated. Its total population is difficult to estimate as it is at its highest abundance in the northern section of the island where point counts were not conducted. Keulemans' comments are sufficiently general that it is reasonable to assume that they were never common in the mountain forest. Thus, a decline cannot be inferred. It is clear that the drongo has a total range of less than 100 km^2, which would qualify the species as Vulnerable D2. Estimates of absolute density in the north should be carried out in the near future.

Príncipe speirops was recently down-listed from Vulnerable C2b to near threatened by BirdLife International (BirdLife International 2001). However, this down-listing appears slightly premature if the IUCN Categories and Criteria (1994) are strictly applied. If we assume its average abundance in the southern lowland forest is indicative of its overall abundance for the island (Table 6.1), there would be *c.* 2,000 individuals. With a continuing decline this species could qualify for Critically Endangered based on its small range, or Endangered based on its small population. However, given the range of estimates of its status over the years, it is not clear that the speirops has in fact been in decline. It is clear that the population tends to be localised and most probably has a total distribution of less than 100 km^2. Príncipe speirops should therefore be listed as Vulnerable based on its very small range regardless of decline. The IUCN category and criterion would be Vulnerable D2 (IUCN 1994).

The status of the eight endemic subspecies is less secure with two qualifying for Critically Endangered, one for Vulnerable, and two for Near Threatened. Exploration of the mountain and southern forest indicate that Príncipe white-eye is at serious risk of extinction. Based on Dohrn's notes (1866) hope remained that Príncipe white-eye was abundant in the mountain forest. With no observations in the mountain forest during this study, despite sixteen days of surveying, it is probable that the species has experienced a decline. With such a small distribution and decline in the number of individuals, Príncipe white-eye qualifies for Critically Endangered B1+2e.

The Príncipe subspecies of the Gulf of Guinea thrush is still considered extremely rare, but its relatively common presence in the primary forest is encouraging. Príncipe thrush has an extremely restricted range and total population figures are certainly below 1,000 individuals. Therefore, the thrush qualifies for the Vulnerable D category based on population figures alone. Given the observations and collections of Fea (Salvadori 1901), Boyd Alexander in 1909 (Bannerman 1914), Correia (1929) and de Naurois (1983), it would appear that this species has always been rare and restricted to its present habitat type. However, further research is required to determine whether the population is in decline.

Príncipe seedeater on Príncipe, has *c.* 11,000 individuals in the southern 45 km^2 of the island. This species is not as threatened as previously suspected. However, due to its sparse population in sections of its range and apparent fluctuations in population, it should be considered as Near Threatened. The reason for the low abundance of this subspecies in the north of the island is unknown and deserves further attention as its counterparts *Poliospiza rufobrunnea thomensis* on São Tomé (de Naurois 1983; Atkinson *et a.* 1991; Christy and Clarke 1998) and *Poliospiza rufobrunnea frade* on Boné de Joquei (Chapter 7) are abundant in most forest types and at all elevations.

Green pigeon was recorded as very common throughout the island by the early collectors (Dohrn 1866; Keulemans 1866). It is now rare to absent in the late successional and primary forest in the southern section of the island. While it still remains relatively common around cocoa plantations and edge habitat, this species should qualify for Near Threatened as it may have undergone a significant population reduction and it appears to have an extremely low abundance throughout much of its range.

Olive ibis was not observed in the explored regions, which is of great concern, as these are the locations where the Ibis was historically reported to have existed. If olive ibis still persists, then it would undoubtedly qualify for Critically Endangered D based on the small number of mature individuals.

The suspected owl species, that has been heard but never seen, was not heard nor seen. If this species is more than a myth, and if it is endemic, it would very probably qualify for Critically Endangered D, based on a very small number of mature individuals.

Finally, African grey parrot is of conservation concern as it is known that this species is harvested for the pet trade. An average parrot hunter will collect about 40 young per year and sell each one for about 50,000 Dobras per bird (approximately US$ 6.50 at current exchange rates). Juste (1996) estimates that 1,500 young are harvested each year plus an unknown number of adults. De Melo (1998) estimates an annual harvest of between 430-550 chicks and 200-300+ adults. The overall effects of this on the population dynamics are unknown. Using the mean abundance per kilometre squared there are *c.* 4,500 African grey parrots in the 25 km^2 of the southern lowlands of Príncipe. This is the region where the parrots are most abundant, and it is therefore unlikely that the total island population exceeds 20,000. Given population figures alone this potentially geographically isolated population would not be considered threatened. However, given its exploitation and the uncertain age structure of the population, the African grey parrot on Príncipe would be listed as Near Threatened. The population trends require further investigation. If a decline could be inferred due to exploitation, this population would soon qualify for Endangered B1+2e.

The dominance of endemics

If the process of the taxon cycle (Ricklefs and Cox 1972,1978; Grant and Grant 1998) was occurring, one would expect the endemic bird species restricted to Príncipe to be the most vulnerable to extinction. However, the endemic birds remain the most common species on the island (Snow 1950), and when the status and distribution of the endemic species and subspecies are compared, it is clear that the endemic subspecies are at greater risk of extinction. Furthermore the only extinctions or extirpations on Príncipe have been non-endemics (Amadon 1953). Here it would appear that the taxon cycle is working in reverse. With the exception of African grey parrot and olive sunbird, only species or subspecies restricted to Príncipe were common in the primary and late secondary forest habitat. A similar relationship has been demonstrated on São Tomé (Peet and Atkinson 1994). There are three main reasons why mainland forest birds may not have been able to become established on the island: (1) tropical rainforest birds are much less likely to migrate to an oceanic island (MacArthur *et al.* 1972) and therefore, new arrivals are extremely rare; (2) Príncipe may be too small for many mainland forest species to persist; (3) the island endemics may out compete new arrivals for limited resources, as has been suggested on São Tomé (Peet and Atkinson 1994). Distance and area may be factors in limiting the number of new arrivals. However, Príncipe is relatively close to continental Africa (220 km) and tropical rainforest habitat is found in large sections of the Gulf of Guinea mainland. There has also been 500 years of European colonisation during which forest birds could have been introduced to the island. While area may be a restriction for some species a great variety of forest birds have colonised small islands throughout the world (see Stattersfield *et al.* 1998). In the case of Príncipe, distance and area on their own appear inadequate to explain the lack of non-endemics in the dense rainforest. Thus, it is possible that competitive exclusion (Lack 1969) plays a role on islands such as Príncipe where there have been few extinctions and high abundance levels of the native avifauna have been maintained despite the introduction of mammalian predators.

Low levels of threat

Islands that were uninhabited until the arrival of European colonists have a higher proportion of threatened species and historic extinctions (Pimm *et al.* 1994; Chapter 3), e.g. Mauritius, the Seychelles and Reunion. It is therefore surprising that Príncipe has only two endemic species that might be considered vulnerable to extinction and that there have been no documented endemic bird historic extinctions. It is possible that there have been undocumented extinctions. However the island has an extremely high number of endemic species and subspecies given its small size (Jones 1994), which indicates that recent extinctions have not been extensive. Although, the absence of ground dwelling forest birds or large flightless species indicates that a few undocumented extinctions may have occurred.

Príncipe has had a unique land use history, which may be responsible for the low levels of present threat. Despite clearance of much of the native forest during the colonial era, shade trees remained for the dominant crops (cocoa and coffee) maintaining a general forest structure. All the endemic species and subspecies appear to have been able to persist in this modified habitat with the exception of Gulf of Guinea thrush and possibly olive ibis. The mountainous region in the centre of the island and, with the exception of roughly a 50 year period, most of the south-west remain a substantial refuge for the island endemic species and subspecies. Unlike most other islands there is now more forest habitat on Príncipe than there has been for the past century.

The inaccessible mountain rainforest would have been a refuge from exploitation during the colonial era and subsequent regeneration throughout the south has greatly decreased the accessibility of the entire region. With the exception of African grey parrot, exploitation is at a very small scale and restricted to easily accessible areas around Santo Antonio and plantations in the north.

The mountain refuge and subsequent regeneration in the south may also play a role in the low levels of threat observed due to introduced predators. At the species level none of the endemic birds appear to be threatened due to introduced predators. However, the cause of rarity of the subspecies olive ibis, Gulf of Guinea thrush, Príncipe white-eye and Príncipe seedeater (in the north of its range) are unknown and may be associated with introductions. The mona monkey was common throughout the primary and late succession secondary forest, rats and mice were rare and no other introduced mammals were observed. While proper trapping is needed to estimate the diversity and density of introduced predators, it appears that many of the human commensual mammalian predators such as cats or feral dogs are at low abundance or absent in the thick tropical rainforest. This dense habitat also provides protection from nest predation. Perhaps this is why rainforest species appear to be less vulnerable in island systems (Paulay 1994).

Finally, Príncipe is relatively close to the mainland (220 km), and Chapter 3 has demonstrated that endemic birds closer to the mainland are less vulnerable to extinction. Endemic species that are closer to the mainland may be less threatened for a number of reasons. The avifauna, as well as other flora and fauna tends to be more specious on islands closer to the mainland (MacArther and Wilson 1967). This would broaden a species evolutionary experience to predators and competitors as well as disease. Islands closer to the mainland are also more likely to be exposed to migrants, strays, or potential colonists. Again this would increase their evolutionary experience to competitors, predators and disease.

Exposure to a broader range of predators or diseases would inhibit the evolution of, or filter out, life-history traits or an immune system that may make a species more vulnerable to extinction once exposed to mainland species. While historic vectors of disease are difficult to identify it is possible to highlight a few of the native predators. Land-crabs have been suggested as a surrogate for mammalian predators (Atkinson 1985). There are a variety of land-crabs found on Príncipe, one of which is present even at the highest point of the island (Cumberlidge *et al.* submitted). There are also two species of snake present on Príncipe, although their date of colonisation is unknown. In addition, there are avian predators such as the black kite *Milvus migrans* and blue-breasted kingfisher.

It is less clear as to why island endemics should be particularly susceptible to competition from mainland species (Pregill & Olson 1981). Especially when it is considered that island endemics may be well adapted to restricted-range environments (Blondel 1991). First, it is possible that they are not less competitive in their native environment, but alteration of their habitat by humans has resulted in island endemics being less competitive than introduced species well adapted to a disturbed landscape. Second, island birds may be isolated from novel competitive adaptations on the mainland. Thus, they are simply exposed to mainland competitive processes at a later stage, making them appear as though they have become less competitive. This process would have the greatest effect on communities that have been isolated for the greatest period of time. Third, birds on distant species poor islands may be more likely to evolve into a new ecological zone or niche. These species may be particularly vulnerable to the introduction of mainland species that traditionally occupy the niche space in to which the island endemics have evolved.

Future threats

Current habitat destruction on the island is minimal and there are encouraging plans to designate the remaining primary forest in south-west and central Príncipe as a National Park. Legislation for establishing a national protected area system has been passed but no specific protected areas have yet been gazetted. The protection of this region is essential for the long-term persistence of the endemic birds. Species particularly dependent on this region are Gulf of Guinea thrush, Príncipe seedeater, Príncipe speirops, and possibly the Príncipe white-eye and olive ibis.

Recent plans to develop over a third of the island as a free trade zone, promoted as Africa's Hong Kong, have now fortunately been abandoned. The current government remains interested in free zone development but is adopting a more cautious approach.

If the recent proposal for a free trade zone had proceeded, then businesses such as multinational oil companies, financial services firms and trading companies would have been encouraged to base their headquarters on a 50 km^2 concession (WADCO 1999). The concession area accounted for 36% of the island's area and would have caused a significant reduction in the already restricted ranges of the island's endemic species and subspecies. Now the government is focusing on oil exploration and the future rapid development of this sector is the single greatest threat to the birds of Príncipe.

Since 1988 the government has gradually been privatising agricultural land to encourage self-sufficiency in food production. After many difficulties, the privatisation programme finally became effective in the late 1990s. However, the privatisation of agricultural land is having important consequences on the environment. Small farmers often cut down the trees on their land immediately on receiving title in order to raise sufficient capital to develop the land further. Low world cocoa prices have also lead to agricultural practices where shade trees are not necessary. In addition, pesticides are now more accessible and commonly used on the island. This process of privatisation will undoubtedly reduce suitable bird habitat outside of the southern forest block.

Conclusion

With bird surveys of the mountain forest and the southern lowland forest, it is now possible to make more robust assessments of the conservation status of the island's endemic species and subspecies on Príncipe. Based on this research I classify two of the seven Príncipe endemic species as Vulnerable to extinction due to their restricted range, Príncipe speirops and Príncipe drongo. The status of the endemic subspecies is less encouraging. Three of the eight subspecies qualify as threatened with extinction (Gulf of Guinea thrush, Príncipe white-eye and olive ibis), and a further two are Near Threatened (the Príncipe seedeater and the green pigeon). Given present population figures in the regions surveyed, the African grey parrot does not appear to be threatened with extinction but has been listed as Near Threatened due to the uncertain age structure of the population. The legendary owl was not seen during this study and its validity remains a mystery.

When Príncipe is considered in the context of other oceanic islands that have been discovered in historic times, the levels of threat and extinction are low. The resilience of the endemic birds appears to be associated with the rainforest habitat and the relatively close proximity of the island to the mainland. However, the central mountainous region and southern section of the island, which have been uninhabited for much of the island's history, have undoubtedly played a strong role in the persistence of these small range island endemics. The future of the endemic birds of Príncipe remains positive as long as large-scale development projects are not encouraged and the government maintains its commitment to conserving the central and southern sections of the island.

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CHAPTER 7

SUPER ABUNDANCE AND PERSISTENCE: LESSONS FROM A SMALL OCEANIC ISLAND

Abstract

The subspecies of seedeater *Serinus rufobrunneus fradei* is restricted to a 35 ha oceanic island called Boné de Joquei, located in the Gulf of Guinea off the coast of West Africa. Its closest relative is *Serinus rufobrunneus rufobrunneus* found on the larger island of Príncipe (139 km^2) only 3 km away from Boné de Joquei. *S rufobrunneus fradei* is unusual, firstly because it has evolved into a distinct form within close proximity to its conspecific, and secondly because it has been able to persist when restricted to a global distribution of less than 1 km^2. Little is known about *S rufobrunneus fradei*, as research has not been conducted on this subspecies since it was described 25 years ago. In this paper, I confirm that *S rufobrunneus fradei* is a distinct evolutionary unit that can easily be distinguished from its conspecifics. I present research on its distribution, abundance and ecology. I compare the Boné de Joquei population to its conspecific on Príncipe and demonstrate that it is found in a broader range of habitats and at a super abundant population density. I suggest that the process of density compensation may be essential for the long-term persistence of many endemic birds restricted to extremely small isolated islands. To effectively conserve these populations it is essential to understand the specific mechanisms associated with super abundance such as lack of avian competition, mammalian predation, and an abundant food supply, so that the conditions associated with super abundance may be maintained.

Introduction

The Príncipe Seedeater *Serinus rufobrunneus* is divided into three subspecies found on different small oceanic islands in the Gulf of Guinea. The Príncipe subspecies *Serinus rufobrunneus rufobrunneus* was the first to be described by Gray in 1862, followed by the São Tomé subspecies *Serinus rufobrunneus thomensis* described by Bocage in 1888 from the collection of Francisco Newton (Jones and Tye 2001). Almost a century passed before de Naurois (1975) described the third subspecies *Serinus rufobrunneus fradei* found on Boné de Joquei, a small island of 35 ha located 3 km off the southeast coast of Príncipe (Figure 7.1). Although sporadic and infrequent, research over the past decade has provided a general understanding of the status, distribution and ecology of Príncipe and São Tomé subspecies (Naurois, 1975; Jones and Tye 1988; Atkinson *et al.* 1991; Christy and Clark 1998; Jones and Tye 2001; Chapter 6). Much less is known about the Boné de Joquei population, as research has not been carried out on this subspecies since it was described by de Naurois (1975).

