British Trust for Ornithology

BTO Research Report No. 97

THE STATUS AND ECOLOGY OF THE ST HELENA WIREBIRD

by
Neil McCulloch

Field work supported by Worldwide Fund for Nature (UK),
International Council for Bird Preservation (UK),
Peter Scott Trust for Education and Research in Conservation.

WWF World Wide Fund For Nature

BRITISH TRUST FOR ORNITHOLOGY,
National Centre for Ornithology,
The Nunnery, Nunnery Place,
Thetford, Norfolk, IP24 2PU.

ISBN No. 0-903793-15-6

Neil McCulloch

THE STATUS AND ECOLOGY OF THE ST HELENA WIREBIRD

Published in August 1992 by the British Trust for Ornithology
The Nunnery, Thetford, Norfolk IP24 2PU, U.K.
Fieldwork supported by Worldwide Fund for Nature (UK),
International Council for Bird Preservation (UK),
Peter Scott Trust for Education and Research in Conservation.

ISBN 0-903793-15-6

CONTENTS

FIGURES

TABLES

SUMMARY

1. The Wirebird *Charadrius sanctaehelenae*, a close relative of Kittlitz's Sand Plover *C. pecuarius*, is found only on the South Atlantic island of St Helena where it is the last surviving endemic bird. First formally described in 1873 the species has been little studied subsequently. The Wirebird must be considered vulnerable because of its restricted range. It was suggested during the 1970's that the species was in decline but no quantitative data on population trends exist. In 1988 a 15-month field study was carried out with the objectives of determining the size of the Wirebird population, and gathering information on habitat requirements, breeding success and feeding ecology and assessing any threats to the species' survival.

2. The best estimate of the current Wirebird population from direct counts is the mean of three full censuses undertaken during this study. This gives a figure of 466 birds. It is improbable that the true population is less than 450 individuals. If it is assumed that, within the census areas, birds overlooked and those counted more than once approximately cancel out and that around 20 birds can be added to allow for those undetected elsewhere then the estimate approaches 500 birds.

3. Wirebirds occur in grassland and semi-desert. Data collected during this study indicate that areas most favoured by Wirebirds can be characterized as pastureland containing a high proportion of Kikuyu Grass *Pennisetum clandestinum* in relation to other grass species; with at least 10% of the ground covered by broad-leaved weeds; mean vegetation height less than 10cm; a gradient of less than 6% and an annual rainfall of 300-500mm. Vegetation structure appears to be more important than community composition, however.

4. Wirebirds take a wide range of invertebrates as prey, amongst which beetles and caterpillars appear to be particularly important. Wirebird density and feeding rate are positively correlated with invertebrate abundance. Feeding rates at semi- desert sites were lower than those on pastureland during the wet season but were slightly higher in semi-desert during the dry period. Feeding in arid areas appears to be less energy efficient, however. Relatively large prey are taken more frequently in pastureland. Foraging accounts for at least 55% of diurnal activity and is most intensive in early morning and late afternoon.

5. Wirebirds appear to be monogamous. Adults are territorial and highly sedentary. They can breed when 10 months old and nest throughout the year, with a dry-season peak from October to February. The clutch is almost invariably two eggs. More than one clutch may be laid in a year. Incubation is shared approximately equally between parents and appears to be more intensive than in Kittlitz's Sand Plover. Eggs are covered when an incubating bird is disturbed and distraction displays are used when chicks, but not usually eggs, are threatened. Less than half the clutches observed produced hatched chicks and chick mortality is estimated to be at least 65%. Survival from egg to independence is probably less than 20%. Nothing is known about the adult survival rate but, in the absence of heavy predation and severe seasonal climatic effects, this is likely to be high. Juveniles disperse widely and, in doing so, may form small flocks. The greater mobility of juveniles probably ensures interchange of birds between all populations on the island.

6. Potential predators of Wirebirds and their eggs occuring on St Helena are cats, dogs, rats and Common Mynahs. Cats are probably the only direct threat to fledged Wirebirds. Human activity, including crop husbandry, and domestic livestock cause some disturbance to breeding Wirebirds at a number of sites. It is not possible to quantify the effects on the Wirebird of predation and disturbance from data gathered during this study but only a small proportion of the Wirebird population is subject to severe disturbance. Predation in general and competition for food between the Wirebird and the Common Mynah require further investigation.

7. The Wirebird does not appear to be threatened at present. However, there may be changes in agricultural practices on St Helena in the future, the impact of which cannot be fully predicted on the basis of the limited data gathered during this study. Regular monitoring of the population is required. More information is needed on effects of pasture management on Wirebirds and on the causes of nest-failure and pre-fledging mortality. An 11-point conservation strategy for the Wirebird is outlined.

Figure 1.1 St Helena: Location

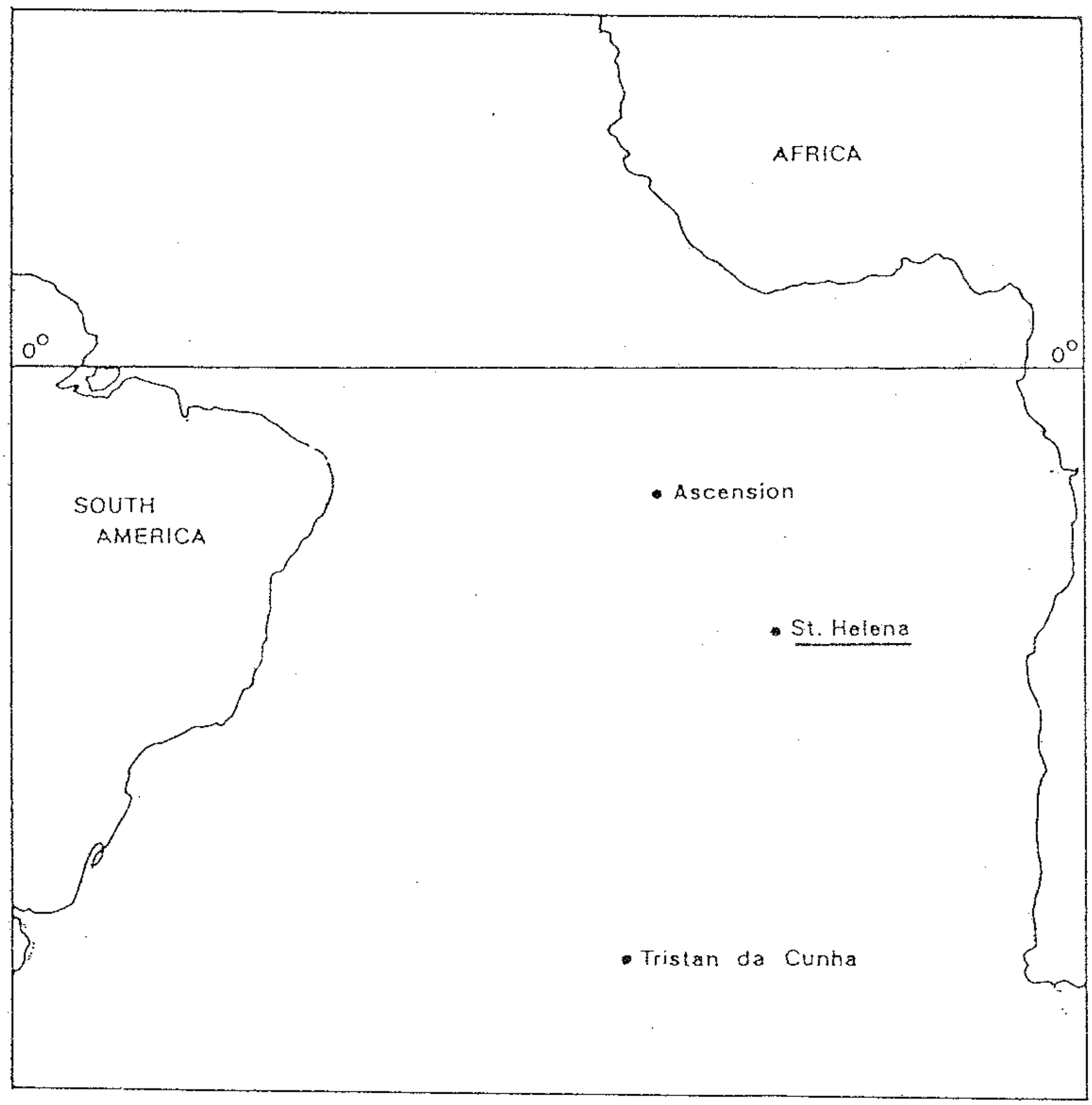
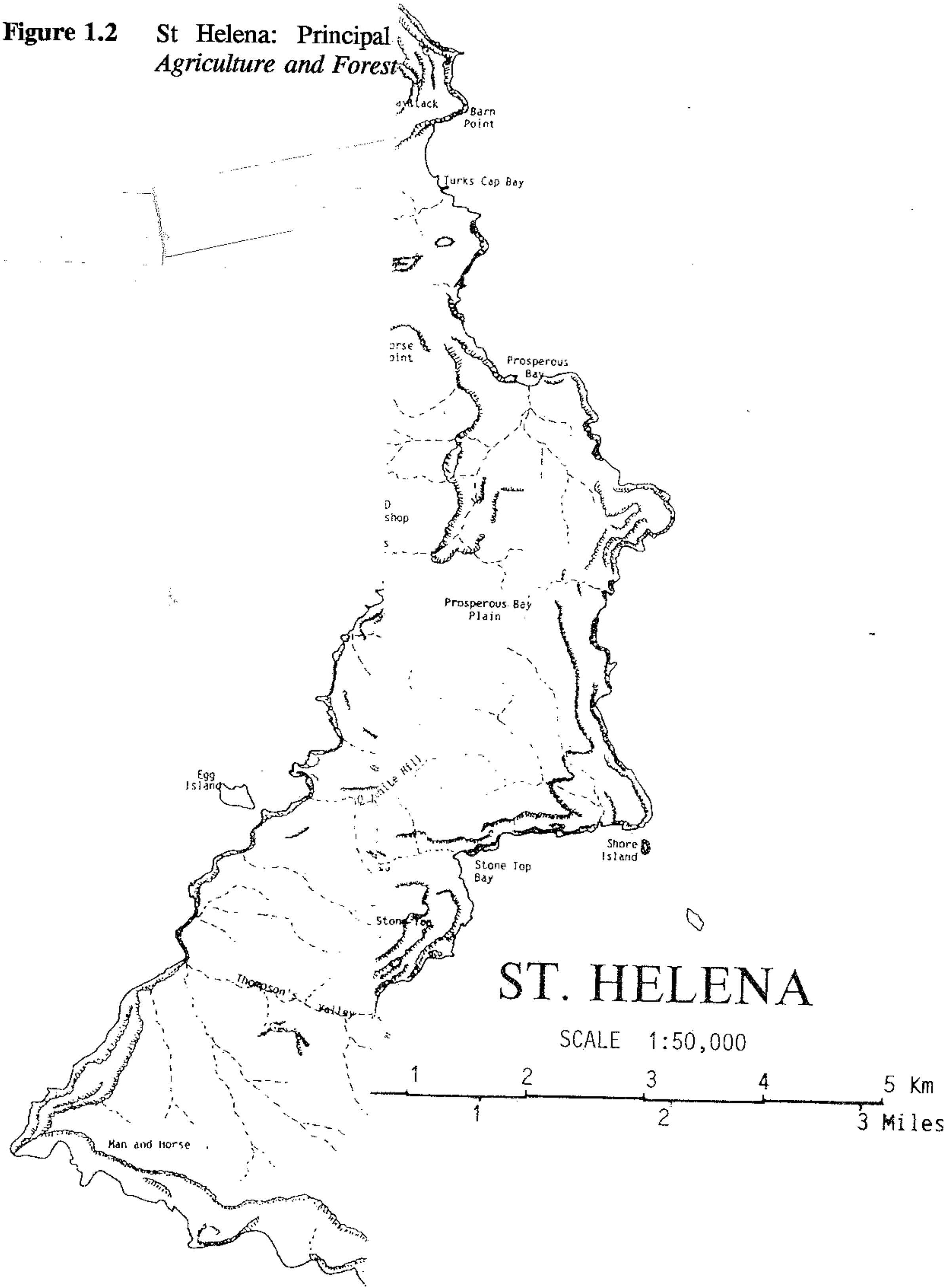


Figure 1.2 St Helena: Principal
Agriculture and Forest



1. INTRODUCTION

The South Atlantic island of St Helena (15° 56'5, 5° 42'W) is one of the most isolated land-masses in the world. It lies some 1900km west of Africa and 3300km east of South America. The nearest land is Ascension Island 1100km to the north-west. Although St Helena covers an area of only 122km^2 and has maximum dimensions of 16km by 10km it's extreme isolation has been a catalyst in the evolution of a surprising number of endemic animals and plants (Brown 1982, Cronk 1987).

It is known from sub-fossil remains that at least nine endemic bird species have occurred on the island (Ashmole 1963, Olson 1975). Six of these species were terrestrial (Table 1.1). The endemic pigeon almost certainly died out prior to human colonisation but all the others persisted into historical times (Olson 1975). It seems likely that other species, probably including small passerines, also existed on St Helena but evidence has yet to be found.

St Helena was discovered by the Portuguese navigator Joao da Nova Castella in 1502. The island's natural vegetation has been almost totally destroyed subsequently, resulting in extensive erosion and land degradation (Cronk 1983, 1986 a, b, 1989). The consequences of this environmental disruption and the introduction of predators such as cats, dogs, rats and pigs included the extinction of all the endemic land-birds with the exception of the Plover, known locally as the Wirebird, and a severe reduction in the numbers and diversity of breeding seabirds.

The terrestrial avifauna of St Helena today consists of eleven breeding species (Table 1.1). All but two of these have been deliberately introduced to the island by Man.

The Wirebird is closely related to Kittlitz's Sand Plover *Charadrius pecuarius* of Africa, from which it probably evolved and with which it has often been treated as conspecific (e.g. Sclater 1924, Bock 1958). Although the Wirebird closely resembles *C. pecuarius* it is substantially larger and differs markedly in its physical proportions: for example, its tarsus length is around 40% longer than that of *C. pecuarius* though its sternum is only 10% longer (Olson 1975).

The Wirebird's wing is more rounded and its pectoral muscles relatively smaller than those of *C. pecuarius*, suggesting the beginnings of evolutionary flight loss. Most of St Helena's other endemic land-birds appear to have been flightless or to have had considerably reduced powers of flight (Olson 1975). The Wirebird's retention of efficient flight has undoubtedly assisted its survival in the face of introduced predators and suggests that its ancestor may have been a relatively recent arrival on the island.

It is not known when the Wirebird's ancestors first reached St Helena but some of the bones found by Olson (1975) appear to date from the early Pleistocene. The birds from which these bones came were all larger than typical *C. pecuarius* so considerable evolutionary divergence may have already taken place by this time. Colonisation of St Helena by African birds during the lower Pleistocene is likely to have been favoured by the greater strength of the South-East Trade Winds at this time (Baker 1970).

Most of the earliest reports describe St Helena as being heavily wooded but it seems probable that substantial areas of the windward side of the island consisted of scrub (Cronk 1989). The more open parts of this were probably the original habitat of the ancestral Wirebirds.

As an open-country species, the Wirebird was probably the only endemic bird to benefit from the widespread deforestation that occurred after human colonisation of the island.

The actual effects of these environmental changes on the Wirebird population are unknown, as the species has been little studied since the English traveller Peter Mundy noted in 1638 that, on St Helena, there was "a small land Foule and butt only that kind to here to be seen" (Temple 1919:413). In 1656 Mundy returned to the island and recorded the first description of the Wirebird, stating that it was "somewhatt like a larke in collour, shape, flightt and note. It would run like a lapwing" (Temple and Anstey 1939: 79). By this time major environmental changes had already occurred. Pigs and goats were present by 1536 (Markham 1911), the latter having possibly been introduced as early as 1513. By 1588 Captain Thomas Cavendish was able to see herds of hundreds of goats during his visit to St Helena (Gosse 1938:18). The presence of feral cats and dogs was noted by Mundy in 1634 (Temple 1914: 330). Black Rats *Rattus rattus* probably first came ashore very soon after the discovery of the island and were certainly a serious pest by 1666 (Gosse 1938: 54). The Brown Rat *R. norvegicus* appears to have become established during the 18th century (Atkinson 1985). Permanent human settlement dates from 1659 when the island passed into the ownership of the English East India Company.

Unrestricted grazing of goats must have severely suppressed natural regeneration of the forests. When the human population began cutting the mature trees for timber and fuel deforestation was rapid. In 1683 the north-east of the island still supported endemic Gumwood *Commidendrum robustum* forest covering some 1200ha (Beatson 1816) but by 1778 fuel wood was in such short supply that the planting of Gorse *Ulex europaeus* for fuel was ordered (Cronk 1986b). The maximum deforestation was probably reached in the mid to late 19th Century, only 162 acres of woodland being recorded in 1884 (Morris 1884). It seems reasonable to assume that Wirebird numbers also reached their peak around this time.

Some contraction of range undoubtedly occurred after the establishment of a fibre industry based on New Zealand Flax *Phormium tenax* in 1907. During this period up to 40% of the pastureland recorded in 1884 was given over to flax production (Brown 1981). The industry declined after the development of synthetic fibres and the last flax mill closed in 1966. Since then some of the flax plantations have been returned to pasture but many have been converted to forest so there has probably been a net loss of Wirebird habitat as a result of flax growing and its consequences.

Housing and amenity developments have also used former Wirebird breeding grounds, especially in the north-west of the island around Half-Tree Hollow and, to a lesser extent, in the Longwood area.

Throughout this period of dramatic environmental change the Wirebird is scarcely mentioned in the literature dealing with St Helena. The earliest specimens in the British Museum (Natural History) collection date from 1842; others were obtained by Layard in 1866 (Layard 1867). The bird was first described as a distinct species in 1873 (Harting 1873), but little information about the Wirebird's behaviour and ecology was obtained until 1984. St Helena's isolation has mitigated against thorough scientific investigation of it's biology and most of the published data on the Wirebird are contained in the anecdotal writings of island residents (Baker 1868, Melliss 1871, Huckle 1924) or the observations of very short-term visitors (Moreau 1931, Benson 1950, Hartog 1984). Some important contributions were made by Haydock (1954), who spent three months on St Helena investigating the avifauna identified 11 Wirebird breeding sites and made the first population estimate for the species; Pitman (1965), who described the eggs and some aspects of breeding behaviour, basing his account largely on the observations of local resident Arthur Loveridge; and Olson (1975), who carried out a valuable study of the island's palaeornithology.

In 1984, following consultations with ICBP, where the Wirebird had been evaluated as deserving threatened status, Alexander (1985) carried out the first major field study of the Wirebird's distribution and ecology. This project was of four months duration and provided much new information on range, breeding and social behaviour. Potential threats to the species survival were also identified.

A number of estimates of the size of the Wirebird population have been published but none has been based on a comprehensive census. As a result the estimates arrived at here have been varied and contradictory, ranging from Haydock's (1954) 100 pairs to Loveridge's (in Pitman 1965) "just under 1000" individuals. It was largely this uncertainty over the numerical staus of so isolated and perhaps vulnerable a species that led Collar and Stuart (1985) to treat the species as threatened and to recommend research on its population dynamics and ecology; they were of necessity unaware of the suggestion that there had been a serious decline in numbers during the last 30 years (Loverige 1974), which might have lent greater immediacy to the call for an investigation. However, following the ICBP's British Section's 1986 decision to support work in British Dependent Territories, a 14-month study was conducted to attempt to establish the true status of the Wirebird and to enlarge on Alexander's ecological work with a view to drawing up a conservation strategy for the species.

The study was carried out between October 1988 and December 1989. It's main objectives were to obtain an accurate estimate of population size by regular census work, to map the distribution of the Wirebird, to establish the species major ecological requirements and to identify any immediate threats. Data were also collected on diet, prey abundance, timing of breeding, breeding success, movements and social behaviour.

During the final two months of the study I was assisted in the field by Mr A. Dunthorn who travelled voluntarily to St Helena at his own expense to contribute to the project.

This report describes the work carried out during the study period and presents analyses principally relating to status, distribution and habitat requirements. Aspects of breeding biology, feeding, social behaviour and environmental problems are also discussed. A series of conservation measures is also suggested.

Table 1.1 Status of known recent land-birds of St Helena

Family	Species	Status	
Phasianidae	Ring-necked Pheasant *Phasianus colchicus*	Introduced	
	Chukar Partridge *Alectoris chukar*	Introduced	
Rallidae	Moorhen *Gallinula chloropus*	Indigenous (?)	
	St Helena Rail *Atlantisia podarces*	Endemic	*Extinct*
	St Helena Crake *Porzana astrictocarpus*	Endemic	*Extinct*
Charadriidae	Wirebird *Charadrius sanctaehelenae*	Endemic	
Columbidae	Barred Ground Dove *Geopelia striata*	Introduced	
	St Helena Pigeon *Dysmoropelia dekarchiskos*	Endemic	*Extinct*
Cuculidae	St Helena Cuckoo *Nannococcyx psix*	Endemic	*Extinct*
Upupidae	St Helena Hoopoe *Upupa antaios*	Endemic	*Extinct*
Sturnidae	Common Mynah *Acridotheres tristis*	Introduced	
Ploceidae	Madagascar Fody *Foudia madagascariensis*	Introduced	
Estrildidae	Java Sparrow *Padda oryzivora*	Introduced	
	Common Waxbill *Estrilda astrild*	Introduced	
Fringillidae	Yellow Canary *Serinus flaviventris*	Introduced	

Failed introductions not included

2. ENVIRONMENT

2.1 GEOLOGY AND TOPOGRAPHY

St Helena is of volcanic origin and is part of the Mid-Atlantic Ridge system, though it lies to the east of the main ridge. The island rises from a depth of 4224m, having first emerged around 20 million years ago. The present land surface covers 122km^2 and has maximum linear dimensions of 16km by 10km. The major axis is aligned north-east to south-west and is surmounted by a ridge rising to 823m at Diana's Peak.

The island comprises the remains of two shield volcanoes, one centred in the north-east of the island around Flagstaff Hill and the other in the Sandy Bay area (Daly 1927, Baker 1970). The north-east volcano is the older and ceased activity around 12 million years ago. About the same time eruptions started at the Sandy Bay centre and continued until extinction 7 million years ago (Baker *et al.* 1967). The younger volcano produced over 75% of the volume of exposed rocks seen today. These rocks consist predominantly of basalts with intrusions of trachytes and phonolytes (A.J.Nicholson in Nunn 1982).

Fluvial erosion since the volcanoes became inactive, has been responsible for most of the present landforms (Nunn 1982). St Helena's topography is dominated by a drainage system radiating from the central ridge. This has produced a series of steep-sided valleys, some up to 300m deep, separated by generally narrow ridges. Between the valley mouths the coastline consists of cliffs ranging from 80m to 570m in height. Some of the bays have pebble or boulder beaches which are generally narrow. Only Rupert's Bay has a small strip of truly littoral sand.

Permanent streams and standing water are rare on St Helena because of the porosity of the rocks, particularly the pyroclastic deposits, and high evapotranspiration rates. Of the streams that do occur, many are highly saline in their lower reaches, having percolated through sodium-rich rock.

2.2 CLIMATE

The climate of St Helena is controlled by the South Atlantic High Pressure Cell and the Equatorial Trough (Mathieson 1990b). Although the island lies well within the Tropic of Capricorn its climate is best described as sub-tropical. The most striking feature of the island's weather patterns is their variability both temporally (between years) and spatially (within the island) so that the concept of a "typical" year has relatively little value. Temperatures are subject to the ameliorating influence of the South-East Trade Winds blowing over the cold Benguela current. Within the island, temperatures vary markedly with altitude. At Jamestown (sea level) the annual mean is 22°C but at Hutt's Gate (627m) only 16°C. The coolest months are normally August and September and the warmest March and April (Table 2.1a).

Rainfall at St Helena is principally caused by orographic disturbance of the flow of the Trade Winds but is also influenced by frontal activity in high southern latitudes (Llewellyn 1982, Mathieson 1990b).