Two unique aspects of the Boné de Joquei seedeater population make it especially interesting from a conservation and evolutionary perspective. First, given that Príncipe is only 3 km from Boné de Joquei, it is remarkable that the interchange between the two populations has been low enough that they can easily be distinguished from one another. Three kilometres appears to be a relatively short distance when considering that the ancestor of *S. rufobrunneus* would have had to have travelled at least 200 km over water to become established, and a further 150 km between Príncipe and São Tomé. Secondly, it is well known that restricted-range species are particularly prone to extinction (Hanski 1982; Simberloff and Gotelli 1984; Gaston and Blackburn 1996; Simberloff 1998; Gaston and Chown 1999). Under the IUCN Categories and Criteria (IUCN 1994), a species is considered Vulnerable D2 if it has a range of less then 100 km^2. The Boné de Joquei population has been able to maintain a viable population within a range of less than 1 km^2, of which a large proportion was used for agriculture prior to independence in 1975.

Understanding the mechanisms that enable the Boné de Joquei population to persist within such a small distribution will aid in its effective conservation by enabling conservationists to ensure that these conditions are maintained in the future. A greater theoretical understanding of small range persistence will also help to evaluate extinction risk of the large number of species that are presently confined to a small global distribution. In addition, further research of this subspecies and its conspecifics provides an excellent opportunity to explore questions such as rates of ecological, evolutionary and behavioural divergence on islands.

This paper is based on research that was carried out in the Democratic Republic of São Tomé and Príncipe between August 22nd and October 11th 1999, of which two days were spent on the island of Boné de Joquei. The validity of the Boné de Joquei population as a distinct evolutionary unit is first discussed based on descriptive notes of coloration and markings, the first photo of a live specimen (Figure 7.2), the first recording of its song (Figure 7.3) and basic morphological measurements. I present results of research conducted on Boné de Joquei on the distribution, abundance and ecology of its seedeater population. This subspecies is then compared with its conspecifics on São Tomé and Príncipe and characteristics and conditions for persistence within a restricted range are discussed, in addition to possible conservation strategies.

Study site and background

Geography

The three islands where the subspecies of seedeater are found vary considerably in size, elevation and distance from the West African mainland. São Tomé is 225 km from the mainland with an area of 836 km^2 and just over 2000 m in elevation. Príncipe is 220 km from the mainland with an area of 128 km^2 (Juste and Fa 1994) and an elevation of 945 m. Príncipe and São Tomé are separated by 150 km and a sea depth of more than 1800 m (Exell 1944; Amadon 1953). Boné de Joquei is only 3 km from the southeast tip of Príncipe and has an area of 35 ha and a height of 300 m (de Naurois 1975). The islands of São Tomé and Príncipe have never been attached; however, Boné de Joquei was likely part of the island of Príncipe when water levels were much lower c12,000 years ago (see Juste and Ibanez 1994) because the sea between the two islands is only 50 m deep (de Naurois 1975).

Avifauna

As can be expected by its relative size, São Tomé has the highest number of bird species with 50 (Jones and Tye 2001) land birds and, depending on the taxonomy followed,15 to 16 single island endemics, followed by Príncipe with 33 landbirds and, again depending on the taxonomy, 5 to 7 single island endemics. De Naurois (1975) records three land birds on Boné de Joquei. He observed 3-4 blue-breasted kingfishers *Halcyon malimbicus dryas,* one couple of Príncipe golden weavers *Ploceus princeps*, and the Boné de Joquei subspecies of seedeater. He states that the Boné de Joquei seedeater was nearly the only terrestrial bird on the island. He also documented two seabirds including the red-billed tropicbird *Phaeton aethereus* and the brown booby *Sula leucogaster.*

Land use history

All three islands have experienced significant habitat modification since their discovery in the late 1400s. On São Tomé and Príncipe the profitable production of sugar cane and, later, cocoa resulted in the cultivation of large sections of the islands (Atkinson *et al.* 1991). However, over the past decade, lack of labour, disease, a crash in the cocoa industry and political instability have lead to the abandonment of most of the cultivated regions, which have now reverted to tropical rainforest. The history of cultivation on Boné de Joquei is less well known. From the observations of this study and of de Naurois (1975), it is clear that virtually all of the accessible growing areas were planted with oil-palm *Elaeis guineensis* and coconut. This represents about 40% of the islands surface area. The local Catholic Priest on Príncipe claims that a man lived on Boné de Joquei prior to independence and that the island was particularly good for crops such as bananas, since the mona monkey *Cercopithecus mona* had not been introduced to Boné de Joquei. However, the steep vertical rock faces are unsuitable for cultivation (Figure 7.1) and if de Naurois (1975) was correct that no one had ever climbed to the top of Boné de Joquei, the dense brush on the summit would have escaped cultivation. The introduction of mammalian predators such as the ship rat *Rattus ratus*, Norway rat *Rattus norvegicus*, house mouse *Mus musculus*, domestic cat, dog, mona monkey *Cercopithecus mona* (Dutton 1994) and civet *Civettictis civetta* (Bruto da Costa *et al.* 1916) have been documented on São Tomé and or Príncipe, but none of the above have been observed on Boné de Joquei.

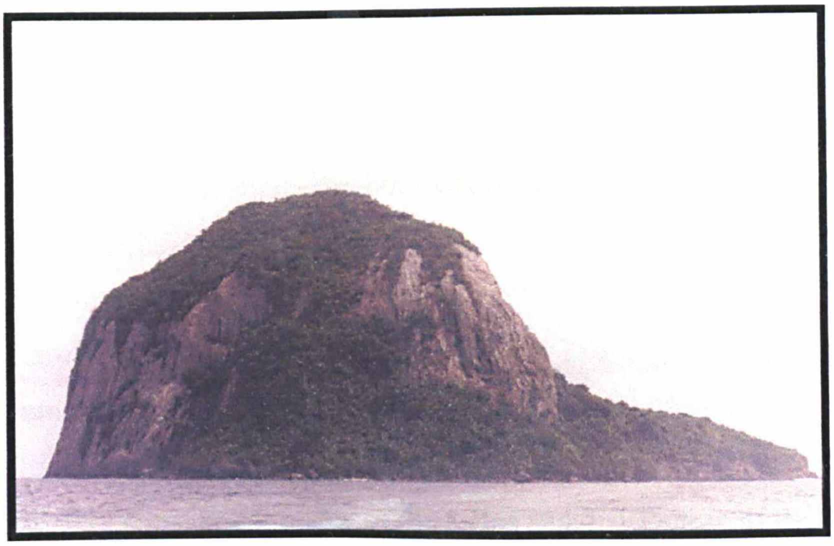


Figure 7.1. The island of Boné de Joquei

Background to the seedeater

Subspecific status

Both the small size of Boné de Joquei and the close proximity of its endemic subspecies of seedeater to its conspecific on Príncipe make it difficult to believe that the population on Boné de Joquei could evolve into a distinct evolutionary unit that can easily be distinguished from the other two subspecies. The validity of this subspecific classification has not been confirmed since *S. rufobrunneus fradei* was described by de Naurois over 25 years ago. Thus, it is reasonable that the subspecific status requires verification (Jones and Tye 2001). In this Chapter I do not wish to enter the debate about species concepts (e.g. Zink and McKitrick1995; Kelt and Brown 2000) or how distinct a population must be before it becomes deemed a subspecies. I simply hope to demonstrate whether or not the Boné de Joquei population is a unique evolutionary unit, defined as a taxon that can be consistently distinguished from its closest relative in morphology or colour. Differences in behaviour or ecology may also provide insight into variation between populations, but it is often difficult to determine whether they are genetically based. De Naurois (1975) describes the unique characteristics of the Boné de Joquei population as having a brighter tint of red, particularly in the rump, throat and abdomen, with faint stripes on the back and no stripes on the abdomen. He states they are slightly heavier, with longer tails and longer, higher, more yellowish beaks than their closest relative, the Príncipe subspecies. The wing length of the Boné de Joquei population is longer than the Príncipe subspecies, but very similar to the São Tomé subspecies (de Naurois 1975).

Distribution and abundance

Early documentation of the status and distribution of the São Tomé subspecies were greatly varied, ranging from uncommon to very common (Salvadori 1903a; Bannerman 1915; Correia 1929; De Naurois 1975). Subsequent to the observations of de Naurois, the São Tomé subspecies has been documented as common to abundant in all forest types (de Naurois, 1983; Jones and Tye, 1988; Atkinson *et al.*, 1991; Christy and Clark, 1998; Jones and Tye, 2001) from sea level to the high mountains, but less common in the northern section of the island (Jones and Tye, 1988). It has also been reported as common around urban areas (Jones and Tye, 1988; Chapter 6).

Until very recently estimates of the status and distribution of the Príncipe subspecies has also been extremely inconsistent ranging from rare to very common (Dohrn 1866; Keulemans 1866; Salvadori 1903b; Bannerman 1914; Correia 1929; Snow 1950; De Naurois 1975; Jones and Tye 1988; Atkinson *et al.* 1991). Christy and Clarke (1998) state that it was observed throughout the island, but is relatively rare in the north and in cultivated areas. This was confirmed in Chapter 6 where the Príncipe population is reported to be rare in the north and almost never seen near inhabited areas, the second most common bird in the southern lowland forest, and the third most common bird in the mountain forest.

In the early 1970s de Naurois recorded the Boné de Joquei population of seedeater as abundant (de Naurois, 1975), with a density estimate of 30 to 40 per ha, suggesting a total of 150-200 individuals in the oil-palm *Elaeis guineensis* forest. He states that it is probable that these birds inhabit more than the gradual slopes of the north face of the island, and that they may also inhabit the forest of the steep incline and the plateau on the summit of the island.

Methods

On September 8th 1999 Boné de Joquei was surveyed for forest bird species, documenting presence or absence, distribution, relative abundance and general notes on ecology. The entire island was covered, including the summit of 300 m. General abundance was based on a system used by Jones and Tye (1988) and the University of East Anglia group (Atkinson *et al.* 1991). Notes were taken on the markings and coloration of the Boné de Joquei population of seedeater in the wild. Photographs were taken with a 300 mm lens and the song was recorded using a microphone and recording system borrowed from the British Library National Sounds Archive, Wildlife Sounds Department. These songs were then compared with earlier recordings conducted by Alexander-Marrack in August 1980 on São Tomé and Ian Sinclair on Príncipe in August 1991. Measurements were taken of four unsexed individuals to determine bill length, width and depth, as well as wing, tarsus and tail length. These were later compared with specimens of the Príncipe and São Tomé subspecies at Tring, The Natural History Museum, England.

The island was also explored to determine the best approach for the point count survey using distance sampling (see Buckland *et al.* 1993) that would take place on October 2 1999. Due to the topography of the island, including a vertical rock face and large unsettled boulders throughout, stratified random sampling was not possible. Therefore two transects were walked around the island, one roughly between 10 and 70 meters from the shoreline and the other between 120 and 250 m. Each point count along the transect line was spaced by at least 100 m; however, ten of the point counts were duplicated along the transect due to the small size of the island. Large distances were not required between transects as the sound of the ocean quickly drowned out bird calls from one site to the next. In total 37 point counts were conducted whenever the light rains permitted between 5:30 AM and 5 PM. At each point count, two minutes were spent waiting for the birds to settle and recording data such as habitat, weather, temperature, elevation and time. The distances of birds from a specific point were then estimated for five minutes. All species of bird heard or seen were recorded. Throughout the survey the island was covered in cloud and temperatures ranged between 22° and 25 °C. Seventy four percent of the observations were based on sound. This data were analysed using Distance software 3.5 (Thomas *et al.*, 1998). Eight distance bands were applied using post stratification. The most distant band was set so that approximately 5% of the most distant estimates would be removed from the analysis.

Results

The Boné de Joquei seedeater population is reddish brown with a slightly more intense reddish tint on the breast and rump. The regions around the eye and chin are darker brown and faint darker lines can be detected running from the top of the head to the mantle. Below the chin the throat becomes slightly lighter reddish brown than both the breast and the chin. With the exception of the head region, the greater wing covers, the primary covers, the secondaries, the primaries and the tail feathers are a deeper brown than the rest of the body. The eye is a dark chestnut colour and the tarsus is a gray/pink (Figure 7.2).

Figure 7.2. The subspecies of seedeater found on Boné de Joquei, *S. rufobrunneus fradei*

Measurements of the bill, wings, tarsus and tail do not indicate any significant difference in morphology between the Boné de Joquei population and the subspecies on Príncipe (Table 7.1).

Table 7.1. Measurements of *S. rufobrunnea.* For each subspecies four unsexed individuals were measured using callipers. The mean is given for each subspecies followed by the lower and upper range. All measurements are in millimetres. All specimens are available at Tring.

Seedeater	Bill length	Bill width	Bill depth	Wing length	Tarsus	Tail length
Boné de Joquei	11.1	6.8	8.4	80	18.9	48.3
Serinus rufobrunnea Fradei	(10.5-12)	(6-7)	(8-9)	(75-82)	(18-19.5)	(46-51)
Príncipe	10.8	6.6	8.5	80.7	18.3	49.5
Serinus rufobrunnea rufobrunneus	(10-11.5)	(6-7)	(8-9)	(77-85)	(18-19)	(48-50)
São Tomé	10.7	6.6	8.9	79.8	17.4	53.5
Serinus rufobrunneus thomensis	(10-11)	(6-7)	(8.5-9)	(77-82)	(16-18)	(50-56)

Recordings of the song indicate that the Boné de Joquei population has a large and varied repertoire consisting of high frequency modulated notes (three to nine Kilohertz) with trills either between whistled notes or at the beginning or the end. The frequency modulation of three to nine kilohertz is relatively standard for the three subspecies and the song structure is similar. The trill rate appears to be similar between the Príncipe and Boné de Joquei populations, but is slightly slower for the São Tomé subspecies (Figure 7.3).

Including the Boné de Joquei population of seedeater, four forest birds were observed during this study, the blue-breasted kingfisher, Príncipe golden weaver and green pigeon *Treron calva virescens*. Two sea birds were also documented, the brown booby and the white-tailed tropicbird *Phaethon lepturus*. The Príncipe golden weavers were commonly seen or heard in groups of two to five below 250 m altitude and were observed nesting on the island. Individual blue-breasted kingfishers were common throughout the island up to 300 m altitude. The green pigeon was seen high in the canopy at lower elevation, although it did not appear to be common. The brown booby was observed on large boulders along the coast and the white-tailed tropicbird was commonly observed in pairs on the ground above 200 m altitude or circling the summit of Boné de Joquei once they had been disturbed. The white-tailed tropicbirds appeared to be nesting, however, the actual nest site was not confirmed due to the inaccessibility presented by loose boulders and large vertical drops.

The Boné de Joquei population of seedeater was found abundant in all habitat types on the island from sea level to 300 m, including oil-palm *Elaeis guineensis* forests, stands of coconut, stands of native trees, sparsely vegetated open areas caused by rock slides, and the dense shrub covering the summit of the island. However, it appeared much less abundant near the summit. It could be found at all levels in the vegetation including small branches close to the ground and perching on large boulders. It could easily be approached within four metres. The Boné de Joquei population of seedeater was seen eating both oil-palm fruits and the flesh from coconut.