The seasonal pattern and quantity of rainfall varies greatly between years (Table 2.1b). Precipitation increases with altitude: Jamestown receives, on average, less than 300mm of rain annually but at an altitude of 800m this rises to over 900mm. In most years rainfall is heaviest between March and September (Table 2.1b, Fig.2.1). This typically occurs in the form of frequent short showers but occasionally low pressure areas may develop in the vicinity of St Helena causing heavy, prolonged precipitation (Llewellyn 1982). Such rainfall may be surprisingly localised and is occasionally sufficiently intense to cause flash floods. Thunderstorms are very infrequent, only seven having been recorded this century up to 1989 (Mathieson 1990b).

Wind direction is dominated by the South-East Trades, which prevail on 70%-80% of days, usually at a strength of Force 4-5. Gales can be frequent between September and November.

The orographic disturbance of the prevailing airstream results in extensive cloud cover, especially at higher altitudes. At Hutt's Gate cloud cover averages over 80% throughout the year while at Jamestown Llewellyn (1982) recorded variation between 46% and 74%. Above 400m, low cloud can cause prolonged foggy conditions between March and November.

Relative humidity is typically 75%-85% but below the 900m isohyet, which approximately coincides with the 600m contour, evapotranspiration generally exceeds rainfall (I.K.Mathieson pers.comm).

2.3 SOILS

The soils of St Helena can be characterised as heavy, acidic clays with a poorly developed crumb structure and a high sodium content (Brown 1978). These properties result in the soils becoming easily waterlogged and putty-like under wet conditions and baking extremely hard when dry. Microbial activity and pH increase with altitude and rainfall (Cronk 1989).

Within the range of the Wirebird, soil types fall into two broad categories, the cambisols of the pasturelands and the xerosols of the arid crown wastes (Brown 1981). The pasture soils can be further divided into three groups. The moist pastures at an altitude of over 500m are underlain by dystric cambisols, the pastures at lower elevations west of the central ridge by eutric cambisols and the drier grazings of the Longwood area by cambisols of intermediate character. The haplic xerosols of the barren, eroded outer fringes of the island contain little organic matter and frequently have high salinity (Brown 1981, Cronk 1989).

2.4 VEGETATION

The present vegetation of St Helena bears little relation to that occurring on the island at the time of its discovery in 1502. Since that date the indigenous plant communities have been almost entirely eradicated by the actions of Man and his livestock and replaced by a wide variety of introduced species.

The distribution of former native vegetation types has been reconstructed by Cronk (1989). Seven assemblages are recognised and a strong relationship to altitude and rainfall is evident. At the lowest levels, below 250m, semi-desert conditions prevailed in many areas. On less saline substrates up to 350m scrubland dominated by the endemic Scrubwood *Commidendrum rugosum* occurred. Rocky areas between 100m and 500m held a community principally comprising St Helena Ebony *Trochetiopsis melanoxylon* and Gumwood *Commidendrum* *robustum*. Relatively dry areas between 300m and 500m were covered by extensive tracts of the drought-resistant Gumwood with spare undergrowth. Such areas included the "Great Wood" of the Longwood district which persisted until the early 18th century. Above 500m Gumwood remained the dominant species but wetter conditions allowed a greater variety of trees, including the Redwood *Trochetiopsis erythroxylon*, and a richer ground flora. In the areas of highest precipitation, above 600m, a woodland comprised of the various endemic cabbage-trees (Compositae) and the tree-fern *Dicksonia arborescens* prevailed. Above 700m the tree-fern was dominant.

Cronk (1989) recognises eight present-day plant communities but these can be simplified into altitudinal/climatic zones. In the following account non-indigenous species are denoted by an asterisk. Below 350m arid conditions prevail and the land surface has been subject to large scale erosion. Such areas are designated the "Crown Wastes". On the eastern (windward) side of the island this zone comprises semi-desert, dominated by the shrub *Suaeda helenae* and large tracts of "creeper" *Carpobrotus edulis**. On the western side, arid areas are typically covered by scrub dominated by either *Lantana camara** or Prickly Pear *Opuntia* spp*.

The former range of the Gumwood in areas receiving less rain annually is now occupied by pastureland and non-indigenous woodland. The main pastures grasses in this zone are Kikuyu Grass *Pennisetum clandestinum**, Wire Grass *Cynodon dactylon** and *Digitaria ciliaris**. The woods are predominantly of *Acacia longifolia*, A. melanoxylon** and *Pinus pinaster**.

On the steeper slopes above 500m, where the annual rainfall is between 600mm and 1000mm, the species composition of both pasture and woodland changes and large areas of land are still covered by relict plantations of New Zealand Flax *Phormium tenax**. Within this zone Brown (1981) recognised two types of grassland which she termed "moist" and "semi-moist". The former, found in areas with more than 900mm of rain per year, is dominated by the grasses *Agrostis tenuis** and *P. clandestinum** while in the latter Mat Grass *Stenotaphrum secundatum** is co-dominant with *P. clandestinum**. Cape Yew *Podocarpus elongata** is a major tree species in the higher altitude plantations. Other important trees are *A. melanoxylon* and *P. pinaster**.

The final vegetation zone consists of relict cabbage-tree/tree- fern woodland. This is restricted to the highest parts of the central ridge arounds Diana's Peak and to a very small area on the east side of High Peak. The woodland contains several endemic tree species but is dominated by *Dicksonia arborescens* and the Black Cabbage-Tree *Melanodendron integrifolium*. During this century the endemic woodland has been heavily invaded by *Phormium tenax**.

2.5 LAND USE

Approximately 75% of St Helena's land surface is heavily eroded semi-desert or scrub, mostly lying below the 350m contour. This area has remained fairly constant over the last 100 years (Fig. 2.2) though its classification has varied. Melliss (1875) included around a third of the arid zone as pasture in his analysis. The grazing of livestock on the Crown Wastes is now illegal.

In 1989 agricultural land occupied around 15% of the total. The greater part of this (11%) was pasture, with the remaining 4% classified as arable land and garden plots. Aerial photography carried out during 1989 revealed, however, that only 77ha of land so designated was under active cultivation, principally for vegetable growing, potatoes being the major crop (Mathieson 1990a). This comprises only 0.6% of the total land area. Substantial areas of arable land currently exist only at Longwood Farm, Broad Bottom and Woody Ridge. The remainder comprises many scattered small plots, usually of less than 1ha.

Most pasture is found between 400m and 600m a.s.l. to the north and west of the central ridge. There are approximately equal numbers of cattle and sheep on the island, around 1200 head of each (ODA 1989), but sheep grazing is confined to the south- western pastures from Thompson's Wood to Man and Horse, Broad Bottom and Woody Ridge. All other pastures carry cattle with the greatest numbers occurring at Deadwood Plain, Broad Bottom, Blue Hill and the Oakbank (Central) pastures. Goats can now only legally be grazed in pens or tethered; no large herds exist.

More than half the area that was under flax at the height of the fibre industry has now been cleared. Most of the remaining flax occurs on the steepest slopes of the central area which is uneconomical to clear. These remnants are often the results of natural dispersal rather than deliberate planting.

The area under woodland has increased in the last 20 years. Between 1978 and 1987 some 680,000 trees were planted on the island (ODA 1989). Most of the new forests have been planted on cleared flaxlands and are intended to produce commercial timber and fuel wood but the establishment of tree cover for soil conservation purposes is also being undertaken at lower altitudes. It is likely that the afforestation of the fringes of the Crown Wastes will increase in the future (Brown 1981, ODA 1989).

The resident population of St Helena in 1987 was 5415 (ODA 1989), of which slightly less than half were located in the Jamestown and Half-Tree Hollow areas. These are the only large settlements in the dry outer zone, the remainder of the population occurring predominantly where there is adequate rainfall for agricultural purposes. The only sizeable inland settlement is Longwood in the north-east. There are smaller centres of population at the Briars, Deadwood, Levelwood, Blue Hill, Sandy Bay Valley, Pounceys, Alarm Forest and Rupert's Valley, but a large proportion of the rural population live in scattered cottages and smallholdings. Built-up areas account for less than 2% of the land.

Table 2.1 Climatic records for St Helena (Data from Mathieson 1990)

a) Monthly temperatures (°C) at Ladder Hill and Bottomwoods(1989)

	Ladder Hill (Alt. 210m)		Bottomwoods (Alt.435m)	
	Max.	Min.	Max.	Min.
January	27.0	20.0	23.6	17.5
February	28.4	21.0	24.7	18.7
March	29.2	21.6	24.7	19.5
April	27.4	20.4	22.3	18.0
May	27.2	19.7	22.1	17.5
June	24.9	17.2	19.9	15.2
July	23.4	16.9	18.8	14.5
August	22.0	16.4	18.1	14.2
September	22.9	16.5	18.4	14.2
October	22.2	16.4	18.1	13.9
November	22.6	16.9	19.1	14.4
December	24.1	18.1	20.7	15.6

b) Monthly rainfall (mm). Mean maxima and minima for Longwood (alt.500m) during 1952-89. 1989 values for Jamestown (15m) and Hutt's Gate (627m)

	Longwood 1952-89			Jamestown	Hutt's Gate
	mean	max.	min.	1989	1989
January	37.6	74.9	6.3	13.5	53.9
February	58.4	170.7	12.7	26.2	39.4
March	72.4	163.6	19.3	9.0	46.2
April	51.6	133.6	4.6	58.4	144.1
May	52.4	146.0	2.3	15.2	77.0
June	69.5	155.2	3.8	55.1	151.0
July	68.7	137.2	16.0	35.1	94.6
August	57.2	144.3	12.7	19.8	91.8
September	44.8	99.1	7.9	5.3	90.0
October	28.2	53.1	1.8	8.0	65.2
November	21.1	43.4	0.0	0.5	55.9
December	21.4	49.0	0.8	3.7	41.2
Total	583.2	860.0	305.6	249.8	950.3

Figure 2.1 Monthly rainfall at Longwood (alt.500m) in 1989

Conditions at this site are similar to those experienced at Deadwood Plain, the principal Wirebird breeding area.

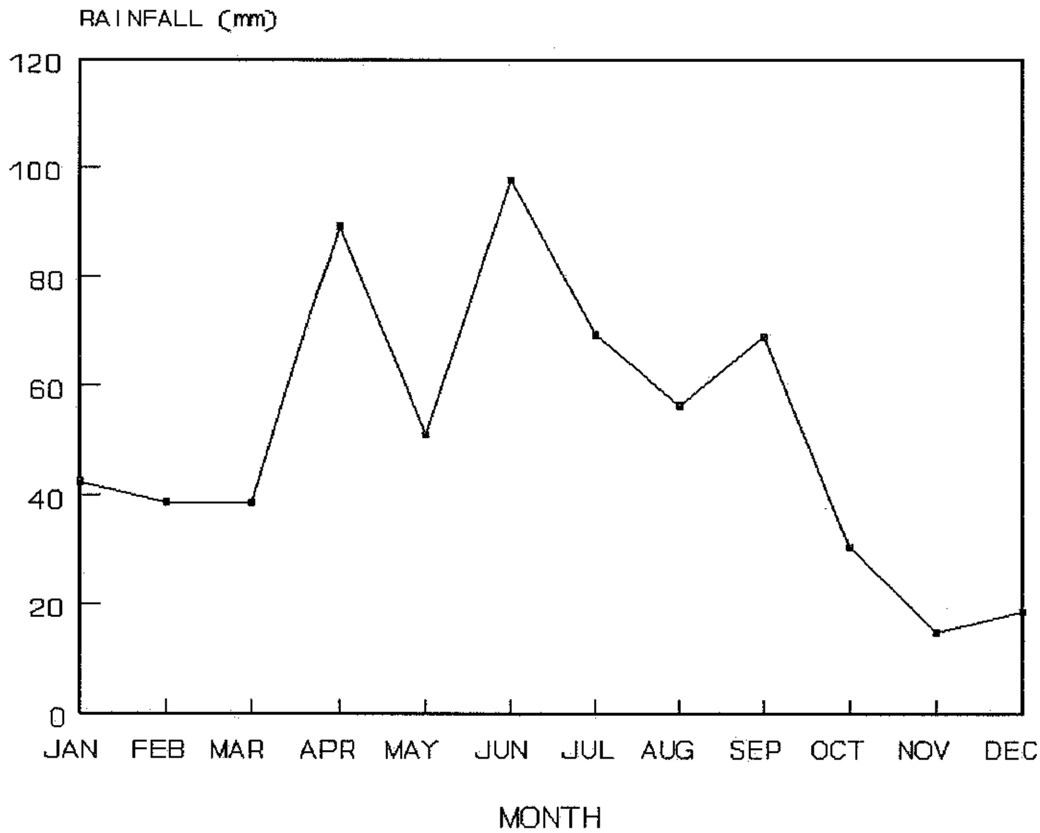
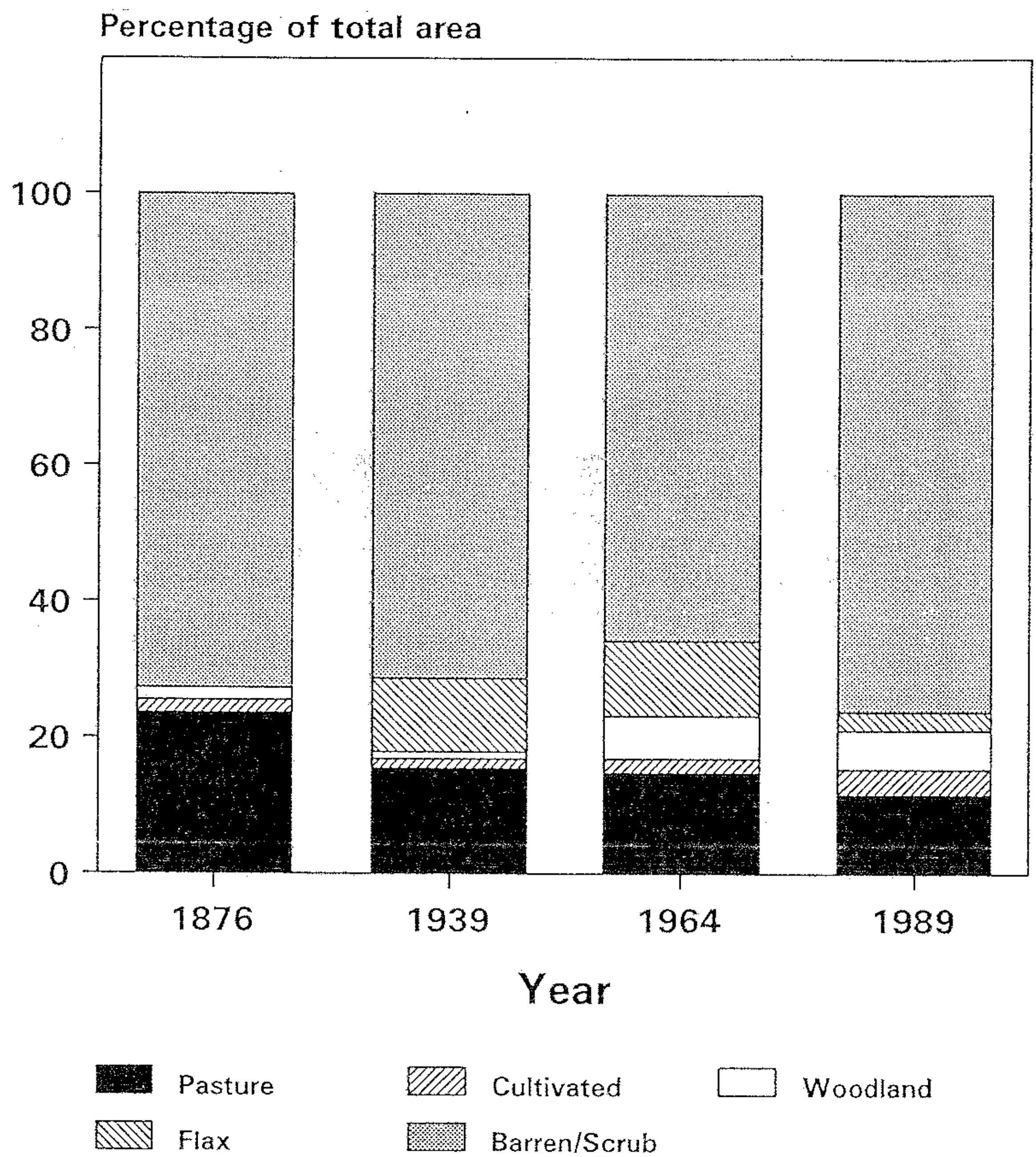


Figure 2.2 Changes in land-use, by percentage area, 1876-1989

Data sources: Anon. (1876) "Precis of Information" ,St Helena Government publication (quoted by Brown 1982)
Stockdale (1939)
Lynn (1966)
Mathieson (1989)



3. DISTRIBUTION AND NUMBERS

3.1 PREVIOUS STUDIES

Several authors have remarked that Wirebirds tend to inhabit the drier, flatter regions of St Helena but few have identified specific breeding sites. Haydock (1954) mapped 11 nesting areas and Alexander (1985) found or heard reports of Wirebirds at 35 sites but was able to confirm breeding at only seven of these.

Prior to the work of Alexander (1985), estimation of Wirebird numbers tended to be based on subjective impressions rather than on systematic counts. Even Alexander's figure was based partly on extrapolation because of incomplete coverage. This has resulted in a disparity of estimates from which it is difficult to discern any recent trends.

Published comments on population size include:

"considerable numbers" Beatson (1816)

"not very numerous" Baker (1868)

"scarce without being rare" Huckle (1924)

"in considerable numbers" Simmons (1927)

"holding its own and breeding all over the island" Moreau (1931)

"not more than 100 pairs" Haydock (1954)

"just under 1000" A. Loveridge (in Pitman 1965)

"now relatively common" Basilewsky (1970)

"quite common" Q.C.B. Cronk (in Collar and Stuart 1985)

"at least a few hundred individuals" den Hartog (1984)

"likely to be 200-300 birds, maximum" Alexander (1985)

The present study is the first to attempt a direct census covering all known breeding areas.

3.2 COVERAGE AND CENSUS METHODS

All Wirebird sites referred to in the literature were visited between October and December 1988, as were any other areas having apparently suitable habitat on the basis of published data on the species' requirements. In effect this included all pastureland and all but the most heavily eroded and precipitous areas of the Crown Wastes.

All sites where Wirebirds were found, or had been recently and reliably reported, were censused at three-month intervals. There were 31 regular census areas. Most of these had obvious topographical or vegetational boundaries but the extensive semi- desert areas of the north-east required the imposition of largely arbitrary divisions to enable them to be worked efficiently. Unoccupied sites were re-checked between census periods as other commitments allowed. The census areas are shown in Figure 3.1 The names used are taken from the current 1:25000 map of St Helena (Directorate of Overseas Surveys 1983) except those in parentheses which are names of convenience for census areas not covered by any single local name.

Initial investigation showed adult Wirebirds to be highly territorial and there was no evidence of regular large-scale movements between sites. The birds can be approached to around 20m without causing serious alarm and are normally reluctant to take flight. This allowed direct counts to be used in censusing the population.

The method used in covering a site during census work depended on the size and topography of the site. At small sites all birds present could frequently be detected by walking round the periphery and scanning with 10x40 binoculars. On narrow ridges a walk down the mid-line often sufficed. At more extensive sites the area was covered in a series of transects, all birds in a strip extending 25m on each side of the observer being counted. As far as was possible, disturbance of birds within each strip was minimized. After familiarization with the species, Wirebirds were usually easily detectable as they tend to inhabit areas of low or sparse vegetation and are also highly vocal. It is unlikely that significant numbers were overlooked. Birds in flight were not counted unless they were seen to take off from a part of the census area not yet covered.

Heavily gullied areas and all but the most open *Opuntia* scrub were not covered after the first census as there was no evidence of their extensive use by Wirebirds and the time required to survey such areas thoroughly was not justified by the relative increase in accuracy of the population estimate.

Large numbers of Wirebirds frequently assembled at bathing and drinking sites at Cook's Bridge in Fisher's Valley and in lower Sheep Pound Gut. Birds at these sites were not included in the census as many birds appeared to be attracted there from relatively long distances and so were likely to have been counted elsewhere. Downy chicks were included in the counts.

3.3 POTENTIAL SOURCES OF ERROR IN THE COUNTS

Some error is likely to have arisen from birds being overlooked or counted more than once within sites. It is not possible to quantify the scale of such error but the relative consistency of counts at major sites between census periods suggests that it is not a serious problem.

Birds which move between census areas may be counted more than once but, equally, may be missed completely, so this introduces imprecision rather than bias. Observations of marked birds indicate that adults tend to be sedentary, so any error is likely to involve juveniles, which make up only some 10% of the population at any one time. Large influxes of juveniles are rare at most sites and are usually readily detectable.

Although birds attending the two major bathing sites were excluded from the census because they were known to include many that had "commuted" from neighbouring census areas, it is almost certain that some previously undetected birds were omitted as a result.

Some birds probably remained undetected in heavily eroded or scrub-covered areas not included in the census sites. There may be as much as 400ha of such country containing some potential Wirebird habitat. If it is assumed that Wirebirds occur within this area at a similar density to those in the Longwood Erosion Zone (0.05/ha), this would provide an additional 20 birds.

The above factors apply to all censuses but there may have been particular sources of inaccuracy in the first and third counts. It is probable that the total for the initial census substantially underestimates the true population, mainly because I was unfamiliar with the Wirebird and its calls. During the June 1989 census a large hatch of caterpillars associated with the shrub *Suaeda helenae* occurred in the arid zone of the north-east, particularly at Prosperous Bay Plain. The number of Wirebirds feeding on caterpillars at this site was three times greater than the highest previous count for the area and it seems certain that birds had been attracted from other sites, so the problem of double-counting or missing mobile birds was more marked on this than other censuses.

3.4 NOTES ON CENSUS AREAS

<u>HIGH KNOLL/COWPATH</u> Sparse, rough grassland and scrub running from High Knoll fort to Ladder Hill around the periphery of the Cowpath area of Half-Tree Hollow. Small numbers of Wirebirds frequently feed around Cowpath in early morning but no evidence of breeding was found. A pair appeared to have taken up a territory within High Knoll fort in October and November 1989.

<u>DONKEY PLAIN</u> Open scrub with extensive areas of exposed rock, bounded by sea-cliffs at its lower extremity and by housing at its upper. This is a heavily disturbed site containing a rubbish dump and a quarry and stone-crushing plant. Wirebirds were most frequently encountered on the lower parts of the plain, below the quarry, and have been seen to fly across Breakneck Valley to feed around the rifle ranges at Ladder Hill.

<u>CLEUGH'S PLAIN</u> Disused arable land and building plots. Wirebirds were found here during only one of the four censuses and there was no evidence of breeding. It is likely that this is only an occasional feeding site.

<u>ROSEMARY PLAIN</u> This relatively small site contains both pasture and arable land, with an area of grassland used as a picnic site. One or two pairs regularly nest on the pasture and the site is used intermittently by small numbers of wandering juveniles. Wirebirds occasionally feed in surrounding gardens.

<u>FRANCIS PLAIN</u> School and public recreation ground in almost daily use. The playing fields hold one or two resident pairs and others (up to eight were observed) may feed there in early morning and evening and during school holidays.

<u>BARREN HILL</u> Includes Barren Hill and upper Lemon Tree Gut. Most Wirebirds are concentrated on the regularly grazed pastures above Woodcot house. Breeding occurred on the lower, Peak Hill, pastures in 1988 but cessation of grazing and planting of trees is making this area progressively less attractive to Wirebirds and none held territories there between February and December 1989. No Wirebirds were ever encountered on the extensive, but steep, pastures in Lemon Tree Gut.

THE DUNGEON A steeply sloping group of upland pastures in the centre of the island. The Wirebird population is very small and no birds were encountered during three censuses. Breeding appears to be irregular but occurred on the west side of Halley's Mount in 1988.

PROSPECT PASTURES A small area of upland pasture surrounded by woodland, normally holds only one pair.

SANE VALLEY Very steep pasture and partially cleared flaxland. Most Wirebirds are found on a relatively flat shelf at around 400m on the west side of the valley but individuals occur throughout the area.

DEADWOOD PLAIN The most important breeding area. The census area includes Flagstaff Hill, Netley Gut and Sheep Pound Gut to its junction with Mulberry Gut. The highest Wirebird densities are found on the upper half of the main plain and the grazed slopes of Flagstaff Hill. The lower paddocks bordered by Deadwood village are subject to heavy disturbance but may hold a large number of birds during severe weather.