Results from the point counts using distance sampling indicate that there were c185 Príncipe golden weavers, c9 blue-breasted kingfishers and c2000 seedeaters. The total estimate of seedeaters is likely to be lower as transects were not run along the vertical rock face or the rocky elevated plateau near the summit where the seedeaters appear to be much less abundant. These areas account for almost half of the islands habitat, therefore assuming the seedeaters are at one fifth of their surveyed population density in these regions the total population would be c1200 individuals. The green pigeon was not observed during the point counts and an estimate is therefore not given (Table 7.2).

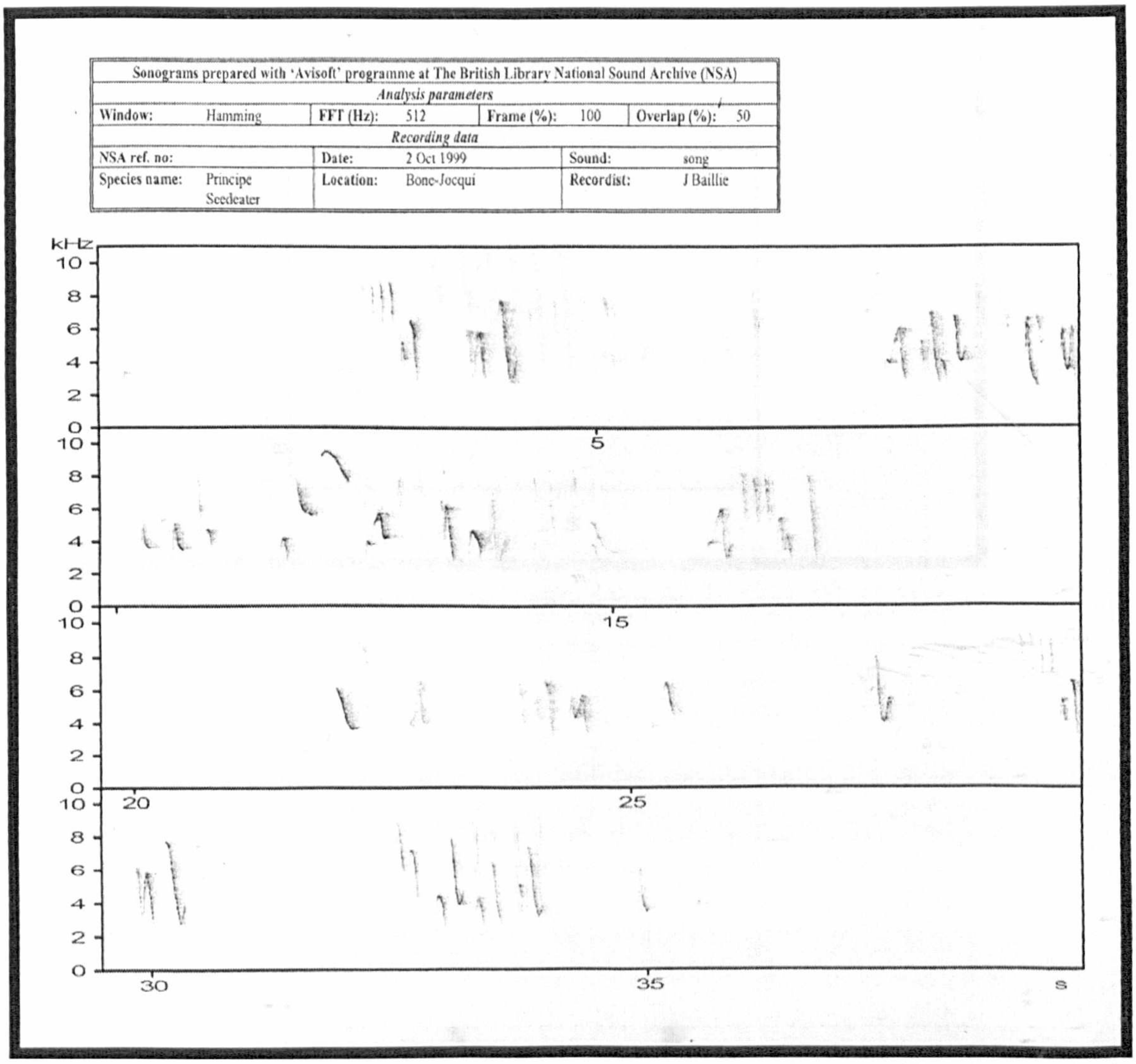
Table 7.2. Relative and absolute abundance as well as maximum elevation of the forest birds of Boné de Joquei.

Boné de Joquei forest birds	Relative abundance	Absolute abundance per km^2, 95 % C.I.	Abundance on Boné de Joquei	Minimum & Maximum Elevation
Green pigeon *Treron calva virescens*	**	-	-	0-200
Blue-breasted kingfisher *Halcyon malimbicus dryas*	***	24.4 (10.0- 46.7)	6	0-300
Príncipe seedeater *Serinus rufobrunnea fradei*	*****	5960.2 (4955.3- 6965.1)	2086	0-300
Príncipe golden weaver *Ploceus princeps*	***	530.8 (293.6-768.0)	186	0-250

Abundant:	*****	50+ seen or heard per day in a specific habitat
Very Common:	****	10-50 seen or heard in a day.
Common:	***	1-10 seen or heard in a day.
Frequent:	**	Seen or heard on more than one occasion in a habitat but not on a daily basis.
Rare:	*	Special record on very few occasions in a certain habitat despite specific attempts to locate them.

Figure 7.3.a,b,c: Sonograms of the Príncipe seedeater (a) *Serinus rufobrunneus fradei*, (b) *Serinus rufobrunneus thomensis,* and (c) *Serinus rufobrunneus rufobrunneus*

(a)



Sonograms prepared with 'Avisoft' programme at The British Library National Sound Archive (NSA)

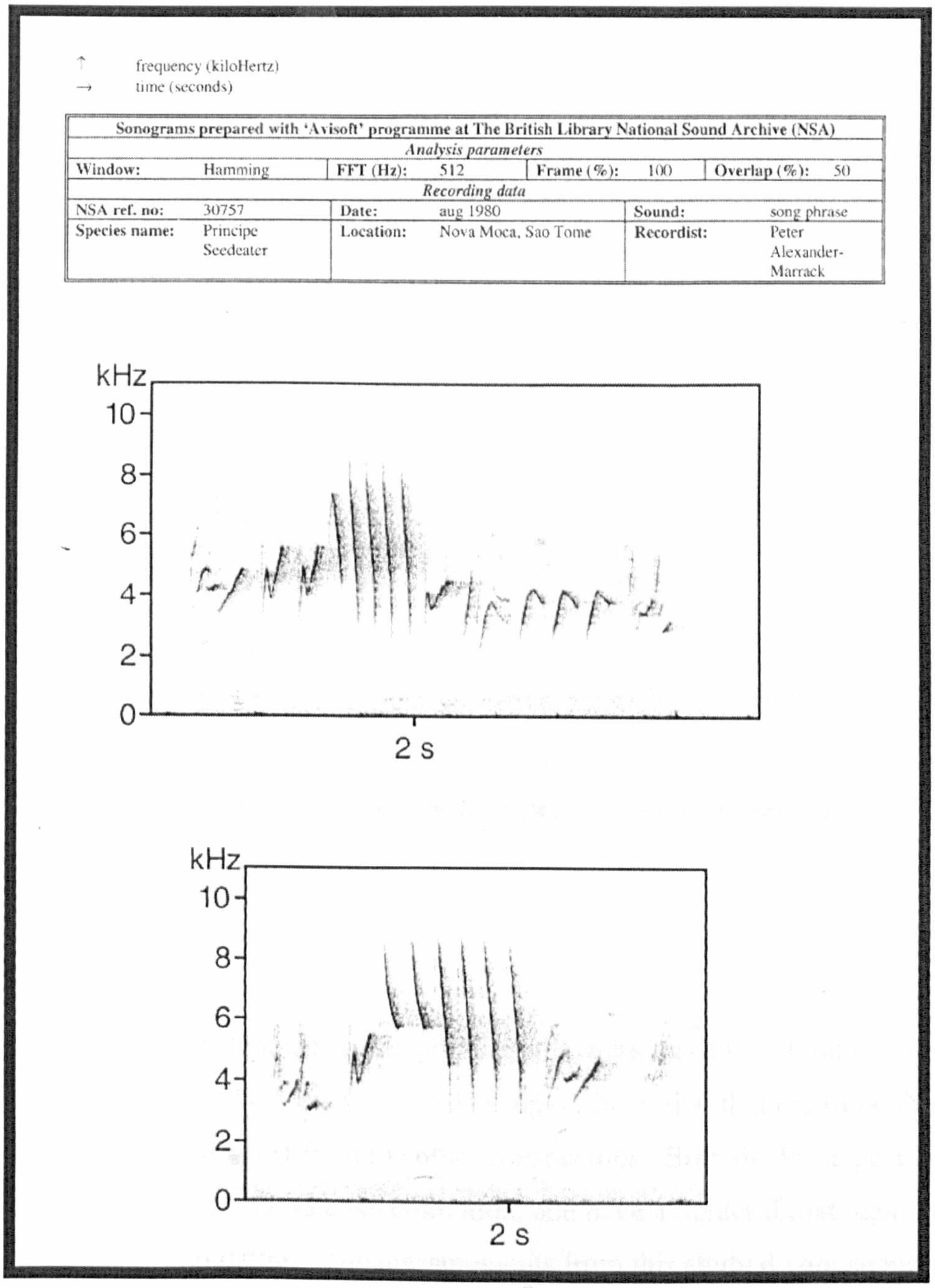
Analysis parameters

Window:	Hamming	FFT (Hz):	512	Frame (%):	100	Overlap (%):	50

Recording data

NSA ref. no:		Date:	2 Oct 1999	Sound:	song
Species name:	Principe Seedeater	Location:	Bone-Jocqui	Recordist:	J Baillie

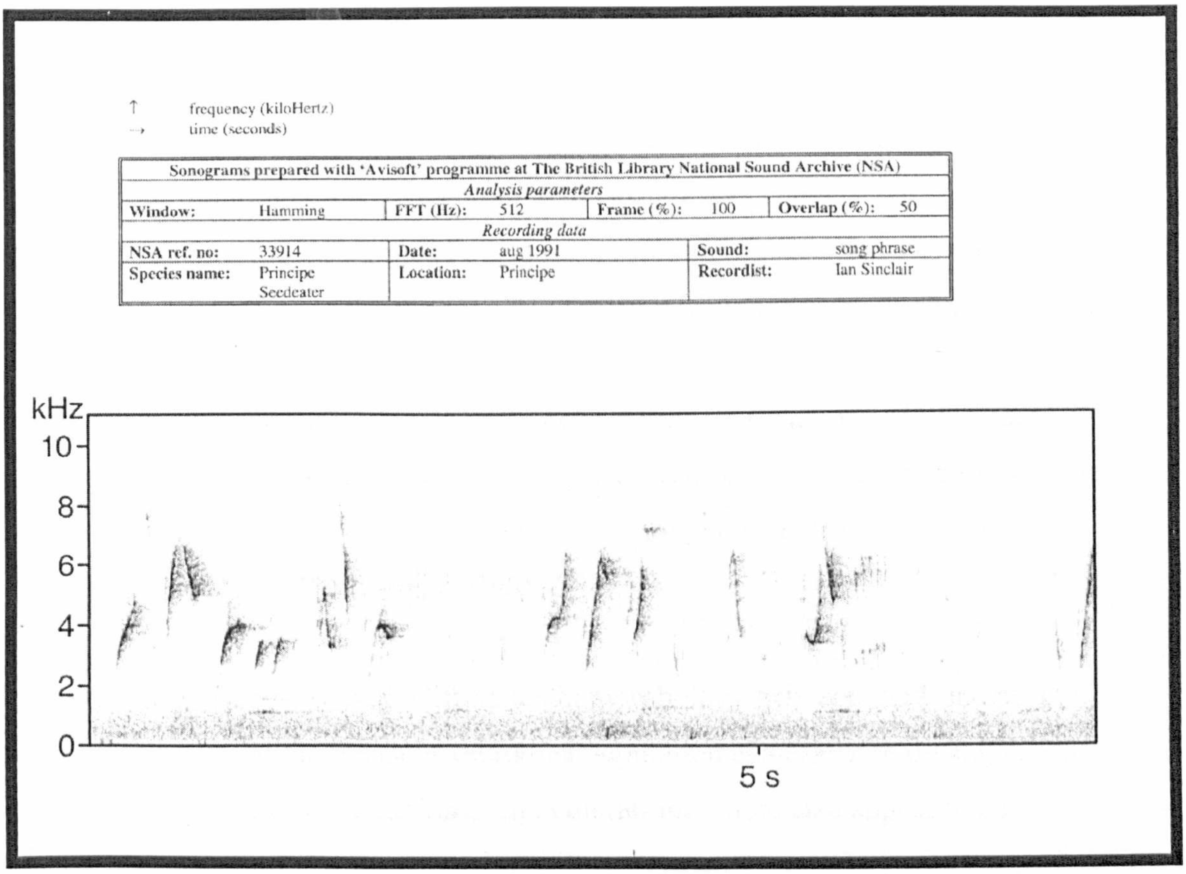
(b)



↑ frequency (kiloHertz)
→ time (seconds)

Sonograms prepared with 'Avisoft' programme at The British Library National Sound Archive (NSA)							
Analysis parameters							
Window:	Hamming	**FFT (Hz):**	512	**Frame (%):**	100	**Overlap (%):**	50
Recording data							
NSA ref. no:	30757	**Date:**	aug 1980	**Sound:**	song phrase		
Species name:	Principe Seedeater	**Location:**	Nova Moca, Sao Tome	**Recordist:**	Peter Alexander-Marrack		

(c)



↑ frequency (kiloHertz)
→ time (seconds)

Sonograms prepared with 'Avisoft' programme at The British Library National Sound Archive (NSA)							
Analysis parameters							
Window:	Hamming	**FFT (Hz):**	512	**Frame (%):**	100	**Overlap (%):**	50
Recording data							
NSA ref. no:	33914	**Date:**	aug 1991	**Sound:**	song phrase		
Species name:	Principe Seedeater	**Location:**	Principe	**Recordist:**	Ian Sinclair		

Discussion

Subspecific status

Observations of the Boné de Joquei population's markings and coloration are very similar to those of de Naurois (1975) and support the notion that the Boné de Joquei population is truly distinct from the other conspecifics. Both the Príncipe and São Tomé subspecies lack the reddish coloration, and have a lighter throat region than the Boné de Joquei population. The measurements from this study do not support de Naurois' assertion that the Boné de Joquei population has a longer tail and wing as well as a higher, longer beak than *S. rufobrunneus rufobrunneus* (see Table 7.2). Measurements from this study should be treated with caution as the sample size is small; however, the remarkable similarity of all the measurements of the Boné de Joquei and the Príncipe subspecies suggests that there are no morphological differences.

This study has demonstrated that the song frequency and structure are very similar between the different populations. Due to the extensive repertoire and variation in song, determination of the extent to which the specific songs have diverged and the variation in repertoire size between the subspecies requires many more hours of recording for all three subspecies.