BANKS' RIDGE An arid area of low scrub and *Carpobrotus* mat holding three or four pairs. Most Wirebirds are found below the 440m contour. Thick *Opuntia* scrub forms the lower boundary of available habitat.

LONGWOOD FARM Wirebirds occur at high density on pasture at Middle Point. Some nesting occurs amongst an extensive area of earth spoil heaps deposited after reservoir construction. The birds frequently feed on newly ploughed fields and nesting on the periphery of potato crops has been recorded.

LONGWOOD GOLF COURSE Wirebird numbers on the course are very variable (0-23 recorded), mainly because this site is a favoured feeding area for non-resident immature birds. The Golf Course probably holds up to five breeding pairs which nest both on the course itself and in the surrounding open scrub despite high levels of disturbance.

BOTTOMWOODS This area of very dry pasture has relatively sparse vegetation with a high proportion of broad-leaved weeds and holds the highest density of Wirebirds on the island. These are evenly distributed throughout the pastures but small numbers are also frequently found feeding amongst the open scrub on the rim of Fisher's Valley where it is probable that nesting occasionally occurs.

LONGWOOD EROSION ZONE A series of heavily eroded slopes and ridges lying between the pasturelands of Longwood Farm and Bottomwoods and Turk's Cap Valley. Nesting occurs at very low density, mainly above 350m.

WEATHER STATION RIDGE A relatively shallow slope running east from the weather station at Bottomwoods. Although sharing the same vegetation type and climate with the Erosion Zone the ridge normally holds a considerably greater density of Wirebirds, perhaps because it is flatter.

HORSE POINT PLAIN A broad, flat ridge dominated by *Carpobrotus* mats. The western end contains a rubbish dump and is therefore subject to regular disturbance. The amount of exposed rock increases from west to east and varies inversely with Wirebird density.

PROSPEROUS BAY NORTH Similar in vegetation to Horse Point Plain but lower in altitude and more heavily gullied. Wirebirds are evenly distributed throughout the area on broad ridges and shallow slopes.

FISHER'S VALLEY Most of this area consists of severely eroded hillsides with extensive gully systems amongst which a few Wirebirds occasionally feed, though no evidence of nesting was found. The valley bottom has a narrow strip of pasture on which two pairs held territories in 1989. Small pools at Cook's Bridge provide a bathing and drinking site which is heavily used, predominantly by non-resident juveniles.

PROSPEROUS BAY PLAIN An area of low-lying, predominantly flat semi-desert with sparse xerophytic/halophytic vegetation. Most Wirebirds are found in the southern half of the site, on the least stony parts amongst scattered *Suaeda helenae* shrubs. The rocky north-eastern parts of the plain are rarely used by Wirebirds.

UPPER PROSPEROUS BAY This large, *Carpobrotus*-dominated arid area lies to the south-west of Prosperous Bay Plain, between Fisher's Valley and Shark's Valley. The lower limit of the census area is approximated by the 320m contour and the upper limit by scrub at around 450m. The majority of Wirebirds occur on the ridge forming the southern side of Fisher's Valley and in the upper parts of Dry Gut.

STONE TOP RIDGE Very similar to the previous area. The few Wirebirds at this site tend to be concentrated on the shallower slopes around Boxwood Hill.

WOODY RIDGE Sheep pasture with a small area of arable land. Wirebirds are found mainly around the eastern end of the ridge. Numbers may vary according to the condition of the grass in this area, being greatest after heavy grazing.

CENTRAL PASTURES An extensive are of upland pasture sometimes referred to in part as Oakbank Upper Lands. It includes Bull Post, Smith's Spring, Alexander's, Crawford's, Beck Doveton's, Blisses and Swampy Gut pastures. Rising to 680m at Sandy Bay Ridge this area appears to provide suitable Wirebird habitat but only two single birds were observed during the present study and no evidence of breeding was found.

POUNCEYS A small area of upland pasture adjoining Pounceys settlement. At 600m-680m this is amongst the highest regular Wirebird breeding sites. Birds frequently move between this site and the Oaklands pastures.

OAKLANDS PASTURES A horseshoe-shaped area of pasture, mostly reclaimed flaxland, lying between Oaklands Hotel and the Clifford Arboretum. This site usually holds 2-3 pairs of Wirebirds on the eastern side of String Gut.

BROAD BOTTOM A major Wirebird site. In addition to Broad Bottom itself, the census area covers the High Peak, Thompson's Hill, Goldmine Gate and Woodlands areas including the French's Gut, Little Broad Bottom, Lemon Valley Head, Cason's, Sebastopol and Myrtle Grove pastures. Although the site is predominantly pastureland rising from 440m-760m there are also substantial areas of arable land at Woodlands and north of Broad Bottom Mill. Most nesting activity was observed on ridges with large areas of bare earth but Wirebirds were often found feeding on the lower sheep pastures or, most frequently, on ploughed land or among growing crops. Nesting among growing potatoes was recorded but it is not known how frequently this occurs.

HORSE PASTURE Wirebirds in the Horse Pasture area occupy a strip of open *Lantana/Opuntia* scrub and grassland 300m-400m wide along the southern rim of Lemon Valley. Grassland is confined to the public picnic site at the south-eastern end and comprises only 10% of the total area. During 1988-89 the picnic area held two resident pairs and was also used as a feeding area by small numbers of non-resident birds. Wirebird numbers in the scrub were variable but at least one pair appeared to be on territory.

BLUE HILL - HEAD O'WAIN A large area of cattle grazings, steeply sloping throughout and rising to 720m. Despite its apparent suitability this site holds very few Wirebirds. The maximum count was five and only one territorial pair was found. The pair occupied the disused cricket pitch to the north of West Lodge, significantly one of the few relatively flat areas.

SOUTHERN PASTURES Extensive pasturelands between Thompson's Wood and White Point including Botley's Lay, Wild Cattle Pound and the Churchyard. Botley's Lay and Wild Cattle Pound are sheep commonages while Thompson's Wood and the Churchyard are grazed by cattle. Almost all the Wirebirds in this area occur on the shallowest slopes of the sheep pasture around Wild Cattle Pound and Botley's Point where heavy grazing has resulted in a high proportion of bare earth.

MAN AND HORSE A dry sheep pasture in the extreme south-west extending from the west side of White Point to around the 360m contour above South-West Point, below which there is thick *Opuntia* scrub, and bounded on the north by Thompson's Valley. This major Wirebird site appears to have been overlooked by all previous authors. Wirebirds are found throughout the census area, the highest density occurring around Joan Hill and West Point.

3.5 COUNTS

Counts obtained in all census areas are presented in Table 3.1 with means and standard deviations. The total count ranged from 389 to 495 birds, with a mean of 447 (s.d. 47.8).

Wirebirds are patchily distributed throughout the island. Most are concentrated in the north-east quarter (Fig. 3.2), approximately 75% of the total being found between Sane Valley and Prosperous Bay Plain. Deadwood Plain is by far the most important site, holding around 30% of the population. No other single site holds more than 10% of the total. Other major sites are Bottomwoods, the south-western sheep pastures especially Man and Horse, and the whole of the arid region including Horse Point Plain, Prosperous Bay North, Prosperous Bay Plain and Upper Prosperous Bay. No Wirebirds were found in the area south of the central ridge including Sandy Bay.

Sites at which Wirebirds had been previously recorded but in which they were not seen in 1988-89 were Fairyland, High Hill (Ebony Plain), White Hill/Sandy Bay Barn, High Ridge, The Barn and Crack Plain. Non-resident Wirebirds were encountered outwith the census areas at Ladder Hill, Plantation House, Knotty Ridge, Jamestown wharf (in flight) and in various gardens in the Alarm Forest area.

3.6 CONCLUSIONS

The best estimate of the current Wirebird population from direct counts is the mean of the second, third and fourth censuses. This gives a figure of 466 birds. It is improbable that the true population is less than 450 individuals. If it is assumed that, within the census areas, birds overlooked and those counted more than once approximately cancel out and that around 20 birds can be added to allow for those omitted at the bathing sites or undetected elsewhere then the estimate approaches 500 birds.

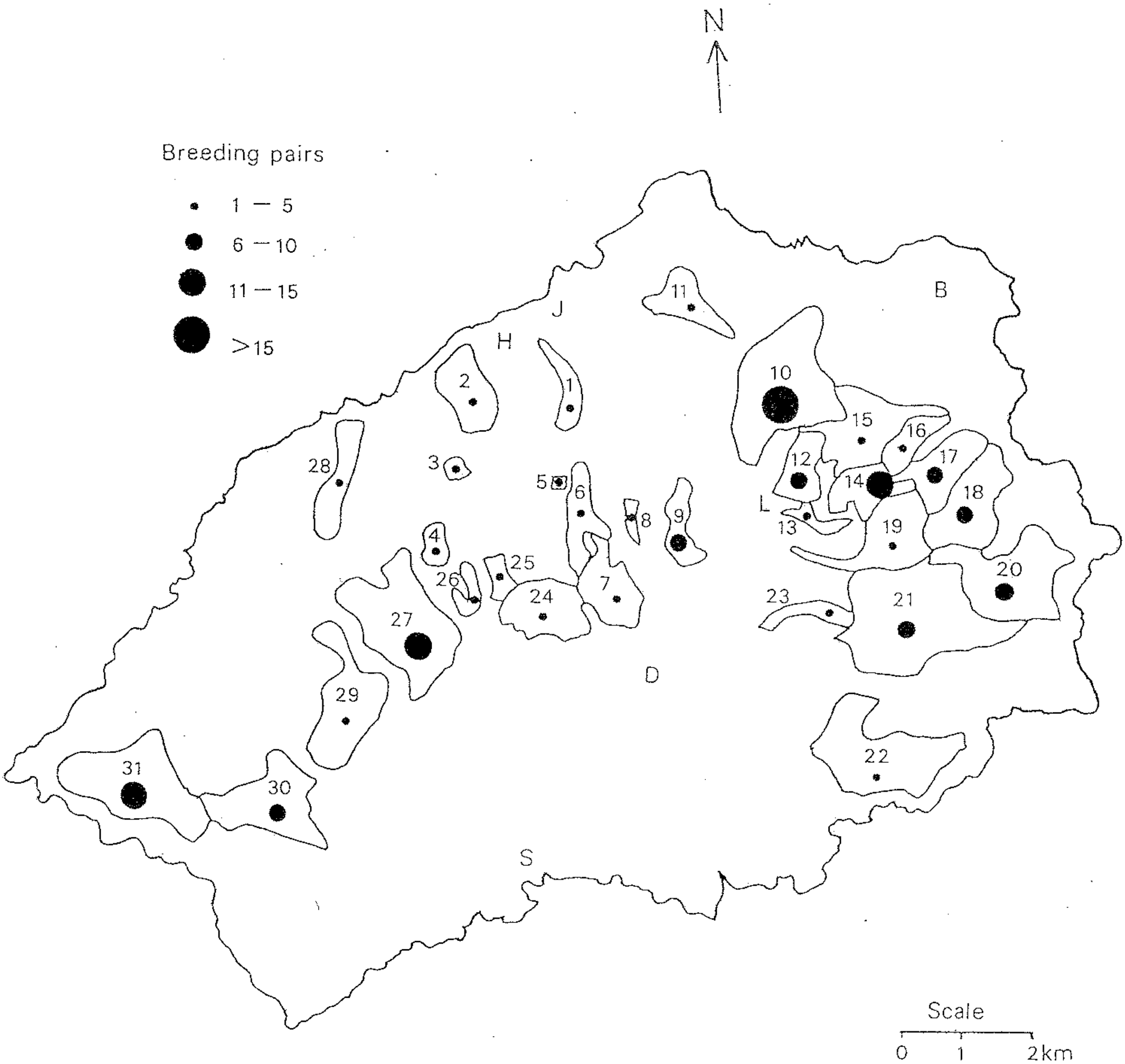


Figure 3.1 Map of St Helena showing Wirebird census areas (numbered), with estimated numbers of breeding pairs, and other principal localities mentioned in the text.

Census areas: 1. Cow Path/High Knoll; 2. Donkey Plain; 3. Cleugh's Plain; 4. Rosemary Plain; 5. Francis Plain; 6. Barren Hill; 7. The Dungeon; 8. Prospect Pastures; 9. Sane Valley; 10. Deadwood Plain; 11. Banks' Ridge; 12. Longwood Farm; 13. Longwood Golf Course; 14. Bottom Woods; 15. (Longwood Erosion Zone); 16. (Weather Station Ridge); 17. Horse Point Plain; 18. (Prosperous Bay, north); 19. Fisher's Valley; 20. Prosperous Bay Plain; 21. (Upper Prosperous Bay); 22. Stone Top Ridge; 23. Woody Ridge; 24. (Central Pastures); 25. Pounceys; 26. Oaklands Pastures; 27. Broad Bottom; 28. Horse Pasture; 29. Blue Hill/Head o' Wain; 30. (Southern Pastures); 31. Man and Horse. Parentheses indicate names of convenience (see text).

Other localities: B = The Barn; D = Diana's Peak; H = Half-Tree Hollow; J = Jamestown; L = Longwood; S = Sandy Bay.

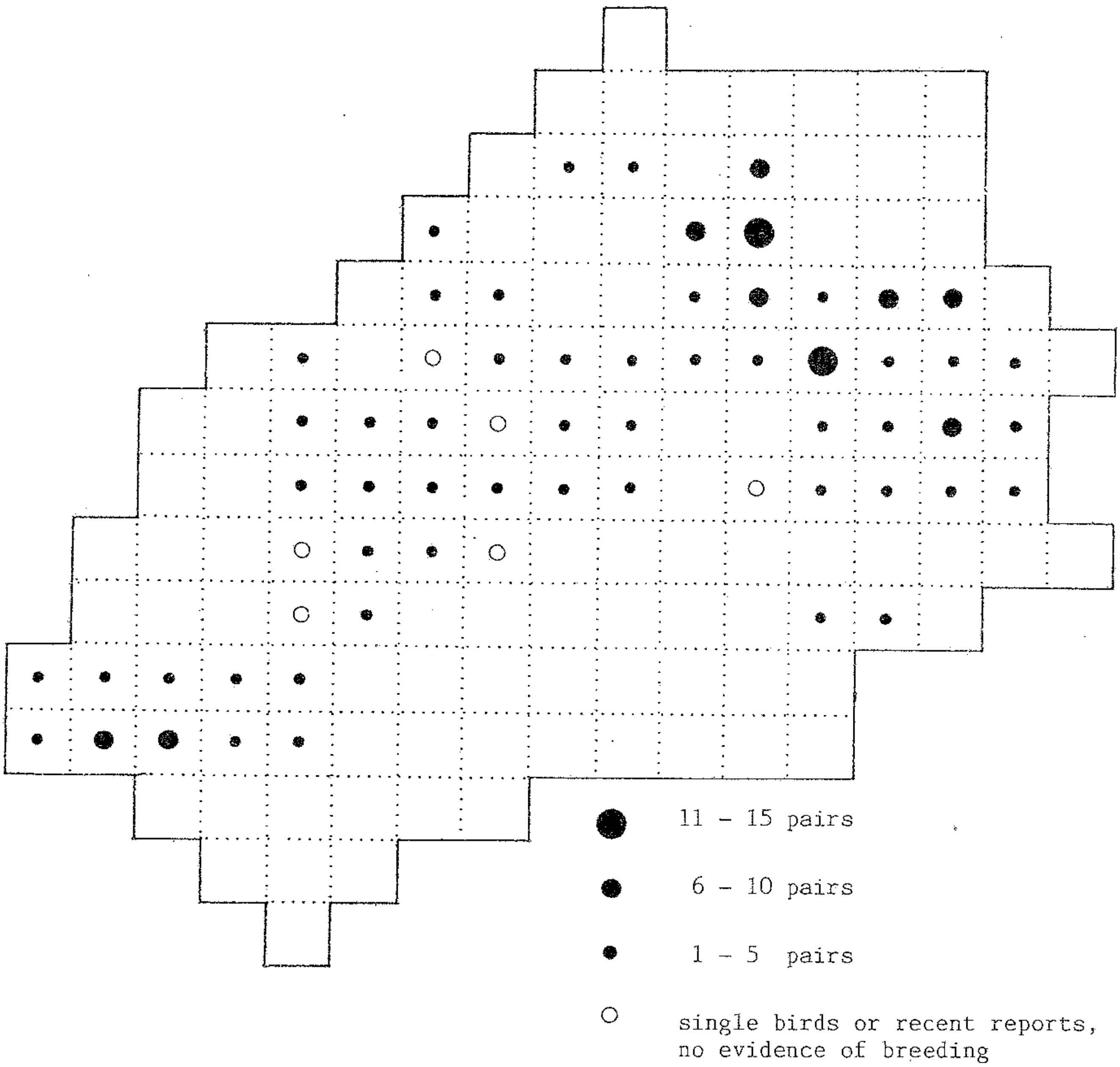
Table 3.1 Censuses of Wirebird populations

	Census Area	Count 1 Oct-Nov 1988	Count 2 Feb-Mar 1989	Count 3 Jun-Jul 1989	Count 4 Oct-Nov 1989	Mean	S.D.
1	High Knoll/Cowpath	-	-	0	2	1	1.41
2	Donkey Plain	4	2	5	4	4	1.26
3	Cleugh's Plain	2	0	0	0	1	1.00
4	Rosemary Plain	0	3	3	2	2	1.41
5	Francis Plain	2	1	6	3	3	2.16
6	Barren Hill	13	9	7	6	9	3.10
7	Prospect Pastures	0	2	2	2	2	1.00
8	Dungeon	5	0	0	0	1	2.50
9	Sane Valley	12	19	13	14	15	3.11
10	Deadwood Plain	129	147	150	121	138	14.01
11	Banks' Ridge	6	6	6	12	8	3.00
12	Longwood Farm	13	22	15	17	17	3.86
13	Longwood Golf Course	18	7	16	6	12	6.13
14	Bottomwoods	37	53	40	47	44	7.18
15	(Longwood Erosion Zone)	6	6	7	5	6	0.82
16	(Weather Station Ridge)	2	6	7	0	4	3.30
17	Horse Pt. Plain	20	13	20	21	19	3.70
18	(Prosperous Bay North)	24	6	17	19	17	7.59
19	Fisher's Valley[a]	1	2	0	4	2	1.71
20	Prosperous Bay Plain	14	9	43	20	22	15.02
21	(Upper Prosperous Bay)	15	10	26	29	20	8.98
22	Stone Top Ridge	-	-	4	6	5	1.41

23	Woody Ridge	2	1	0	13	4	6.06
24	(Central Pastures)	1	1	0	0	1	0.58
25	Pounceys	5	2	1	4	3	1.83
26	Oaklands Pastures	2	5	5	1	3	1.06
27	Broad Bottom	19[b]	38	42	38	34	10.34
28	Horse Pasture	11	6	9	8	9	2.08
29	Blue Hill-Head o'Wain	0	4	5	4	3	2.22
30	(Southern Pastures)	3[b]	16	13	20	13	7.26
31	Man and Horse	23	31	33	47[c]	34	9.98
	Total	389	427	495	475	447	47.79
	Mean total, based on counts 2, 3, 4 only					466	34.95

- Not covered
a Excluding Cook's Bridge
b Poor visibility
c Census area extended

Figure 3.2. Breeding distribution of Wirebirds during 1988-89 based on 1 kilometer squares.



4. HABITAT

The previous section has shown that Wirebirds are not evenly distributed throughout St Helena. The major environmental factors influencing distribution, other than food abundance (which will be dealt with separately), are likely to be topography (i.e. steepness of slope), climate (particularly rainfall), and vegetation. These factors are presented for each census area in Table 4.1. The density of Wirebirds at a particular site is the best available indicator of the overall suitability of the site, so the relationship between density and each of the above variables was investigated.

Density was estimated by dividing the mean number of birds counted at a site during the four censuses by the area of the site. The area was calculated from the 1:25000 map of St Helena by scale drawing on squared paper. Area was estimated to the nearest 5ha for sites larger than 10ha, to the nearest 1ha for smaller sites.

4.1 TOPOGRAPHY

The literature and initial field observations suggested that Wirebirds prefer relatively flat areas. An inverse relationship between bird density and gradient would be expected if this were the case.

An average gradient was calculated for each census area, again using the 1:25000 map, by expressing the altitudinal increment along the axis of the dominant slope as a percentage of the horizontal distance. In the case of valley sites the mean of the constituent gradients was taken.

Regression of population density on gradient revealed a significant inverse correlation ($r = -0.61$, $P<0.01$, $n = 31$). To minimize bias resulting from overestimation of density on small sites, the correlation coefficient was re-calculated with sites of less than 10ha excluded. It was still significant ($r = -0.46$, $P<0.05$, $n = 29$). An improved description of the relationship, explaining 29% of the variance in Wirebird density, was obtained by the addition of a quadratic term to the equation ($r= -0.nn$, $p<0.nn$, $n = 29$: see Fig.4.1). Interpretation of these results is, however, complicated by the generally low bird densities found at semi-desert sites which are likely to be mainly unrelated to topography. Repetition of the curvilinear regression using only data from pastureland sites confirmed the existence of the relationship ($r = -0.74$, $p<0.01$, $n = 16$), explaining 55% of the variance in Wirebird density.

The total area of all census sites was divided into six gradient classes and the hypothesis that Wirebird distribution is unrelated to gradient was tested by the application of a G-test for goodness of fit (Sokal and Rohlf 1981) to the numbers of birds observed and expected in each class. Prior to testing, these figures were divided by three to allow for individual Wirebirds not being independently distributed, a substantial proportion of the population being found as territorial pairs or family parties. This will tend to increase the between-site variance and thus inflate the value of G. The creation of "pseudo-groups" of three in the analysis reduces this effect. Pairs and solitary birds will greatly outnumber family groups at any particular time, therefore the G-value resulting from a "pseudo-group" size of three will be conservative. This method was applied to all G-tests in Table 4.2.

The G-test revealed a highly significant non-random distribution (Table 4.2a). Sites with a gradient of less than 6% held an excess of birds and all other classes held fewer than expected. The analysis is fairly crude and fails to take into account the tendency of Wirebirds at sites with a high mean gradient to congregate on the flatter parts. Thus the effective area of many census sites is considerably smaller than that delimited by apparently suitable vegetation. These results do, however, support the hypothesis that Wirebirds find areas with a gradient greater than 10% relatively unattractive.

4.2 RAINFALL

Annual rainfall for each census area was estimated from a recent map of isohyets (Mathieson 1990b) as the mean of the isohyet values within which the site lies. No correlation between Wirebird density and annual rainfall was found ($r = -0.03$, $n = 29$). However, this analysis assumes a linear relationship and application of a G-test to the numbers falling into five rainfall classes showed a significant excess of birds in areas receiving between 300mm and 700mm rain annually (Table 4.2b). The most favoured areas, between the 300mm and 500mm isohyets, hold 72% more Wirebirds than would be expected if distribution were random.

The exact nature of the influence of rainfall on Wirebird distribution is unclear but is probably related to its effects on prey availability and plant growth. In areas receiving least rain invertebrates appear to occur at low density (see Section 5) and in high rainfall areas, although invertebrates may be less scarce, they may be difficult to find amongst the longer, denser vegetation. The greater frequency of rainfall and low temperatures in the latter areas may also make the successful rearing of chicks less likely, as feeding time will be restricted by the increased requirement for brooding. These ideas remain untested.

4.3 VEGETATION

4.3.1 COMPOSITION OF VEGETATION

Wirebirds were found in a variety of vegetation types. The only general statement that can be made about their distribution in relation to vegetation is that they avoid woodland and thick scrub. The remaining open areas occupied by Wirebirds fall into two broad classes: grassland and semi-desert. "Grassland" includes vegetation types 1 and 2 of Table 4.1 while "semi-desert" includes types 5 and 6.

Mean Wirebird densities (log-transformed) were compared between these two vegetation types by single-classification analysis of variance, using only sites larger than 10ha. The means for grassland and semi-desert were 0.29 birds/ha and 0.09 birds/ha, which differ significantly at the 5% level ($F(1,24) = 4.45$). Within the grassland there was also a significant difference between the mean density on intermediate pastures (0.36 birds/ha and that on upland pastures (0.13 birds/ha) at the 5% level ($F(1,15) = 5.90$). (Although closely resembling intermediate pastures in species composition the Longwood Golf Course was excluded from this analysis because of the atypical variability of Wirebird numbers at this site. Its inclusion would have strengthened both differences.)