In the absence of genetic studies it is difficult to know the extent to which the population has been isolated. Immigration might be expected given the close proximity of Príncipe; but if immigration were common the differences between the species would probably be smaller. However, if there is strong selection for specific traits on an island the population may maintain differences despite periodic colonisation (Grant and Grant 1998). It is quite possible that they have evolved in complete isolation, as birds that have colonised distant islands often become poor dispersers (Diamond 1981; Grant 1998). Molecular studies could provide great insight into the extent of isolation and the process of divergence, whether it is a result of selection, genetic drift (Wright 1940) or the founder effect (Mayr 1954; Berry 1998).

Although there appears to be little difference in morphology between the Príncipe and Boné de Joquei population, the Boné de Joquei population can easily be distinguished from its conspecifics based on markings and coloration. There also appear to be ecological and behavioural differences that will be discussed later. In the absence of molecular tests the extent of the genetic divergence remains unknown. However, it is clear that the Boné de Joquei population is a distinct identifiable evolutionary unit.

Species present

During this study two birds are recorded that de Naurois (1975) did not document, the green pigeon and the white-tailed tropicbird. However, de Naurois documented the red-billed tropicbird that was not observed during this study. With the combined observations there are still only four forest birds and two sea birds that have been seen on the island. With the few sightings of the green pigeon and an estimated population of 8 individuals for the blue-breasted kingfisher, it is unlikely that they are isolated from the populations on Príncipe. The Príncipe golden weaver may be isolated to Boné de Joquei, but with a small estimated population of 186 it is also likely that there is interchange with the Príncipe population.

Distribution and behaviour

The distribution of the Boné de Joquei seedeater population is similar to that of the subspecies on São Tomé and Príncipe in that it is found in a broad range of forest habitats (Christy and Clark 1998; Jones and Tye 2001). Different from both of its conspecifics, the Boné de Joquei subspecies is commonly found exposed in sparsely vegetated open areas as well as occupying low, dense brush that covers much of the upper sections of the island. Behaviourally, the Boné de Joquei population was much more tame than its conspecifics, allowing approach within four metres. It was observed commonly perching very close to the ground or on large boulders. Thus, the Boné de Joquei population appears to differ from its conspecifics both in its ecology and behaviour. However, it is not known if these differences are genetically based.

Abundance

The Boné de Joquei population also differs in that it is found at much greater abundance throughout the island. Using the estimate of 1200 for the total population of the island the population density would be c34 individuals per hectare. This is an extremely high population density when considering that the Príncipe population's highest abundance is 3.3 individuals per hectare (Chapter 6). Furthermore, the Príncipe subspecies is the second most abundant species in the south of Príncipe and the third most abundant species in the mountain forest (Chapter 6). If the Boné de Joquei population had a similar abundance to that of the Príncipe subspecies there would be c115 individuals on Boné de Joquei, a very small population to maintain a subspecies for thousands of years.

The estimate of c34 species per hectare on Boné de Joquei requires a discussion of potential biases that may lead to an inflated estimate simply because the abundance level is alarmingly high. Using point counts and distance sampling the observer is trying to identify the number of individuals and their estimated distance during a snapshot in time. Highly mobile birds at high densities are more likely to fly into a survey site during the time when a point count is being conducted. If the species are not observed flying into the survey site they will be included in the point count and therefore the species will be over-represented. This problem is intensified when surveys are largely based on calls. In addition curious or island tame species may be more likely to be attracted to the observer. Although this may have resulted in a slight inflation of the abundance estimate, it is indisputable that the Boné de Joquei population is found at extremely high levels of abundance unparalleled on Príncipe.

Keys to persistence

Isolated island environments may provide conditions that enable some species to live at a level of super abundance and, therefore, greatly increase their probability of long term persistence within a restricted range (Manne *et al.* 1999) by mitigating the negative effects associated with small populations confined to a very small area. Such negative effects are environmental stochasticity (Gilpin and Soulé 1986; Lande, 1993), demographic stochasticity (Richter-Dyn and Goel, 1972; Pimm *et al.* 1988), and inbreeding and loss of selectable variation (Frankel and Soulé 1981; Soulé 1987). With a super abundant population the seedeaters on Boné de Joquei would be less susceptible to extinction due to periodic environmental influences such as storms (Spiller *et al.* 1998). In turn, this would decrease the chance of the population being reduced to a size that is susceptible to stochastic demographic extinction, bottle necks and inbreeding depression.

Avian competition

The low number of forest birds (four) on Boné de Joquei may have allowed the Boné de Joquei population to broaden its niche and access a greater proportion of the island's resources, a process known as density compensation, competitive release or density inflation (MacArthur *et al.* 1972; Crowell 1983; Blondel 1991; Manne *et al.* 1999). This is supported by the broad range of habitat types currently occupied by the Boné de Joquei subspecies. Most of the Príncipe species would have once been represented on Boné de Joquei, as it was part of the island of Príncipe c12,000 years ago. Why most of the Príncipe species were unable to persist on Boné de Joquei is unknown. We can only guess as to whether it was a process of competitive exclusion (Lack 1969, 1976), lack of appropriate habitat or resources, chance or a combination of the above. Ironically, it is likely that many of the local extinctions resulted in an increase of the seedeaters probability of long term persistence, as the absence of competitors may have enabled it to access a broader range of resources and sustain a higher population density.

It is unknown whether the presence of the abundant seedeater on Boné de Joquei restricts the successful colonisation and persistence of other species. However, it is interesting to note that the small birds from Príncipe that could be considered competitors, such as the Dohrn's thrush-babbler *Horizorhinus dohrni* or the Príncipe white-eye *Zosterops ficedulinus*, are not present, while the only other common forest birds on Boné de Joquei, the Príncipe golden weaver and the blue-breasted kingfisher, primarily focus on food resources outside of the seedeater's range, such as larger insects, snails and small birds (see Christy and Clark 1998).

Abundant food supply

Oil-palm fruit and seeds (de Naurois 1975) appear to be the most common food sources of the Boné de Joquei population; however, the other subspecies have been observed to forage on both fruits and insects (Christy and Clarke 1998). Such a generalist feeding strategy indicates that the seedeater may be able to access a much broader range of resources in the absence of competitors. Despite the negative or positive effects of competition, there must be an abundant food resource available in order for the seedeater to sustain such a high population density. The island's vegetative landscape prior to cultivation is unknown, but oil-palm is currently one of the most dominant trees on the island and may now be essential for the maintenance of their high population densities.

Mammalian predation

The population density of the seedeaters on Boné de Joquei may also be higher due to the lack of mammalian predators. The only potential predator observed on Boné de Joquei was the blue-breasted kingfisher, which has been documented to have eaten small birds on Príncipe (Keulemans 1866; Correia 1928-9; Snow 1950). São Tomé and Príncipe have a broad range of introduced mammalian predators (Dutton 1994) and some of these may be present on Boné de Joquei; however, there are a number of clues that indicate that destructive mammalian predators have not yet reached the island. First, the white-tailed tropicbird appeared to be nesting on the ground above 200 m altitude on Boné de Joquei. They were not observed nesting on Príncipe and on São Tomé they are only found in the mountain interior, presumably where mammalian predation is lower. Secondly, there is a large reddish land crab found at extremely high levels of abundance throughout Boné de Joquei but not common on Príncipe. The distribution of land crabs is often limited by mammalian predators (Hartnoll 1988). Finally, perching close to the ground and island tameness should be less common with the presence of mammalian predators.

Conservation

Habitat destruction, the most common threat to island birds (Stattersfield 1998), does not appear to be an imminent threat on Boné de Joquei. Conservation attention should focus on factors associated with the extremely high abundance of the Boné de Joquei seedeater population. I believe these factors are lack of avian competitors, abundant food supply, and lack of mammalian predators. However, further work is required to identify the dominant mechanism or mechanisms enabling super abundance. The island should be monitored on a periodic basis to assess if any potential avian competitors have become established. It is important to determine whether mammalian predators have been introduced to the island. If extensive trapping indicates that they have not yet been established or that there are few mammalian species, efforts should be made to educate the local fishing community and tourist operators about the importance of not transporting mammals to the island. Although the seedeaters have presumably survived on natural vegetation for thousands of years, cultivation in the last century and the introduction of non-agricultural exotics may have substantially changed the ecosystem dynamics. For example, succession of a single aged stand of oil-palm may lead to the sudden loss of food supply. We need to learn more about this species' feeding habits and requirements and monitor the island to ensure that there is an abundant food supply. A general conservation lesson can also be learned from the Boné de Joquei seedeater population. When conservationists are attempting to manage small isolated island populations that have already been disturbed they must consider that the population may have once existed at super abundant levels and such population densities may be essential for its future survival.

Conclusion

This study has confirmed that the Boné de Joquei population of seedeater is distinct from the Príncipe and São Tomé subspecies and has persisted on the small island of Boné de Joquei at least long enough to evolve different coloration and markings, and potentially unique ecological, and behavioural traits. I demonstrate that the Boné de Joquei population is found to be at least 10 times more abundant than its closest relative on Príncipe. The high level of abundance appears to be driven by lack of avian competition, abundant food resources, and absence or low species diversity of mammalian predators. I suggest that conditions specific to a small isolated island have enabled the seedeater to sustain a super abundance and, therefore, reduce its extinction probability by mitigating the negative effects of small populations, such as stochastic events and inbreeding depression. I recommend that conservation attention focus on the mechanisms driving super abundance to ensure that these conditions are maintained on Boné de Joquei. Conservation efforts should include monitoring the island for avian competitors or mammalian predators and ensuring that there is a continued abundant food supply. The study of this extremely restricted-range subspecies has demonstrated that all restricted-range species are not equal. Specific conditions of an isolated small island may allow a species to live at higher densities and persist for thousands of years within a range size that would not be possible under mainland or higher diversity conditions.

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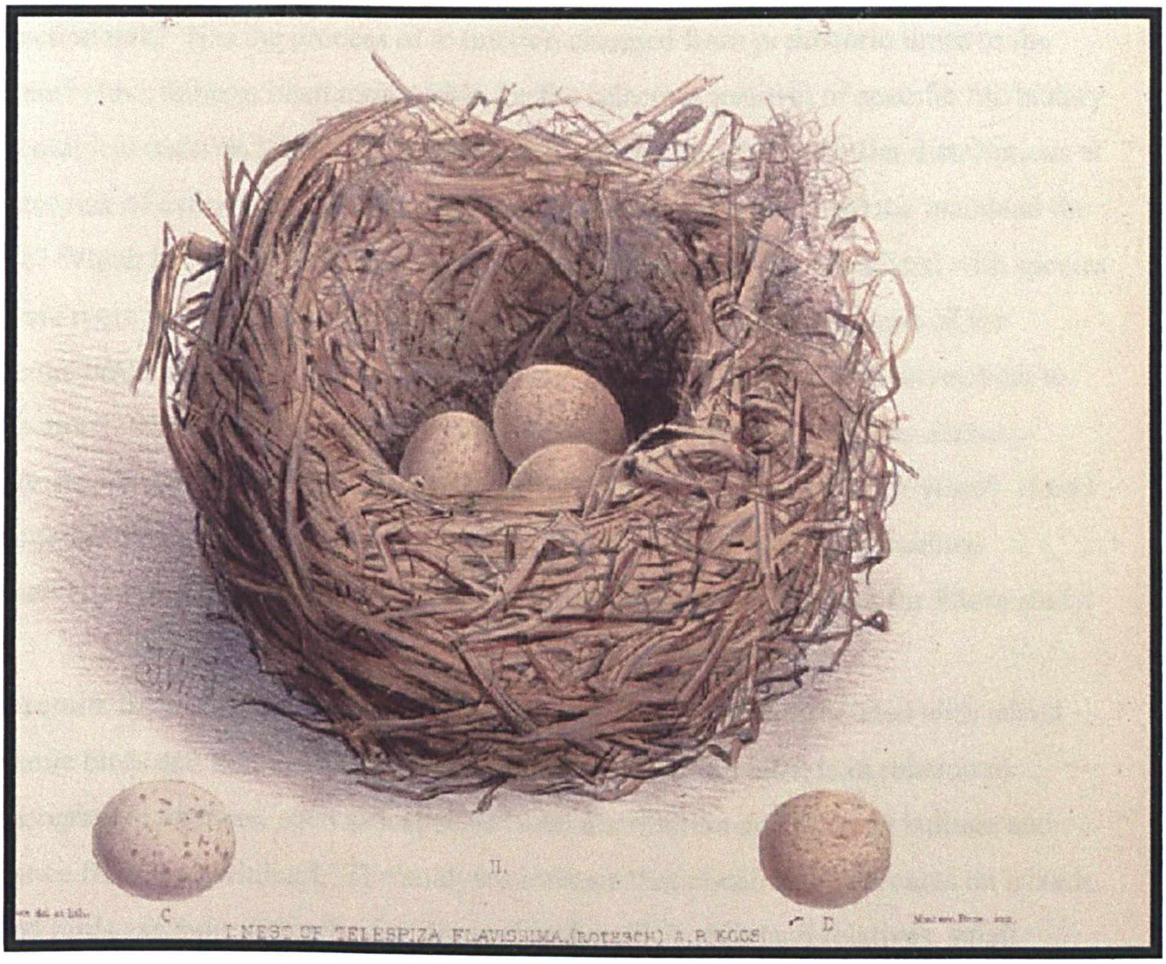
CONCLUSION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I. NEST OF TELESPIZA FLAVISSIMA, (ROTHSCH.) & A.B EGGS

The aim of this thesis has been to provide insight into the process of extinction on islands by exploring the extrinsic processes of extinction in relation to traits or conditions associated with persistence or vulnerability. I have addressed nine main questions in this thesis: Are there unique traits associated with island endemic birds? Have prehistoric human-caused extinctions influenced present patterns of avian extinction risk? Has the process of extinction changed from prehistoric times to the present? Have humans been responsible for the selective removal of specific life history or ecological traits on islands? Are island or mainland birds with similar distributions at greater risk of extinction? Are the extinction processes on islands and the mainland the same? Which life history, ecological, or morphological traits are associated with species that are more vulnerable to extinction? What is the status and distribution of the endemic birds of Príncipe and why has this community of species been so resilient to extinction? What traits or conditions have enabled the Príncipe seedeater *Serinus rufobrunnea fradei* to persist on an islet of less than 1km^2 for thousands of years? Here I summarise the main findings of the thesis, discuss the theoretical and practical conservation implications of the research, and outline interesting areas for future study.

The results from Chapter 2 indicate that there are unique traits associated with island endemic birds and that many of these traits also vary within islands in relation to biogeographic features, such as a species' total distribution and average latitude and distance from the mainland. The analyses indicate that clutch size decreases on islands, island birds are more sexually size dimorphic than their mainland relatives, small species tend to get larger on islands and there is a non-significant trend for large birds to get smaller. Within islands, clutch size decreases with a species total distribution and, for passerines, it increases with greater distance from the equator and decreases with distance from the mainland. It is also noteworthy that oceanic island endemic birds do not follow Bergmann's rule, as they are not larger in body size at greater distance from the equator.

Given that there are consistent differences between island and mainland species it is reasonable to assume that island endemic birds may respond in different ways to extrinsic threat processes. In some cases the differences may be associated with greater risk of extinction, such as the island trend toward the evolution of flightlessness (Diamond 1981; McNab 1994; Roff 1994). However, other traits may be neutral in terms of extinction risk, or reduce a species vulnerability to extinction. The traits that were demonstrated to consistently change in an island environment such as sexual body size dimorphism or clutch size were not associated with elevated rates of extinction (see Chapter 5). Many traits or conditions have been associated with island birds, but few have been rigorously tested. To understand more about island birds and why they may be particularly extinction prone or resilient we must establish which traits or conditions can be truly generalised. Research into trends on islands such as mating systems, parental care, fidelity, territoriality, nesting location, annual fecundity, age of maturity, longevity, survivorship, niche shifts, and density compensation would all greatly improve our understanding of the unique nature of island endemic birds. It would also be interesting to explore how these traits vary with different stages of endemism.

Analyses in Chapter 3 support the notion that endemic birds on islands that have been exposed to humans for a long period of time have experienced lower rates of recent extinction. This indicates that there have been 'extinction filters' (Coope 1995; Balmford 1996) whereby past threats have stripped out vulnerable species leaving a more resilient though less diverse species complement. Evidence of an extinction filter can be found in both the Pacific and non-Pacific. There is a similar, but much weaker relationship between the length of time an island has been colonised by humans and the proportion of species that are threatened with extinction. A closer examination of the threat processes indicates that birds on islands that have been colonised by humans for a long period of time are less threatened by the introduction of exotic species. No relationship is found between the extent of human colonisation and the proportion of species that are threatened by exploitation or habitat loss.

The examination of extinction filters enables us to infer important processes of extinction in the distant past and gain insight into whether the dominant processes of extinction have changed over time. If extinction processes in the distant past are similar to recent threat processes, then birds on islands that have been colonised by humans for a long period of time should now appear more resilient to extinction. If the dominant threat processes change or intensify, there may be no relationship between past resilience and present or future persistence. This is because new or more intense extinction processes are novel to all species. The strong relationship between the date of first human colonisation of an island with the proportion of species that have recently gone extinct, but weak relationship with the proportion of birds that are at present threatened, indicates that the dominant processes of extinction may be changing.

If species are more resilient to a specific threat process on islands that have been colonised for a long period of time, then the specific threat process was likely a significant cause of prehistoric human-caused avian extinctions. Thus, the introduction of exotic species was likely a dominant process of extinction when humans first colonised oceanic islands.

The analyses from Chapter 3 support that the first human colonists to oceanic islands have been responsible for extensive endemic bird extinctions on islands throughout the world and that the process of extinction has recently changed. The role of humans as an extinction filter is supported by subfossil records of extinct island endemics (Olson and James 1982; Diamond 1982, 1984, 1989; Cassels 1984; Olson 1989; Dye and Steadman 1990; Milberg and Tyberg 1993; Pimm *et al.* 1994; Steadman 1990,1993, 1995, 1998). The changing process of extinction, as well as the past importance of introduced species as an extinction process, are supported by the analysis in Chapter 1, demonstrating that recent extinctions were primarily caused by introduced species, but now habitat loss is becoming the dominant process of extinction (also see King 1985; Johnson and Stattersfield 1990; Collar *et al.* 1994; Stattersfield *et al.* 1998; Russell 1998; Simberloff 2000).

This study reinforces that researchers focusing on island endemic species must consider that the flora and fauna remaining today may only represent a small subset of what existed prior to the arrival of humans. It also demonstrates that it is important to have an understanding of historical extinction processes, as past causes of extinction can have a strong influence on present patterns of susceptibility. However, in the case of islands, as habitat loss intensifies, resilience to past extinction processes will have little influence on a species future probability of survival. Habitat loss is also a relatively non-selective extinction process (Russell 1998) which may function more as an extinction blanket than an extinction filter. For future studies of this nature it may be interesting to further refine categories of threat. For example, divide species threatened by introductions into those threatened by competitors and those threatened by predators, or divide species threatened by exploitation into species that are hunted for food and those that are collected for the pet trade.

The analyses in Chapter 4 indicate that species inhabiting oceanic islands that have been exposed to humans for a long period of time are less likely to be ground nesters, flightless birds, and non-forest specialists. There was no significant association when a species' clutch size or body size was considered. These analyses indicate that the presence of human-related threats has radically altered the selection regime on oceanic islands. Humans may have been responsible for the virtual eradication of specific traits of island endemic birds. Assuming this is true, endemic species found on islands today are not a random subset of those that existed prior to the arrival of humans.

If the traits most vulnerable to extinction are associated with higher levels of endemism, then a disproportionate number of the phylogenetically unique island species may have been driven to extinction. For example, flightless extinct species such as the dodo, moas or flightless waterfowl of Hawaii represented unique lineages. Many of the remaining flightless birds are also very unique, such as the kagu or kakapo. The findings from Chapter 4 also indicate that the traits associated with greater extinction risk may rapidly change as a new extinction process is introduced. For example, flightlessness or ground nesting may not have rendered a species at greater risk of extinction prior to the arrival of humans. Here only flightless or poorly flighted birds, ground nesting species, and non-forest-restricted endemics have been identified as traits that may be in the process of being filtered from the island system. It would be interesting to search for other traits that are also being selectively removed. Traits that may be of particular interest are sexually selected characteristics, mating systems, and specific guilds.

Chapter 5 demonstrates that there is no significant difference between the overall extinction risk of oceanic island and mainland birds, if species with similar distributions are compared. However, when the processes of threat are examined individually, island birds are significantly more threatened by introduced species. The analyses from chapter 3 and 4 in addition to the subfossil remains of extinct island endemic birds provide strong evidence that threat rates may now be similar simply because many of the vulnerable species have already been driven to extinction. The analyses conducted here compare island and mainland species with similar distributions. However, a more refined analysis with exact distributions for mainland species may provide greater insight into the processes of extinction for which island and mainland birds are particularly susceptible. The fact that island birds are disproportionately vulnerable to introduced species highlights the importance of introduced species eradication programs on islands in conjunction with greater controls on the transport and introduction of exotics (see Simberloff 2000).

The results from Chapter 5 also suggest that on oceanic islands, flightless species and habitat specialists are at present more threatened with extinction than other species. If only birds that have been exposed to humans for less than 1000 years are considered, then ground nesters and larger birds are also at greater risk of extinction. Regardless of whether species have or have not been exposed to humans for a long time, sexually size dimorphic birds, dichromatic species, and birds with a small clutch size are not associated with a greater probability of extinction.

Chapters 3, 4, and 5 suggest that we should think carefully before we make generalisations about extinction prone traits. The traits that we identify as extinction prone will depend on the specific threat process (Owens and Bennett 2000; Chapter 4) as well as the extinction processes that have taken place in the distant past (Chapter 3). Thus, traits that are associated with more vulnerable species in one region many not be applicable to another if the processes of extinction are different, or the extinction filters have acted on different temporal scales. We must develop a much more sophisticated understanding of the temporal and spatial relationship between process of extinction and traits associated with greater vulnerability if we wish to make sound predictions about which species will be the most vulnerable to future extinction.

Research carried out on Príncipe in the Gulf of Guinea suggests that two of the seven island endemic birds qualify as vulnerable to extinction, based on the IUCN Categories and Criteria (see IUCN 1994). The vulnerable species are Príncipe speirops *Speirops leucophaeus* and Príncipe drongo *Dicrurus modestus*, and have been classified as threatened based on their relatively small distributions. Two of the eight subspecies qualify as critically endangered (Olive Ibis *Bostrychia olivacea rothschildi* and Príncipe White-eye *Zosterops ficedulinus ficedulinus*) and one as vulnerable (Gulf of Guinea Thrush *Turdus olivaceofuscus xanthorhynchus*). No recent endemic bird extinctions have been documented on Príncipe, and the native island birds still remain the most abundant species on the island (Snow 1950). The endemic birds of Príncipe are extremely resilient considering that roughly one quarter of the endemic birds on islands off the coast of Africa have gone extinct over the past 500 years and that 42% of African island endemic birds are at present threatened with extinction (see Chapter 1).

Their resilience is even more remarkable given that most of the island was at one point under cultivation, virtually every mammalian predator that has been a menace on oceanic islands has been introduced to the island, and many of the endemic birds have been subject to human exploitation.

The key to their persistence appears to be a combination of biogeographic features and land-use history. First, Príncipe is relatively close to the mainland (220 km) which may result in a greater species area relationship than exists in equivalent, more distant islands, as well as greater exposure to migrants or vagrants. This would result in the island endemics having greater evolutionary experience with competitors, predators, and disease than species on more remote islands or archipelagos. Greater extinction risk on more remote islands is supported by the analysis in Chapter 3. Second, the thick rainforest environment provides excellent cover and nesting sites that may reduce species susceptibility to introduced predators. Observations in the rainforest also indicate that human commensal predators are much less abundant in this environment. Third, the agricultural transformation of the landscape resulted in the removal of much of the native vegetation, but crops such as cocoa maintained a forest structure. Fourth, the land use history of Príncipe is relatively unique. Most of the island is now covered in thick tropical rainforest, but at the beginning of the 1900s only the mountain forest and a small section of the southern lowlands remained uncultivated. In the early 1900s, the mountain forest and the southern lowlands likely served as a refuge, providing native habitat and an environment with reduced predation by introduced predators and human exploitation. If the land use history of Príncipe followed that of most other oceanic islands, the present threatened status and the number of recent extinctions of the avifauna would undoubtedly be similar.

This case study suggests that island endemic birds may be extremely resilient to extinction if their native habitat is maintained and they have had at least limited historic exposure to competitors, predators, and disease. This reinforces the point that conservationists' main objective should be to maintain and regenerate native habitat on oceanic islands, and on remote islands to focus more energy on the eradication or reduction of introduced competitors or predators. It is rarely a viable option to conserve island endemic birds without their native habitat. Such conservation efforts often lead to expensive and unsustainable strategies such as captive breading and supplementary feeding. If we are serious about maintaining viable endemic bird populations into the distant future, then we need to focus on protecting species for which adequate habitat remains or can realistically be regenerated.

Chapter 7 demonstrates that the Príncipe seedeater *Serinus rufobrunnea fradei,* located on Boné de Joquei in the Gulf of Guinea, is found in all habitat types on the island and has an extremely high population density. Competitive release and or density compensation are often observed in island endemic bird populations (Crowell 1962; MacArthur *et al.* 1972; Blondel 1991) and may help to explain why many island birds are able to persist within extremely small distributions (Manne *et al.* 1999). Higher population densities will reduce a species risk of extinction due to environmental or demographic stochasticity as well as the negative genetic effects associated with small populations. Density inflation and or density compensation may be dependent on few competitors, few predators, and an abundant food supply. Understanding and managing for the driving mechanisms that allow for higher population densities may be essential for the future survival of many restricted-range island endemic populations.

It would be useful to have a better understanding of the extent to which elevated population densities occur on oceanic islands. However, it is important to note that the introduction of predators or competitors to islands may have greatly reduced the occurrence of this phenomenon. Many species on small oceanic islands may not appear particularly threatened because they have average population densities. Such species may be overlooked by conservationists, while in actuality, their long-term persistence is greatly compromised by the recent loss of super-abundance.

The results form this thesis suggest that (1) there are convergent life history or morphological trends that occur when species become endemic on oceanic islands; (2) patterns of prehistoric human-caused extinctions influence the areas where recent extinctions have occurred, but will have little influence on where future extinctions take place; (3) extinction processes are changing on islands, as many of the species that were particularly prone to introductions are now extinct and habitat destruction has recently intensified; (4) species with specific life history or ecological traits may have been selectively removed from oceanic islands by human-related threats; (5) extinction risk is similar for oceanic island and mainland species when species with similar distributions are compared; (6) the processes of extinction are similar on islands and the mainland, but island species are particularly vulnerable to introduced species; (7)

oceanic island birds that are flightless, ground nesting, large bodied or forest restricted may be at greater risk of extinction than other birds; (8) the resilience of the endemic birds of Príncipe may be associated with the unique land use history, rainforest habitat and their relatively close proximity to the mainland; (9) super abundant population densities may be essential for the long term persistence of birds on small isolated islands. The aim of this thesis has been to further our understanding of the process of extinction occurring on oceanic islands and it is hoped that the research presented here will have both theoretical and practical applications for the conservation of island-endemic species.

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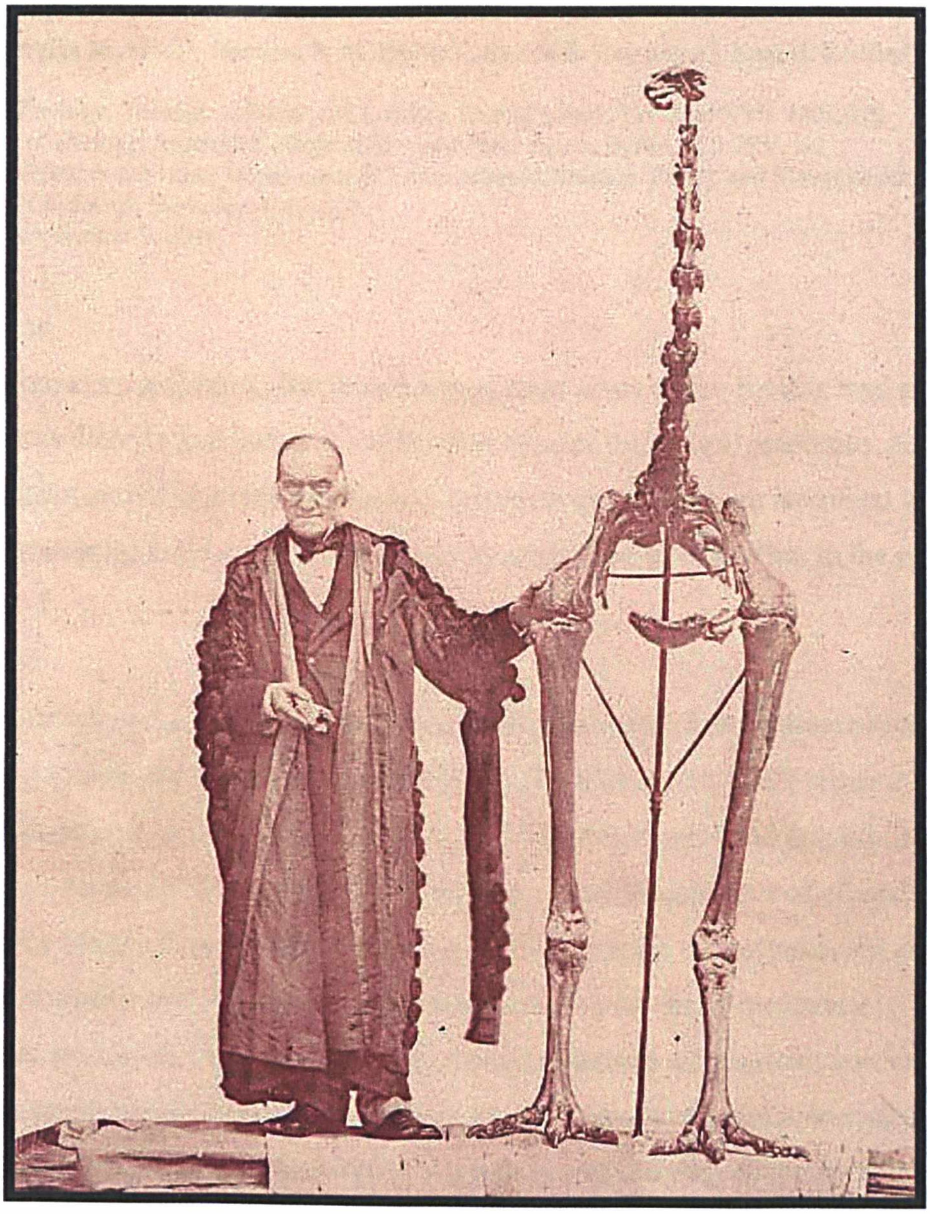
Appendix



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ASSESSMENT AND MANAGEMENT OF SPECIES AT RISK

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Introduction

A massive human population, distributed across most areas of the Earth's land surface, now competes directly and indirectly with other species for natural resources. As a result of human activities many species have gone extinct, others are restricted to tiny islands of remaining habitat, and still others are committed to extinction in the near future.