Further evidence of a preference for intermediate pasture was provided by the result of a G-test carried out on the observed and expected numbers of Wirebirds for the three vegetation types. The observed distribution was significantly non-random, the total number of

Wirebirds on intermediate pasture being twice that expected and fewer than expected being found in the other classes (Table 4.2c).

The vegetational composition of 19 census areas was sampled using quadrats of 0.25m area. The number of quadrats allocated to an area was equivalent to one quadrat/ha. At large sites quadrats were laid in sub-sets of 10 to 20, which were distributed so as to ensure a fully representative coverage of the whole area: where more than one vegetation type was apparent within a census site quadrats were allocated to each type in proportion to its area; within each sub-set the position of each quadrat was randomized. The direction taken and distance moved between individual quadrats were determined using a table of random numbers. Two series of numbers were used. The first, varying between 1 and 12, determined direction from the starting point in terms of a clock-face. The second series, ranging from 1 to 100, indicated the number of paces to be moved. All species present within each quadrat were listed and the percentage of the total area covered by each species, or by bare earth or rock, was recorded. "Rock" includes bedrock, boulders and gravel of greater than 2cm diameter. Finer gravels were included in "bare earth". The mean percentage cover was calculated for each species at all sites sampled. The analysis includes data adapted from Brown (1982) for the "Southern Pastures" census area.

Table 4.3 shows the major components of the plant communities at pastureland sites. Differences in the mean percentage cover of all the major grass species, broad-leaved weeds and bare earth between intermediate and upland pastures were tested by single- classification analysis of variance. The two pasture types differ mainly in the proportion of *Agrostis tenuis* present, this being greater in upland pastures which have generally more grasses and less bare earth (Table 4.4). Bottomwoods is atypical of the intermediate pastures, having much less extensive grass cover (though this varies seasonally) and a higher proportion of broad-leaved weeds and bare earth (Table 4.3). However, all significant differences between the pasture types still hold when Bottomwoods is removed from the analysis.

Linear regression of Wirebird density on pastureland components revealed significant positive relationships with percentage Kikuyu Grass and percentage broad-leaved weeds ($r = 0.58$, $p<0.05$ and $r = 0.92$, $p<0.001$). The slopes of the relationships with *Agrostis tenuis*, Mat Grass and Cow Grass were negative but not significant. There was also a positive correlation between density and percentage bare earth ($r = 0.84$, $p<0.001$). Mean coverage by Hay Grass was significantly greater on upland sites while broad-leaved weeds and bare earth occurred over a greater area of Intermediate pastures (Table 4.4).

Table 4.5 presents the vegetational composition of semi-desert areas (Crown Wastes). There is little species overlap between these areas and pastureland. Typically more than half the area is unvegetated and creeper *Carpobrotus edulis, Atriplex semibaccata* and *Suaeda helenae* are the dominant plant species. Although *C. edulis* is the most important single plant, dead material comprises more than half the area covered by this species. This forms an extensive ash-like layer around the growing plants. No correlation was found between Wirebird density and percentage cover of any component species.

4.3.2 VEGETATION HEIGHT

In section 4.2 it was suggested that taller vegetation might reduce Wirebird density because it reduced both detectability of the prey and mobility of the birds. This might partially explain the relative scarcity of Wirebirds on upland pastures. It is difficult to investigate the effect of vegetation height on bird density by comparison of different sites as elimination of other contributory factors is difficult. It was, however, possible to study the effect of varying vegetation height within a single census area, (Deadwood Plain), thus largely controlling for other environmental parameters.

Deadwood Plain is grazed by cattle throughout the year. Grazing is rotated amongst a number of paddocks. During the dry season (approx. November-February) the combined effects of grazing and dehydration keep the grass uniformly short throughout the area. After the onset of the rains (usually around March) a mosaic of grass-lengths is produced, the mean length in any particular paddock being related to the time since it was last grazed.

Such mosaic conditions prevailed in April and May of 1989. In April the paddocks were subjectively classified as "long" or "short" with respect to grass length. Five paddocks were selected from each group, the total area covered by each category being approximately equal. Twenty-five random point measurements of grass length, to the nearest 1mm, were made in each paddock. Means were compared within groups by single-classification analysis of variance and found not to differ significantly between paddocks. The combined data were then used to compare the group means, which differed significantly ("long" = 11.99cm, s.d. 5.26; "short" = 3.62cm, s.d. 1.56; $F(1,248) = 289.3$. $p<0.001$). Wirebirds were counted in each paddock, at the same time of day, for nine consecutive days until the grazing regime was changed. The mean daily count within each group did not differ significantly between days. The data were combined to compare group means, which differed significantly ("long" = 12 birds, s.d. = 3.6; "short" = 52 birds, s.d. = 12.1; $F(1,14)= 108.2$, $p<0.001$). The equivalent group totals from the February census, when the grass was uniformly short, were 41 and 35 birds respectively. These single observations were compared with the April group means by a t-test (Sokal and Rohlf 1981). The total for the "short" group did not differ from those found there after the rains ($t = 1.34$, 8 df) but the "long" group total was significantly higher than in April ($t = 7.71$, 8 df, $p<0.001$). This suggests a movement away from areas of ungrazed grass after the resurgence of growth stimulated by the rains.

At all grassland sites at which quadrat sampling was carried out, the height of the vegetation was also measured at 0.5m intervals along a 20m line transect originating from the centre of every fifth quadrat. Mean vegetation heights are shown in Table 4.3. Regression of Wirebird density against mean vegetation height revealed a significant inverse relationship ($r =0.63$, $P<0.05$, $n = 12$: see Fig.4.2).

4.3.3 VEGETATION DENSITY

Wirebird distribution may also be affected by the density of vegetation in terms of the number of plants or stems per unit area. This was not measured directly during my study but, as density will tend to be strongly influenced by the abundance of sward forming species, the percentage total grass cover may give some indication of density. Amongst pastureland sites there is a significant negative correlation between Wirebird density and this total ($r = -0.89$, $p<0.01$, $n = 12$: see Fig.4.3) but the high significance level of the relationship is dependent on the inclusion of the atypical Bottomwoods. Although it has a higher Wirebird density than any other major site, the total vegetation cover at Bottomwoods is comparable with that at semi-desert sites which typically have very low bird densities. Vegetation density at this site is more rainfall dependent than any of the other pastureland areas, but despite this variability growth is always relatively sparse. If, however, Bottomwoods is excluded from the analysis the relationship, though weaker, remains significant ($r = -0.66$, $P<0.05$, $n = 11$).

It appears that an area with a sparse but evenly distributed vegetation cover, like Bottomwoods, is more attractive to Wirebirds than one with a similar amount of vegetation distributed in discrete, more dense patches, probably because of differences in food abundance and detectability.

No evidence of an effect of percentage ground cover on bird density was found when this was compared between the two groups of paddocks at Deadwood Plain that differed significantly in vegetation height and Wirebird numbers, the mean percentage cover being similar in both groups.

This analysis does not provide conclusive evidence that vegetation density is an important factor in determining Wirebird distribution, but suggests that it may indeed have some influence. A major programme of Kikuyu Grass planting was initiated in the 1950's with the aim of stabilising over-grazed pastures under threat from erosion (Humphrey 1957). The species has subsequently spread widely throughout the island. Although methodological differences preclude statistical comparison of the results obtained in this study with extensive sampling carried out by Brown (1982) these suggest that Kikuyu Grass has continued to become more abundant since the latter study, largely supplanting Wire Grass and other less robust species at many sites. One can only speculate as to whether the dense, springy swards formed by Kikuyu Grass in well-watered upland areas has affected their attractiveness to Wirebirds.

4.4 CONCLUSIONS

Data collected during this study indicate that areas most favoured by Wirebirds can be characterized as pastureland containing a high proportion of Kikuyu Grass *Pennisetum clandestinum* in relation to other grass species; with at least 10% of the ground covered with broad-leaved weeds; mean vegetation height less than 10cm; a gradient of less than 6%; and an annual rainfall of 300-500mm. Wirebird distribution may not necessarily be directly influenced by all of these factors, however.

Table 4.1 Census areas: Environmental parameters and Wirebird density (birds/ha)

Census Area	Area (ha)	Wirebird density	Altitudinal range (m)	Mean gradient (%)	Vegetation type	Rainfall
High Knoll/Cowpath	20	0.05	280-580	2	3	2
Donkey Plain	85	0.04	160-410	18	3,4	1,2
Cleugh's Plain	10	0.05	360-430	20	2	2
Rosemary Plain	15	0.13	500-600	10	2	4
Francis Plain	2	1.50	450	0	2	3
Barren Hill	35	0.25	420-550	13	1,2	2,3,4
Prospect Pastures	7	0.21	520-560	15	1	4
Dungeon	55	0.02	500-680	19	1	4,5
Sane Valley	40	0.36	400-540	22	2	3,4
Deadwood Plain	300	0.46	530-640	4	2	2
Bank's Ridge	75	0.10	320-500	11	3,5	1
Longwood Farm	35	0.48	440-530	8	2	3
Longwood Golf Course	15	0.79	500-530	3	23	
Bottomwoods	45	0.98	440-500	6	2	2,3
Longwood Erosion Zone	125	0.05	240-510	12	6	1,2
Weather Station Ridge	55	0.07	280-430	13	5,6	2
Horse Point Plain	80	0.23	360-430	6	5,6	2
Prosperous Bay (North)	110	0.15	240-400	13	5,6	2
Fisher's Valley	120	0.02	300-440	8	2,6	2
Prosperous Bay Plain	150	0.14	280-320	2	5,6	1,2
Upper Prosperous Bay	360	0.06	240-460	7	5,6	1,2
Stone Top Ridge	195	0.03	200-490	13	6	1,2
Woody Ridge	25	0.16	450-560	8	2	3
Central Pastures	80	0.01	520-680	25	1	5
Pounceys	15	0.20	600-680	12	1	4,5
Oaklands Pastures	15	0.22	560-640	9	1	4
Broad Bottom	200	0.20	440-680	19	1,2	4
Horse Pasture	60	0.14	200-580	21	2,4	2
Blue Hill-Head o'Wain	125	0.03	520-720	21	1,2	4
Southern Pastures	160	0.10	400-690	13	1,2	3,4
Man and Horse	145	0.23	400-680	20	2,3,4	2,3

Key:

Vegetation type (after Cronk 1989)

1 : Upland pasture
2 : Intermediate pasture
3 : Opuntia scrub
4 : Lantana scrub
5 : Creeper waste
6 : Eroded desert

Rainfall

1 : <300mm
2 : 301-500mm
3 : 501-700mm
4 : 700-900mm
5 : >900mm

Table 4.2 Wirebird distribution in relation to gradient, rainfall and vegetation types

a)

Gradient (%)	No. Wirebirds Observed	Expected
0-5	174	77
6-10	111	115
11-15	55	115
16-20	74	81
21-25	13	34
26-30	28	33

G = 49.3, 5df, p<0.001

b)

Annual rainfall (mm)	Observed	Expected
<300	65	163
300-500	268	156
500-700	73	51
700-900	48	71
>900	1	13

G = 59.3, 5df, p<0.001

c)

Vegetation type	Observed	Expected
Intermediate pasture	281	139
Upland pasture	56	94
Semi-desert	101	205

G = 65.1, 5df, p<0.001

Figure 4.1 Relationship between Wirebird density (birds/ha) and mean gradient (percent) in census areas of at least 10ha.