For still larger numbers, the future looks extremely uncertain. Recent assessments of the global conservation status of species (IUCN 1996, Oldfield *et al.* 1998) suggest that more than 10 percent of birds and around 20 percent of mammals and amphibians are now threatened with extinction (table 2). Comprehensive assessments of all native U.S. species by the Nature Conservancy show that over 60 percent of molluscs and crayfish, 40 percent of freshwater fishes and amphibians, and 50 percent of freshwater invertebrates are at risk. Extinction risk also is demonstrably nonrandom; species within some phylogenetic clades tend to have higher or lower levels of extinction risk than across taxa as a whole, thereby increasing the loss of evolutionary diversity from species extinctions (Russell *et al.* 1998, Purvis *et al.* 2000a). Extinctions are also nonrandom with respect to the ecological roles that species play, so that loss of species will have an impact on ecosystem and community (Jernvall and Wright 1998).

The situation is more serious still for some taxonomic groups in especially vulnerable habitats. Certain dramatic evolutionary radiations have been almost completely eliminated. For example, until the mid-1980s over 120 land snail species of the snail family Partulidae were distributed across the islands of Polynesia; almost all are now either critically endangered or extinct as a result of the introduction of a predatory snail (Mace *et al.* 1998). The introduction of the Nile perch (*Lates niloticus*) to Lake Victoria in East Africa has now led to the extinction of up to 200 species of haplochromine cichlid fishes that once formed a unique "species flock" with extraordinary levels of morphological, ecological, and behavioural specializations. These examples illustrate the intensity and potential of the current extinction spasm.

From the perspective of a research agenda, we need to analyze the causes and understand the processes that ultimately lead to species extinction, and thus identify methods and approaches to mitigate the problem. In this chapter we review some key issues for the assessment and management of species at risk.

Processes Leading to Extinction: Habitat Loss, Overexploitation, and Introduced Species

Species have always gone extinct. The fossil record bears testament to the extinctions of both species and entire evolutionary radiations, and extant species probably represent only about 2-4 percent of all species that have ever lived (May *et al.* 1995). The fragmentary nature of the fossil record makes direct comparison of ancient extinctions with modern extinction problematic (Jablonski 1995). Most paleontological data come from marine invertebrates, usually of abundant and widespread taxa, while modern extinctions have mostly been cataloged for terrestrial vertebrates, many of which were relatively rare and narrowly distributed. Some authors have suggested that, based on the average persistence time of species in the fossil record of between 0.5 and 10 million years, the current extinction rate may be from 100 to 1,000, and perhaps 10,000, times higher than background extinction rates (May *et al.* 1995, Pimm *et al.* 1995).

Extinction rates have varied throughout the fossil record, with noticeable peaks during periods of mass extinction (Jablonski 1991, Benton 1995, May *et al.* 1995). The rates that we expect over the coming centuries may begin to approach the most severe periods of extinction in the earth's history (Jablonski 1995). Unlike the mass extinctions of the past, however, the driving processes are not attributable to abiotic geological changes nor extraterrestrial impacts. Instead, the direct and indirect causes are almost entirely due to human activities. Our analysis of the nature of extinctions must therefore start with a consideration of these ultimate driving processes.

The major processes leading to extinction are anthropogenic and result from habitat loss, overexploitation, introduced species, and the interactions among these (Diamond

1989). These processes may be regarded as the extrinsic drivers, the ultimate causes of extinction as described by Simberloff (1986), or the agents behind the "declining population paradigm" described by Caughley (1994).

Habitat loss is probably the most common problem, especially for continental species (WCMC 1992, Mace and Balmford 2000). Human population growth and development lead to the appropriation of extensive areas of land for settlement, agriculture, and resource extraction, and the infrastructure to support these activities causes further loss and fragmentation. Habitat loss does not just imply clearance but also all kinds of degradation and fragmentation that limit the potential for wild species to persist. Over large continental areas, for example in northwest Europe and eastern North America, natural habitats are now reduced to a tiny proportion of their historical extent, and many of the land areas set aside for wildlife are degraded and left for conservation management largely because they are unsuitable for development. As the patches of remaining habitat become smaller and more isolated, the species living within them are more likely to go extinct and individuals from neighboring patches are unable to immigrate to repopulate the patch. In eastern North America, species extinctions have been recorded at a rate consistent with simple models concerning the effects of habitat loss (Pimm and Askins 1995). Other regions, such as the species-rich eastern coastal forests of Brazil, which have endured relatively recent yet extensive clearance, have so far suffered few recorded extinctions. However, there are large numbers of species restricted to small remaining patches of forest which, though not extinct, appear to have very bleak prospects (Brooks and Balmford 1996). Following their isolation in habitat remnants, species may persist for some time before finally succumbing, (Brooks *et al.* 1999, Cowlishaw 1999) perhaps giving us too optimistic a view of the eventual impact of our current activities.

Overexploitation can take a variety of forms, from large-scale commercial extraction of fishes and forests to local, subsistence hunting. There are often limited controls to the access to wildlife resources providing little incentive to manage the resource sustainably (Hardin 1999). This creates competition that is hard to regulate efficiently, even when there are technical and financial resources to do so (Ludwig *et al.* 1993). Despite extensive research into methods for sustainably harvesting natural populations, there are still many difficulties in estimating key parameters and implementing and enforcing management plans (Ludwig *et al.* 1993, Lande *et al.* 1994). As a result, for example, although the total commercial catches of marine fishes have been relatively constant over the last few decades, FAO data show a shift in catch records from long-lived, high trophic level, piscivorous bottom fish toward short-lived, low trophic level invertebrates and planktivorous pelagic fish. These trends signal unsustainable exploitation of marine resources and seem likely to have both direct and indirect impacts on oceanic food webs and communities (Pauly *et al.* 1998). Indeed, several commercially exploited fish species now show continuing declines in abundance despite international agreements to control their harvest rates (Cook *et al.* 1997, Myers *et al.* 1997, Matsuda *et al.* 1998). Large, long-lived, and slowly reproducing species appear to be the most vulnerable to declines from commercial fishing, (Jennings *et al.* 1998) and one such species, the barndoor skate (*Raja laevis*), now appears to be close to extinction (Casey and Myers 1998).

At more local scales, overharvesting for food, fuel wood, pets, ornaments, and trophies continues to threaten many species. Although international agreements limit the trade in wild species among countries, there are difficulties in controlling exploitation within countries, especially where the wildlife products are of high commercial value (e.g., elephants (Milner-Gulland and Beddington 1993)). Many wild species are also unsustainably harvested in tropical forests as a source of protein (e.g., neotropical vertebrates; Alvard (1997)). For bushmeat there is a serious threat to many wildlife species because the characteristics that make species attractive as a source of protein, such as large body size, also make the species especially vulnerable to overhunting (Robinson and Redford 1991).

Introductions and translocations of species to areas outside their natural ranges are now, and have been, a major driver of anthropogenic extinctions. Many species, especially in areas that have been settled by people from distant lands, have already been driven extinct by introduced species. Pimm *et al.* (1994) estimate that the Polynesians wiped out 500 to 1,000 bird species in their early explorations across the Western Pacific, and introductions continue to pose a serious threat to island species (WCMC 1992). Similarly, the Australian mammal fauna has suffered directly and indirectly from introduced species, especially European native species brought by early settlers (Burbidge and McKenzie 1989). The highly diverse endemic plant radiation of the Cape Floristic province of South Africa is threatened by both invasive species and land use changes. Successful invasive species generally tend to be short-lived, with high intrinsic rates of increase, i.e., early successional species. Although they outcompete native species in the short term, over the long term, the ability of some invasive species to persist may be limited. In contrast, the species that are most susceptible to the effects of introduced species are those that inhabit isolated regions and occupy habitats that have been heavily modified by anthropogenic influences, (Godfray and Crawley 1998) where they may suffer population declines and extinction from competition, predation, or hybridization.

Consequences of Extrinsic, Human-caused Perturbations

A species' vulnerability to extrinsic threats is often influenced by its ecology, life history, physiology, or distribution. Intrinsic characteristics of extinction-prone species have been more thoroughly investigated by research biologists than have the effects of the external drivers and the interactions between the two (Caughley 1994), leading to some debate about the relative importance of each. However, it is clear that both factors should be considered if we are to improve the reliability of predictions about extinction risk (Hedrick *et al.* 1996, Beissinger and Westphal 1998).

Several kinds of evidence provide information about the most vulnerable species. First, empirical studies have identified intrinsic characteristics of extinction-prone species. Rates of local extinction have been shown to be higher for species that have restricted ranges or occupy a small number of sites (Hanski 1982, Simberloff and Gotelli 1984, Thomas and Mallorie 1985, Happel *et al.* 1987, Gaston 1994, Gaston and Blackburn 1996, Gaston and Chown 1999), are local endemics (Terborgh and Winter 1980, Cowling and Bond 1991) or have low abundances, high temporal population variability, and poor dispersal (Karr 1982, Diamond 1984, Pimm *et al.* 1988, Newmark 1991, Gaston 1994). These studies are all open to the criticism that they may only be investigating correlates of extinction-prone characteristics, since body size, dispersal ability, range size, population variability, and local population density are all interrelated (McArdle *et al.* 1990, Pimm 1992, Gaston 1994, Gaston and Blackburn 1996). In studies where interrelationships among life history traits and the geographical sampling can be controlled, extinction risk has been shown to be higher for species with low population density, small range size, and habitat and diet specializations (Foufopoulos and Ives 1999, Purvis *et al.* 2000b). The response of a species to a threat is complicated and depends on its life history, the local environmental conditions and the specific perturbation. For example, the stability of fluctuating populations is reduced by exploitation; (Beddington and May 1977), the response of primates to logging is a function of their home range size and the latitude at which they live (a correlate of habitat variability); (Harcourt 1997) and extinction of carnivores within reserves is higher for those with large home ranges (Woodroffe and Ginsberg 1998).

Second, there are some useful insights from ecological and life history theory. It can be shown that small populations are more extinction-prone because of their susceptibility to demographic stochasticity (Richter-Dyn and Goel 1972, Goodman 1987), the increased expression of recessive deleterious alleles under inbreeding (Soulé 1980, Soulé and Mills 1998), the change in quantitative characters that allow adaptation, and the accumulation of mildly deleterious mutations (Hedrick and Miller 1992, Frankham 1995a).

Lande (1998) has reviewed these various processes in terms of the minimum viable population sizes that they imply. This has shown that demographic stochasticity is unlikely to be important for any population that has more than one hundred individuals, but random environmental variation or catastrophes are important for populations of all sizes, and they become more significant as environmental variability becomes large in relation to the population growth rate (Lande 1993).

In terms of genetic effects, deleterious recessive alleles become more likely to be expressed when populations are reduced in number. The resulting inbreeding depression may increase short term extinction probabilities for Ne's up to 50 – 100 (Mills and Smouse 1994, Allendorf and Ryman in press), translating to effects on actual population size in the range of 200 to 500 individuals (Soulé *et al.* 1986, Mace and Lande 1991, Frankham 1995b). To preserve quantitative trait variation, larger populations are needed. One estimate is that to maintain high levels (more than 90 percent) over thousands of years will require minimum effective population sizes of at least 5,000, and to prevent the accumulation of mildly deleterious mutations over tens of thousands of years will require minimum effective population sizes of around 10,000 to 100,000. Because of difficulties in estimating key parameter values for these calculations (Franklin and Frankham 1998, Lynch and Lande 1998), the critical population sizes from these theoretical studies are best interpreted as guides to the relative importance of different characteristics rather than real thresholds for management (Lande 1998). Moreover, this approach is deficient because it lacks a treatment of the feedbacks between genetics and demography (Soulé and Mills 1998).

Our analysis of the extrinsic and intrinsic factors associated with increased extinction risk has covered much of the field of ecology and evolutionary biology. In order to identify key questions, we now analyze issues that are of practical significance for conservation practitioners.

Critical Gaps in Knowledge

In discussing the critical gaps in our knowledge about how to protect species at risk, we examine six major areas. Research priorities for these six areas are given in table 1. The research areas are:

- Patterns of species at risk
- Dynamics of threatening processes
- Dynamics of population persistence in a changing world
- The effectiveness of different management strategies
- Conservation in practice
- Adaptive management monitoring

Each of these subjects is discussed below, and pertinent research questions are identified. First we discuss research questions, then move on to management actions.

Research Questions

1. Identifying Patterns of Species at Risk

The first set of research questions requires an analysis of patterns - a simple accounting of where the most species are located and what their relative risks of extinction, endemism, and diversity are. Along with patterns of biodiversity it is important to document the distribution and intensity of dominant processes of threat throughout different regions of the world. The above issues are particularly relevant to the design of networks of protected areas (Soulé and Terborgh 1999). This approach has been widely explored and used for planning at both global and regional levels. Through such studies, high-priority areas, habitats, and ecosystems have been identified and targeted for action (Myers 1988, Myers 1990, Pressey *et al.* 1993, Beissinger *et al.* 1996, Williams 1998). Species are not distributed evenly over the earth's surface and neither are the centers of richness, endemism, or threat particularly well correlated across taxa (WCMC 2000), especially in certain regions such as the United Kingdom and South

Africa (Prendergast *et al.* 1993, vanJaarsveld *et al.* 1998). In other areas, there are higher congruence patterns of species' complementarity among sites, such as forest patches in Uganda (Howard *et al.* 1998). In general, however, the concordance among diversity, endemism, and threat--three different measures of the conservation importance of an area--also varies with scale and location (Balmford and Long 1995, Kershaw *et al.* 1995) and presents some difficult choices for those setting conservation priorities (Margules *et al.* 1988, Pressey *et al.* 1996).

2. Dynamics of Threatening Processes

Analyzing patterns provides only a partial solution. The viability of populations and species ultimately depends upon population and evolutionary dynamics. Within any particular area, species will not share similar future prospects. Those that are highly adaptable (genetically, behaviourally, or both), have good dispersal abilities, or with populations whose prospects are more favorable will be expected to have enhanced viabilities. Therefore, we consider the dynamics of threatening processes and their likely impact upon affected species.

3. Dynamics of Persisting in a Changing World

A simple consideration of threatening processes reveals that these change in nature and intensity over both time and space--sometimes at alarming rates. This is one reason why analyses of patterns do not provide a sufficient basis for management (Smith *et al.* 1993, Balmford *et al.* 1998). Our third set of research topics considers studies on how species at risk can cope with dynamic change.

Currently, dynamic changes are accentuated as a result of the rapid human population expansion. Numbers are still increasing rapidly, although at different rates in different areas of the world (Cohen 1995). Globally, human numbers are expected to double over the next 60 years (McNeely *et al.* 1995). While some regions, such as Europe and North America, are expected to meet their resource needs without further land conversion for agriculture, many other areas are still undergoing rapid development alongside high population growth. Food requirements may double in Central and South America and Asia, and perhaps increase fivefold in Africa (WCMC 2000). Land use changes will therefore proceed inexorably in some areas of high biodiversity. This demand, and its likely impact on wild species, needs to be understood and managed if conservation activities are to be successful. Even in more stable areas of the world, changing patterns of work and leisure are leading to migrations from urban to rural areas, with significant consequences for land use planning. Habitat loss and fragmentation will continue but at different rates and in different ways than in the past.

One of the difficulties with the dynamic nature of land changes is that past trends are often not a reliable predictor of the future. Human activities also present a new challenge in the form of global climate change. Current predictions about changes in average temperatures suggest that the impacts will vary regionally and across habitats. There may be profound influences on marine ecosystems, which could experience an increased frequency and intensity of oceanic perturbations with consequences for many marine fish and corals. Global patterns of seawater circulation are expected to alter as a result of increased surface temperatures, which may have consequences for sea levels and for climate in both island and continental areas. Some parts of the land surface, especially temperate and arctic zones, are expected to face large temperature changes, and there is already evidence that European bird and butterfly species ranges are shifting to higher latitudes and the animals are altering egg-laying dates in response to current warming trends (Crick and Sparks 1999, Hill *et al.* 1999, Thomas and Lennon 1999). Under systematic warming, species persistence will depend on a different set of traits than those that offer high fitness in more stable habitats. All this underlines the importance of studying and understanding the spatial, temporal, and adaptational characteristics of species. For example, a study of a forest savannah in Cameroon indicated that, although ecotones have generally been regarded as unimportant areas, natural selection operating on birds in the ecotone may be important for generating evolutionary novelties (Smith *et al.* 1993).

Management Actions

The final three groups of research priorities discussed below focus on ways to use knowledge gained from research in the development, implementation, and assessment of management activities. Many conservation practices have been tried in the past, some with much more success than others. Unfortunately these experiences are often poorly documented and knowledge disappears with the people who were responsible for it. There is a need for a more systematic approach to analyzing and synthesizing alternative approaches.

4. Assessing the Effectiveness of Different Management Strategies

In this section, we focus on the more biological aspects of management at both the population and ecosystem levels. Fundamental principles from population biology were first developed a couple of decades ago (Soulé 1987). There are now a variety of ever more sophisticated techniques for population management that incorporate environmental and human processes in various forms of Population Viability Analysis (PVA) (Boyce 1992, Burgman *et al.* 1993). While some empirical evidence suggests that these models are reliable predictors of future population trends (Brook *et al.* 2000), it is unclear how robust they are as management tools when vital rates are well known (Fieberg and Ellner 2000), let alone under uncertainty and catastrophic change (Mangel and Tier 1994, Ludwig 1996), and it is also unclear how best to incorporate many different variables and their interactions into such models (Beissinger and Westphal 1998).

5. Conservation applied

Culture and place affect the choice of conservation tactics. For example, the United States has strong species-based legislation that provides protection for the habitats of listed species in their native areas, whereas in Australia and New Zealand translocations, introductions, and reintroductions have been extensively used for some highly endangered species (Serena and Williams 1994). The role of captive breeding has been widely debated (Hutchins *et al.* 1995, Balmford *et al.* 1996, Snyder *et al.* 1996). The practitioners of many regions focus conservation efforts on the design, implementation, and management of protected areas and reserves (Soulé and Terborgh 1999). In a rapidly changing environment and landscape it is increasingly difficult to design protected areas that will be efficient in the future. Placing reserves at natural landscape scales with edges at natural boundaries should be efficient (Peres and Terborgh 1995), but the designs and configuration of reserve areas may need to be altered to cope with systematic environmental changes, especially climate change.

We recognize both the challenges and benefits associated with local human communities whose immediate needs and aspirations may conflict with those of biodiversity conservation. While some apparent conflicts are illusory, in other cases strategies and approaches can be taken that will be more effective at achieving multiple short- and long-term goals. It is in this area in particular that conservation biologists must move into more interdisciplinary scientific communities and work with economists, sociologists, land planners, and human demographers to achieve effective results.

6. Adaptive Management and Monitoring

A long-term approach to management that includes both monitoring, analysis of actions, and adaptive management is important. Once management plans are in place, evaluate the predetermined goals and objectives regularly; if the actions are not proceeding according to plan, then the reasons need to be identified and alterations made (Margoluis and Salafsky 1998). For effective adaptive management, a great deal of planning must be undertaken at the start, with agreement among various stakeholders about what the indicators of altered management might be. Biologists should play an active role in such planning to ensure that the biological principles at the heart of any management plan are not compromised as implementation proceeds.

Table 1. Research Priorities

Identifying Patterns of Species at Risk

(1) Which regions, habitats, taxa, and species are most threatened or soon will be?

(2) What are the major processes threatening biodiversity and where are they currently focused? How do these processes change over time and space?

(3) What are the current population trends of species in different locations? Can a valid index of community or ecosystem health based on many species and processes be developed?

(4) What do studies of recent and historical correlates among extinction rates, anthropogenic processes, and biological features of species indicate about simple measures that can be used to direct conservation activities? What is the evidence that extinction filters, selective processes of past extinction, have already stripped out vulnerable taxa and communities? Can such knowledge ensure that conservation efforts be directed toward systems that have been less exposed to threats and are therefore more vulnerable to them?

(5) Can habitat loss be used as a surrogate to estimate rates of extinction? If so, how will factors such as species richness, habitat type, and latitude influence the calibration?

(6) Are indicator, keystone, or flagship species effective conservation monitoring tools, and if so, which species or complex of species best represent the status of a larger system?

Dynamics of Threatening Processes

(1) How do aspects of species ecology, behaviour, genetics, phylogenetic status, and life history affect a species' ability to acclimate and persist in response to the following: habitat loss, fragmentation, and modification; introduction of exotic species; exploitation for sustainable use; introduction of new diseases; and other anthropogenic threats and disturbances?

(2) To what degree do extinction lag effects inhibit the identification of species that are at great risk of extinction?

(3) What determines when extinction is the endpoint of a decline? Are species that have successfully adapted to the human landscape simply behaviourally preadapted, or are some species better able than others to adapt through learning?

(4) What are the best methods for diagnosing population decline? Experimental and comparative methods for diagnosing causes of population decline need to be developed and tested.

(5) How important are cumulative threats to the persistence of species? What kinds of interactions between threats are the most severe?

(6) What combination of spatial patterns and biological or physical factors (i.e. nutrient balance, rarity, and abundance) are the most efficient and useful indicators of changing population and ecosystem processes?

(7) Can new approaches, such as molecular genetic methods, be used to obtain rapid insight into a species' population dynamics when long-term data are lacking?

Dynamics of Persisting in a Changing World

(1) What determines variation in the resilience of communities or ecosystems? How is it affected by recent isolation, species richness, trophic level distribution, alien species, humidity, latitude, niche occupation, life history, functional redundancy, and keystone species?

(2) How do population dynamics and persistence vary in relation to life history attributes, population structure, environments, and phylogeny? How are habitat types and ecological factors such as ecotones, marginal habitats, niche availability, or the edge of a species range associated with persistence?

(3) How much and at what spatial scales does demography vary within a metapopulation and across landscapes? Can sources and sinks be identified given their true definitions? How often do different types of metapopulations and source-sink dynamics occur in nature?

(4) What is the relative importance of demographic and environmental stochasticity in affecting extinction compared to biological features of species and anthropogenic factors?

(5) To what degree and under what conditions does genetic variation influence demography and persistence? How does inbreeding in small populations affect persistence? How does outbreeding depression affect persistence in admixed populations? What is the relative importance of gene flow versus local adaptation for population persistence? How does genetic architecture of a trait influence its potential for adaptive change?

Management Actions

Assessing the Effectiveness of Different Management Strategies

(1) How can the models used in decision-making be improved? What is the appropriate context for use of Population Viability Analysis (PVA), decision analysis, and other analytical techniques that are intended to guide managers?

(2) How should reserves be designed to reflect dynamic landscapes? How large need reserves be so that difficult and expensive management regimes are not required to replace former ecological processes?

(3) What conservation strategies maximize both species and community conservation and fulfill specific human needs? When is it best to focus conservation resources on strictly protected areas versus integrated land use areas? What are the biological and economic costs and benefits of strategies that focus on prevention versus cure? What are the biological and economic costs and benefits of focusing on reversible threats and species that can be saved while rejecting difficult cases, compared to focusing on saving the most threatened first (i.e., triage approaches)?

(4) How useful are rules of thumb for conservation planning and population viability assessment? Can they be tested using a combination of modeling techniques and empirical studies?

(5) What are the biological and economic costs and benefits of captive breeding, reintroductions, and translocations? How frequently does adaptation to captive propagation prevent successful reintroductions of plants and animals? How can the process of domestication and adaptation be reversed in captive animal and plant populations?

(6) What incentives can be used to encourage conservation organizations to share information and pool resources for common projects?

Conservation in practice

(1) What are the most useful approaches to involve local communities in conservation projects? What can we learn from projects that have and have not been successful in accomplishing this? How can we ensure that local support for conservation projects is sustainable over long periods of time?

(2) What organizational models lead to improved implementation, coordination, and scientific direction of endangered species recovery programs?

(3) How can we plan protected areas and other management units so that they require minimal long-term management, or political and social controls?

Adaptive Management and Monitoring

(1) How should managers monitor, assess, and disseminate results of conservation projects? What can be learned from implementation of management recommendations that should feed back into the research agendas and future planning options?

(2) What aspects of structure, power, and authority in governmental and nongovernmental organizations enhance or decrease the implementation of adaptive management approaches in decision making?

(3) How can management interventions be structured to test theory and collect data to learn from crises?

(4) Where should assessment and monitoring be targeted--individual organisms, populations, subspecific units and species, or assemblages of species that are grouped by habitat, ecoregion, phylogeny, or functional criteria? What are the economic and biological consequences of adopting any one of these for a specific instance?

Table 2. Summary results of the application of IUCN criteria to various higher taxonomic groupings. The approximate number of species assessed is estimated from IUCN (1996) and Oldfield *et al.* (1998). The figure in parentheses indicates the proportion assessed of the total species diversity on the group. Since assessors may focus on the most threatened species, and on those that are well known, the threat and data deficiency rates may become more unrepresentative as the proportion of species assessed decreases.

Taxon	Approximate number of species assessed (percent total)	percent threatened of those assessed	percent DD of total assessed
Mammals	4763 (100 percent)	23 percent	5
Birds	9946 (100 percent)	11 percent	1
Reptiles	1480 (20 percent)	17 percent	5
Amphibians	600 (12 percent)	21 percent	7
Molluscs	>3000 (4 percent)	31 percent	18
Trees	10,091 (?0.1 percent)	59 percent	4

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A new species of freshwater crab (Brachyura: Potamoidea: Potamonautidae)from Príncipe,Gulf of Guinea, Central Africa

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Synopsis

A new species of freshwater crab of the genus *Potamonautes* Macleay, 1838 is described from Príncipe (Democratic Republic of São Tomé and Príncipe), an island in the Gulf of Guinea off the coast of Central Africa. The specimens were collected during a recent zoological expedition by the Zoological Society of London. This is the first record of the occurrence of freshwater crabs on the island of Príncipe.

Introduction

The freshwater crabs reported on here were collected during a zoological expedition to the island of Príncipe, made recently by the Zoological Society of London. The island of Príncipe, together with the island of São Tomé, constitute a small independent republic (The Democratic Republic of São Tomé and Príncipe) in the Gulf of Guinea. Príncipe is the second in a chain of islands that make up the Atlantic Ocean Islands group, that lies off the coasts of Cameroon, Equatorial Guinea and Gabon. The other islands in this group are Bioko, São Tomé and Annobon. Bioko is closest to the mainland and has two species of freshwater crabs, *Sudanonautes floweri* (De Man, 1901) and *S. granulatus* (Balss, 1929), both of which are also found in nearby Cameroon (Cumberlidge, 1993, 1995, 1999). São Tomé is the third island in the group, and has one species of endemic freshwater crab, *Potamonautes margaritarius* (A. Milne-Edwards, 1886). There are no records of freshwater crabs occurring on Annobon, the fourth island in the chain, and the furthest from the mainland.

Until the present report freshwater crabs were not known to be present on Príncipe. The new species from Principé was observed in streams, and collected in cloud forest in the remote roadless highlands. The new species is compared to *Potamonautes anchietae* (Brito-Capello, 1871) and to *P. margaritarius*, but differs from each in a number of important characters (Bott, 1953, 1955, 1964). Although the specimens from Príncipe are both subadult females, and ideally an adult male is needed to make a definitive identification, a preliminary description is provided here, based on several unique somatic characters of the specimen. Characters of the gonopods, male abdomen, and male chelipeds will be described when more material (including an adult male) becomes available.

Figures were prepared using a *camera lucida*, and the specimens were deposited in the Natural History Museum, London, U.K. (NHM). Abbreviations: cw, distance across the carapace at the widest point; cl, carapace length measured along the median line, from the anterior to the posterior margin; ch, carapace height, the maximum height of the cephalothorax); fw, front width measured along the anterior margin; s, thoracic sternite; e, thoracic episternite; s4/s5, s4/s5, s5/s6, s6/s7, s7/s8, sternal sulci between adjacent thoracic sternites; s4/e4, s5/e5, s6/e6, s7/e7, episternal sulci between adjacent thoracic sternites and episternites; P1-P5, pereiopods 1-5, a1-a6, abdominal segments 1-6, a7, telson of the abdomen.

Systematic account

Family Potamonautidae Bott, 1970

Genus ***Potamonautes*** Macleay, 1838

Potamonautes principe sp. n.

(Figure. 1, 2)

Diagnosis

Postfrontal crest straight, smooth, spanning entire carapace, ends meeting anterolateral margins at epibranchial teeth. Exorbital tooth small, pointed; epibranchial tooth represented only by small granule; anterolateral margin posterior to epibranchial tooth raised, completely smooth, continuous with posterolateral margin. Carapace surface completely smooth; highly arched, height greater than front width (ch/fw 1.5). Pleural (vertical) suture on carapace sidewall Y-shaped, ends meeting exorbital and epibranchial teeth. Suborbital margin raised, completely smooth. Ischium of third maxilliped with deep vertical sulcus. Third sternal sulcus s3/s4 deep, v-shaped, meeting sterno-abdominal cavity. Thoracic episternal sulci s4/e4, s5/e5, s6/e6 and s7/e7 distinct.

Anterior inferior margin of merus of cheliped lined by row of small sharp teeth, with large pointed tooth near junction with carpus.

Distribution

This species is known only from the summit of the Pico do Príncipe: (01° 34', 51'N and 07° 22', 57"E) at 945 meters, The Democratic Republic of São Tomé and Príncipe, Gulf of Guinea, Central Africa.

Material

HOLOTYPE. NHM reg. 1999:xxxx) 1 subadult female, cw 40.5, cl 27.5, ch 14.8, fw 10.5 mm, summit of Pico do Príncipe (01° 34' 51"N and 07° 22' 57"E), 945 m, coll. J. E. M. Baillie, 26 Sept. 1999.

Other Material

Príncipe. 1 subadult female, paratype, cw 33.2, cl 22.8, ch 11.6, fw 10.0 mm (NHM reg. 1999. xxxx), summit of Pico do Príncipe (01° 34' 51"N and 07° 22' 57"E), 945 m, coll. J. E. M. Baillie, 1 Sept. 1999.

Description

Carapace ovoid, wide (cw/fw 3.88), highly arched (ch/fw 1.45); surface completely smooth semi-circular, urogastric, transverse branchial grooves faint. Front straight, relatively narrow, about one-quarter carapace width (fw/cw 0.26), anterior margin sharply deflexed. Postfrontal crest distinct, smooth, straight, spanning entire carapace, consisting of fused epigastric, postorbital crests; ends of postfrontal crest meeting anterolateral margins at epibranchial teeth. Anterolateral margin between exorbital, epibranchial teeth smooth, lacking intermediate tooth; anterolateral margin posterior to epibranchial tooth raised, completely smooth, continuous with posterolateral margin. Exorbital tooth small, pointed; epibranchial tooth represented only by small granule. Suborbital margin raised, completely smooth. Suborbital, subhepatic, pterygostomial regions of carapace sidewall all completely smooth; sidewall divided into three parts by longitudinal (epimeral) suture (dividing suborbital, subhepatic regions from pterygostomial region), and by Y-shaped vertical (pleural) groove (dividing suborbital from subhepatic regions). Superior ends of Y-shaped vertical groove meeting exorbital, epibranchial teeth. First thoracic sternal sulcus s1/s2 deep; second sulcus s2/s3 deep, running horizontally across sternum; third sulcus s3/s4 deep, v-shaped, meeting sterno-abdominal cavity. Thoracic episternal sulci s4/e4, s5/e5, s6/e6 and s7/e7 distinct. Third maxillipeds filling entire oral field, except for transversely oval respiratory openings at superior lateral corners; long flagellum on exopod of third maxilliped; ischium with deep vertical sulcus. Epistome prominent, smooth, triangular. Mandibular palp two-segmented; terminal segment single, undivided, with hair (but no hard flap) at junction between segments. Subadult female abdomen subcircular, segments a1-a6 of female abdomen four-sided, telson (a7) a broad triangle with rounded apex; segments a5-a6 broadest.

Major cheliped of subadult female slim, with elongated dactylus and propodus, palm of propodus swollen; fingers of digits of cheliped with small even teeth, forming long slim interspace when closed. First carpal tooth of inner margin of carpus of cheliped large, pointed; second carpal tooth pointed, half size of first tooth. Posterior inferior margin of merus of cheliped smooth, with few small teeth distally; medial inferior margin with row of small sharp teeth along entire length, large pointed tooth at distal end; superior surface of merus smooth. Pereiopods P2-P5 slender, P3 longest, P5 shortest. Dactyli of P2-P5 tapering to point, each bearing four rows of downward-pointing short, sharp spines. Adult size range of *P. principe* sp. n. beginning at cw 41 mm. The colour of the specimens when freshly caught (before alcohol preservation) was creamy white with a very light purplish tone, however one specimen was more white than the other. This coloration was relatively uniform throughout the body including the dorsal carapace, underside, and legs. The purplish tone was darker on the carapace just behind the eyes, which turned to an orange reddish color once the specimens were placed in alcohol.

Ecological notes

The island of Principé is ovoid in outline, with a total land area of 139km^2 (Figure 3). The highest point on the island is the Pico de Principé (945m), a volcanic mountain whose lower slopes are vegetated by lowland rainforest that grades into cloud forest along the summit of the mountain. The climate of Príncipe is tropical, hot, and humid, and there are two dry seasons and two wet seasons. The driest months are July and August, and from the end of December to beginning of January, while the wettest months are October, November, March and April. Rainfall levels are high, averaging 1000mm in the north and up to 5,000 mm per year in the south, and monthly temperatures range between 25° and 31° C (Bredero *et al.*, 1977). The two specimens were collected from the summit of the Pico do Príncipe at 945 meters above sea level on two separate occasions. The terrain at the summit of the Pico do Príncipe is volcanic and mountainous, and the vegetation cover is cloud forest with small stunted trees, and a high abundance of epiphytes and bryophytes. The thick cloud cover and regular rainfall keep the soil and leaf litter very damp. On both occasions when crabs were collected the weather was extremely damp and the mountain top engulfed in cloud cover. Both specimens were collected on land from under damp and decaying leaf litter. There was no river or body of water near the location where the specimens were found. The nearest stream was observed at lower altitudes (830 m), but temporary small pools form near the summit after heavy rain. It is likely that *P. principe* can breathe air, given its extremely terrestrial lifestyle. When crabs were disturbed by removing the leaf litter cover, they ran rapidly across the forest floor and took cover under leaf litter or any available crevasse. Holes that might have been dug by these crabs were found near where the crabs were collected, but crabs were not actually observed moving in or out of these holes.

Comparison

Potamonautes principe sp. n. is closest to *P. anchietae*, a medium-sized species of freshwater crab from Angola (Brito-Capello, 1871, Bott, 1953, 1955, 1964). This species was most recently described and illustrated by Bott (1955, p. 247-249, figures. 24, 76, 77, pl. IX, figure. 1a-d) as *P. (Isopotamonautes) anchietae*. *Potamonautes principe* sp. n. and *P. anchietae* are similar in that both species have a highly arched carapace, a prominent and complete postfrontal crest, a pointed exorbital tooth, a small granular epibranchial tooth, a v-shaped thoracic sternal groove s3/s4, and a similar-sized first carpal tooth on the carpus of the cheliped. However, there are a number of characters that distinguish the specimens from Vissabenguilla, Angola (SMF 1890) described by Bott (1955) as *P. (I.) anchietae*) from the specimens from Príncipe under consideration here.

For example, the carapace height of *P. principe* sp. n. is greater than that of *P. anchietae* (ch/fw *P. principe* 1.45, *P. anchietae* 1.19), and the frontal margin of *P. principe* sp. n. is narrower than that of *P. anchietae* (fw/cw *P. principe* sp. n. 0.26, *P. anchietae* 0.39). Further, the anterolateral margins of the carapace of *P. principe* sp. n. are completely smooth and lack teeth of any kind, whereas these margins in *P. anchietae* are distinctly granular. The medial inferior margin of the merus of the cheliped of *P. principe* sp. n. has a row of distinct pointed teeth along its length, whereas this margin in *P. anchietae*, lacks teeth, and is either granular or smooth. Finally, the suborbital and pterygostomial regions of the carapace sidewall of *P. principe* sp. n. are smooth, whereas these regions are distinctly granular in *P. anchietae.*

Bott (1953, 1955, 1964) described two subspecies of *P. anchietae: P. (I.) a. biballensis* Rathbun, 1905, and *P. (I.) a. machedoi* Bott, 1964, both of which are found in Angola. However, comparison of the types of these taxa with *P. principe* sp. n. indicates that each one differs substantially from the new species described here. For example, the epibranchial tooth of *P. (I.) a. biballensis* is large and pointed whereas that of *P. principe* sp. n. is small and granular, and the carapace of *P. (I.) a. biballensis* is flattened, whereas that *P. principe* sp. n. is high (ch/fw *P. principe* sp. n. 1.45, *P. (I.) a. biballensis* 1.25). Similarly, the epibranchial tooth of *P. (I.) a. machedoi* is large and pointed whereas that of *P. principe* sp. n. is small and granular, and the frontal margin of *P. principe* sp. n. is narrower than that of *P. (I.) a. machedoi* (fw/cw *P. principe* sp. n. 0.26, *P. (I.) a. machedoi* 0.33).

Potamonautes principe sp. n. was compared here with a specimen of *P. margaritarius* from São Tomé (SMF 2668), and the two taxa can be distinguished by the following characters. The carapace of the latter species is distinctly flattened (ch/fw *P. margaritarius* 0.95, *P. principe* sp. n. 1.45), the anterolateral margin of *P. margaritarius* behind the epibranchial tooth is clearly toothed (whereas this margin is completely smooth in *P. principe* sp. n.), and the ischium of the third maxilliped of *P. margaritarius* is smooth and lacks a vertical suture (whereas this suture is deep in *P. principe* sp. n.).

Taxonomic remarks

The new species is assigned to *Potamonautes* because it possesses the following combination of characters: the anterolateral margin lacks an intermediate tooth between the exorbital and epibranchial teeth; the mandibular palp is two-segmented; and the third maxilliped exopod has a long flagellum. *Potamonautes* is a widespread genus of African freshwater crabs found throughout Africa from Senegal to the Horn of Africa, and from Egypt to South Africa. Bott's (1955) revision of the freshwater crabs of Africa recognised some 34 species in this genus. Since then the number of species of *Potamonautes* has risen to more than sixty (Bott, 1959, 1960, 1964, 1968, 1970; Stewart *et al.*, 1995; Stewart, 1997a,b; Daniels *et al.*, 1998; Cumberlidge, 1999; Corace &

Cumberlidge, 2001). Although Bott (1955) recognised fifteen subgenera of *Potamonautes*, the authors of the present study prefer to follow Cumberlidge (1999) and use *Potamonautes* [*sensu lato*] for all species, pending a revision of the entire genus (Cumberlidge, unpublished).

It is not normally good practice to describe a new species from a subadult female. However, we have decided to establish this taxon in the light of the distinct nature of the available morphological characters, and because of the isolated nature of the study area which may mean that further specimens of *P. principe* sp. n. are unlikely to become available for some time. Characters of the gonopods, adult male chelipeds, abdomen and sternum are not at present known because the only specimens of *P. principe* sp. n. are subadult females. Nevertheless, there are a number of unique characters that distinguish *P. principe* sp. n. from other species in the genus.

Etymology

The species is named for the island of Príncipe where it was collected. The species name *principe* is a noun in apposition.

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Figures

Figure. 1. *Potamonautes principe* sp. n. Holotype subadult female, cw 40.5 mm, NHM xxxxx. A, carapace, dorsal view; B, cephalothorax, frontal view; C, left third maxilliped; D, abdomen; E, anterior sternum; F, right cheliped, frontal view; G, left cheliped, frontal view; H, carpus and merus of right cheliped, dorsal view; I, carpus and merus of right cheliped, inferior view. Scale = A, H, I, 13.1 mm; B, D, C, E, 10.5 mm; F, G, 8.3 mm.

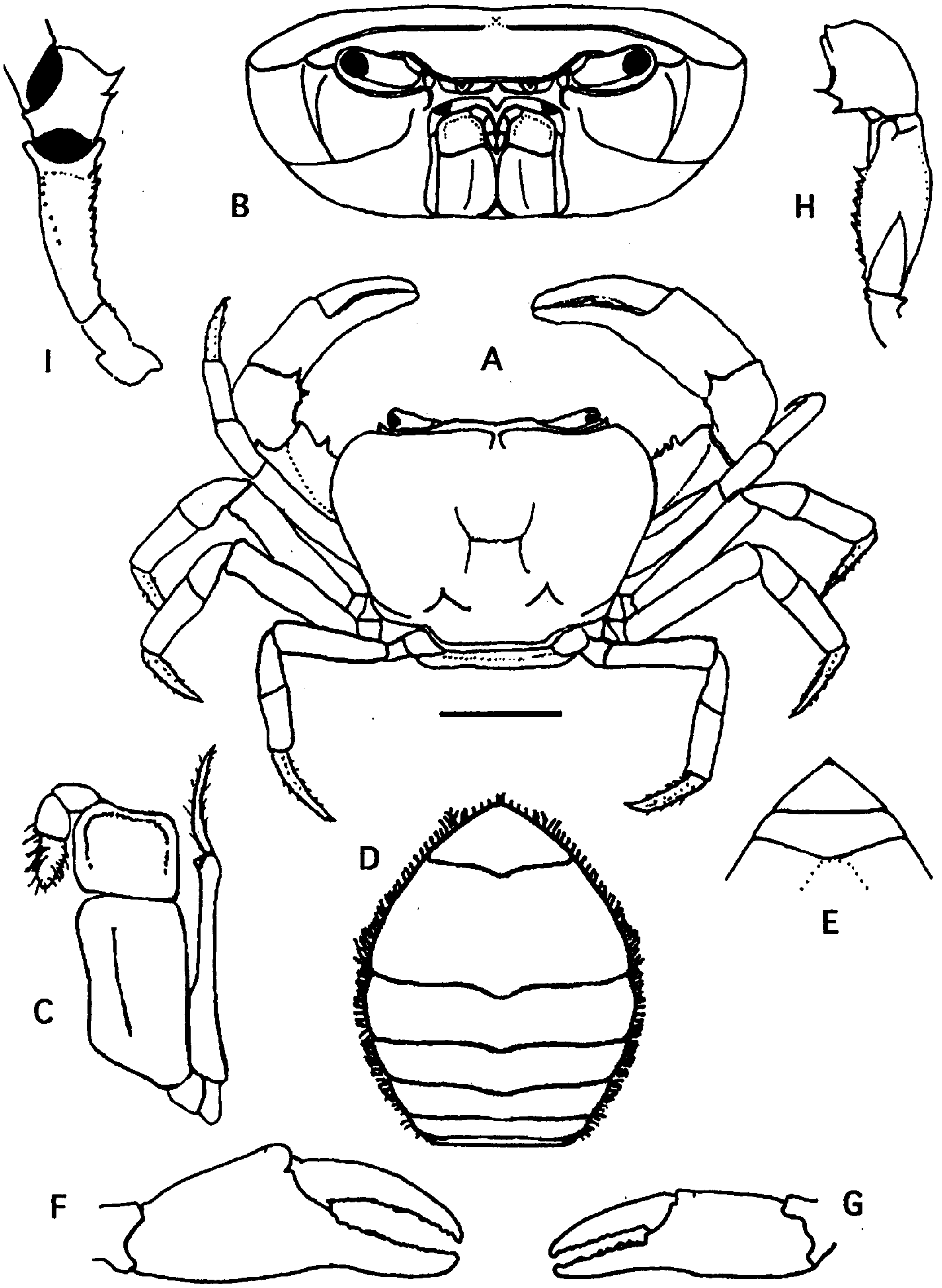

Figure. 2. *Potamonautes principe* sp. n. Holotype subadult female, cw 40.5 mm, NHM xxxxx. A, dorsal view.

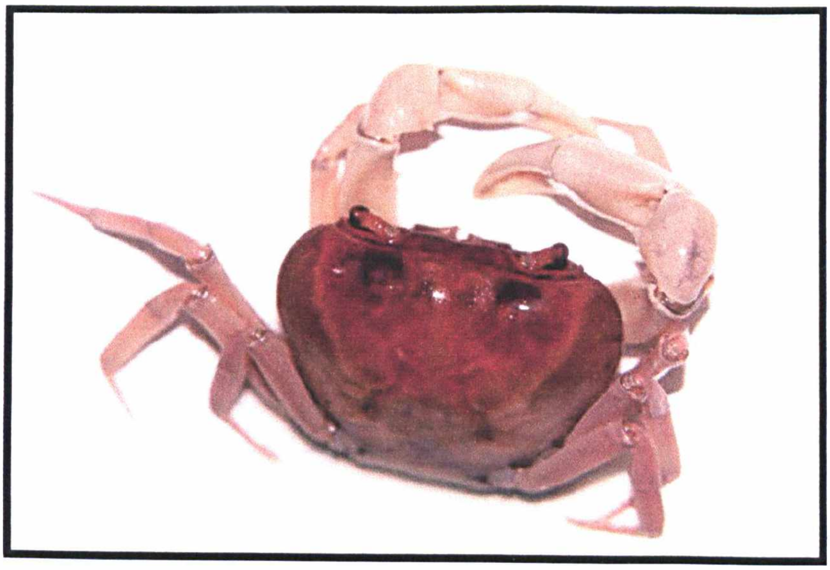

Figure. 3. Map of Príncipe showing the type locality of *Potamonautes principe* sp. n.