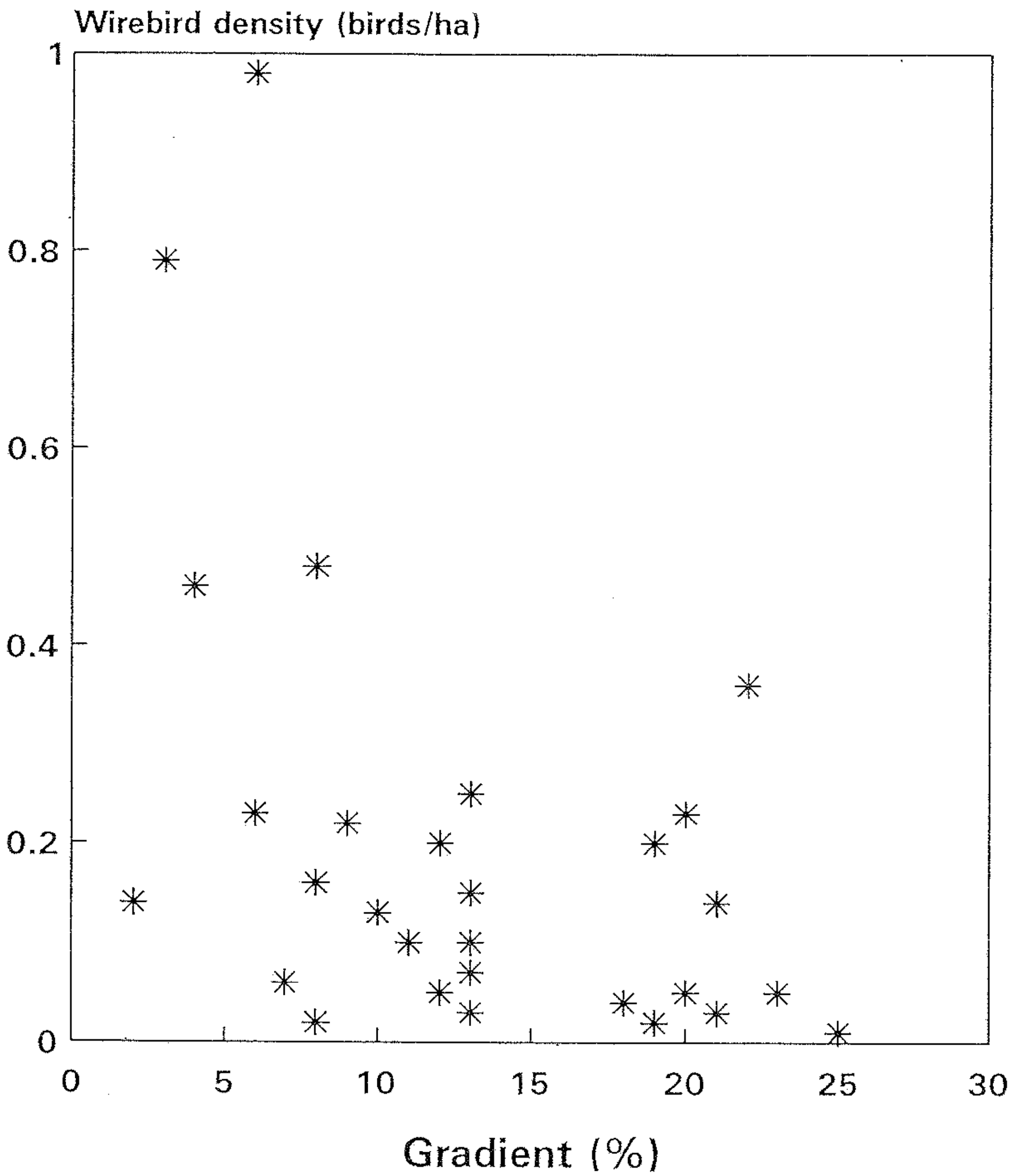


Table 4.3a Vegetational composition of Wirebird breeding sites on pastureland, expressed as percentage cover.

	Intermediate pasture					
	SV	DWP	LF	SP*	MH	BW
Kikuyu Grass *Pennisetum clandestinum*	47.3	49.2	50.3	32.1	42.2	2.2
Mat Grass *Stenotaphrum secundatum*	27.9	0.3	1.8	27.3	0.4	0
Hay Grass *Agrostis tenuis*	0.4	1.2	0.1	0.6	0.2	0.5
Wire Grass *Cynodon dactylon*	0.1	0.5	1.6	3.8	9.4	3.9
Cow Grass *Paspalum scrobiculatum*	0	0.1	0	1.1	1.0	0
Other Grasses	6.8	15.9	3.0	19.8	3.4	0.4
Gorse *Ulex europaeus*	0	0	0	0.1	1.0	0
Lantana *Lantana camara*	0.2	0.2	0.6	0	1.0	0.8
Creeper *Carpobrotus edulis*	0	0.1	2.3	0	0	1.6
Wild Pea *Vicia sativa*	0.4	6.0	1.5	0	0	0
Broad-leaved Weeds	2.6	15.1	12.3	4.8	8.0	32.8
Bare Earth	4.6	9.2	20.4	9.5	26.1	53.1
Vegetation height (cm)	**7.1**	**8.2**	**7.1**	-	**6.0**	**6.6**

* Data from Brown (1982)

Key:
SV = Sane Valley
DWP = Deadwood Plain
LF = Longwood Farm
SP = Southern Pastures
MH = Man and Horse
BW = Bottomwoods

Table 4.3b Vegetational composition of Wirebird breeding sites on pastureland, expressed as percentage cover.

	Upland pasture						
	BH	D	CP	P	O	BB	BLH
Kikuyu Grass *Pennisetum clandestinum*	65.1	37.9	61.1	33.3	42.5	52.9	54.5
Mat Grass *Stenotaphrum secundatum*	2.3	17.7	2.6	3.1	0.1	16.5	23.7
Hay Grass *Agrostis tenuis*	2.5	12.2	10.6	30.8	20.0	10.2	9.1
Wire Grass *Cynodon dactylon*	2.6	0.9	0	0	0	0.1	0
Cow Grass *Paspalum scrobiculatum*	0	10.7	4.2	15.4	5.5	0.5	0.4
Other Grasses	1.1	4.7	14.7	11.5	19.3	8.6	6.5
Gorse *Ulex europaeus*	0.1	0.3	0	0	0.3	0.2	0.1
Lantana *Lantana camara*	0	0	0	0	0	0.1	0
Creeper *Carpobrotus edulis*	0	0	0	0	0	0	0
Wild Pea *Vicia sativa*	0	0	0	0	0	0	0
Broad-leaved Weeds	8.1	3.6	1.2	1.9	8.3	5.5	2.2
Bare Earth	6.5	3.7	2.0	3.2	2.0	6.6	2.2
Vegetation height (cm)	**8.2**	**13.3**	**13.0**	**7.2**	**9.4**	**8.6**	**9.4**

Key: BH = Barren Hill
D = The Dungeon
CP = Central pasture
P = Pounceys
O = Oaklands
BB = Broad Bottom
BLH = Blue Hill-Head O'Wain

Table 4.4 Mean percentage covered by major vegetational components in intermediate and upland pastures, with results of comparison by single - classification analysis of variance.

	Intermediate Pastures Mean	Upland Pastures Mean	F(1,11)
Kikuyu Grass *Pennisetum clandestinum*	38.2	49.6	1.69
Mat Grass *Stenotaphrum secundatum*	9.6	9.4	0.00
Hay Grass *Agrostis tenuis*	0.5	13.6	12.16**
Wire Grass *Cynodon dactylon*	3.2	0.5	4.04
Cow Grass *Paspalum scrobiculatum*	0.4	5.2	4.06
All Grasses	60.1	87.9	6.33*
Broad-leaved weeds	12.6	4.4	3.69
Bare Earth	20.5	3.7	6.15*
Vegetation height (cm)	**7.0**	**9.9**	**8.82***

Key: * $P<0.05$, *** $P<0.001$

Table 4.5 Vegetational composition of Wirebird sites in the Crown Wastes (semi-desert).

	Percentage Cover				
	BR	HPP	PBN	PBP	UPB
Creeper *Carpobrotus edulis* (live)	7.0	14.2	7.7	5.2	19.5
Creeper *Carpobrotus edulis* (debris)	9.5	24.4	11.9	6.3	11.8
Atriplex semibaccata	2.7	6.7	2.4	5.2	6.9
Suaeda helenae	2.4	0	6.7	5.8	8.0
Eragrostis cilianensis	0	0	0.5	3.1	1.5
Broad-leaved Weeds	0.6	0.6	1.0	0.9	0.1
Ice Plant *Mesembryanthemum crystallinum*	0.1	0.6	0.9	0.1	1.5
Prickly Pear *Opuntia* spp.	0.3	0.4	0.3	0	0.4
Wild Coffee *Chrysanthemoides monilifera*	1.3	0	0	0	0.1
Baby's Toes *Hydrodea cryptantha*	0	0	0	0.1	0
Lantana *Lantana camara*	0.1	0	0	0	0
Lichens	2.0	0.3	1.3	1.4	1.5
Bare Earth	58.0	39.2	55.1	44.1	37.3
Rock	14.8	13.7	12.7	28.1	10.7

Key: BR = Banks' Ridge
HPP = Horse Point Plain
PBN = Prosperous Bay North
PBP = Prosperous Bay Plain
UPB = Upper Prosperous Bay

Figure 4.2 Relationship between Wirebird density (birds/ha) and mean vegetation height (cm) at 12 pastureland census areas.

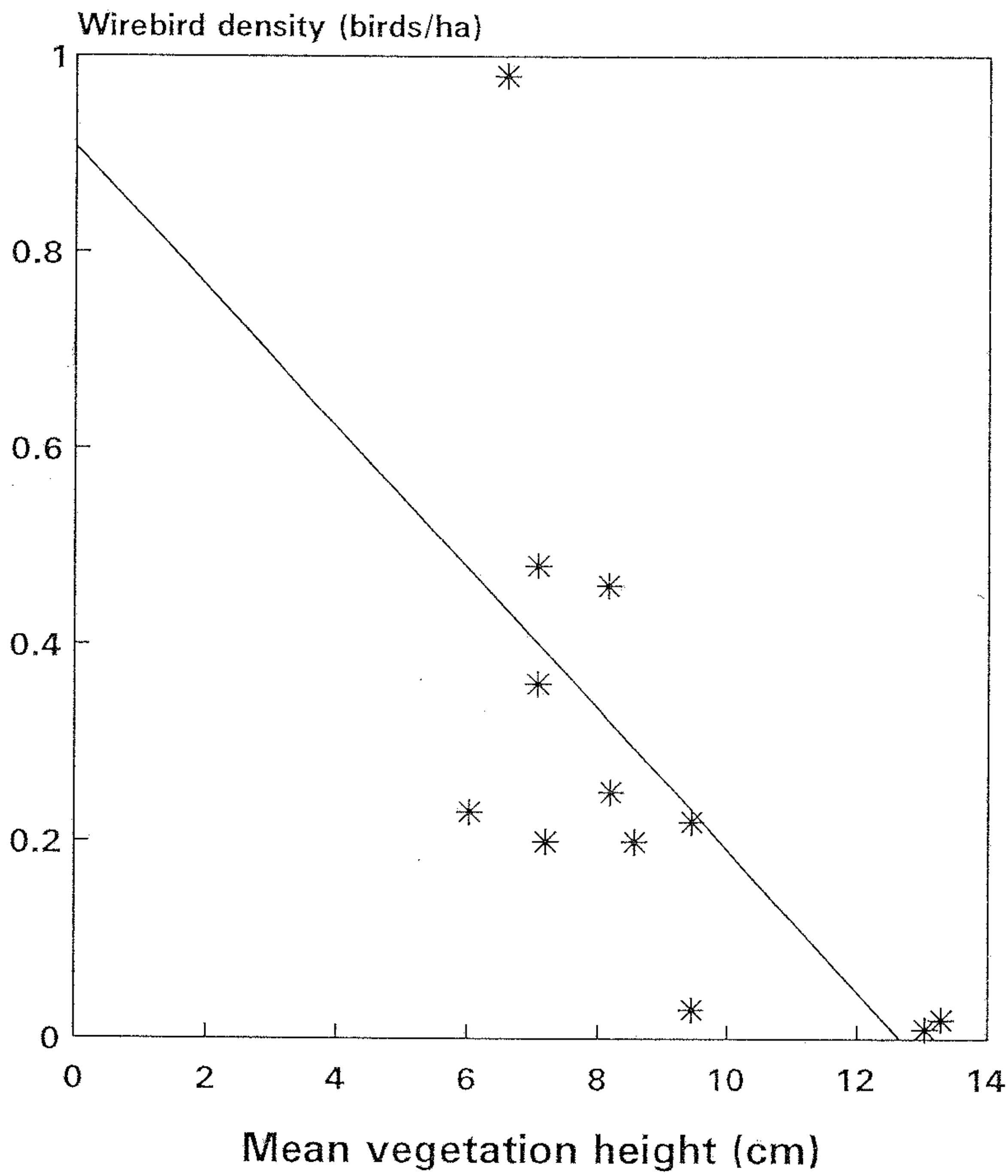
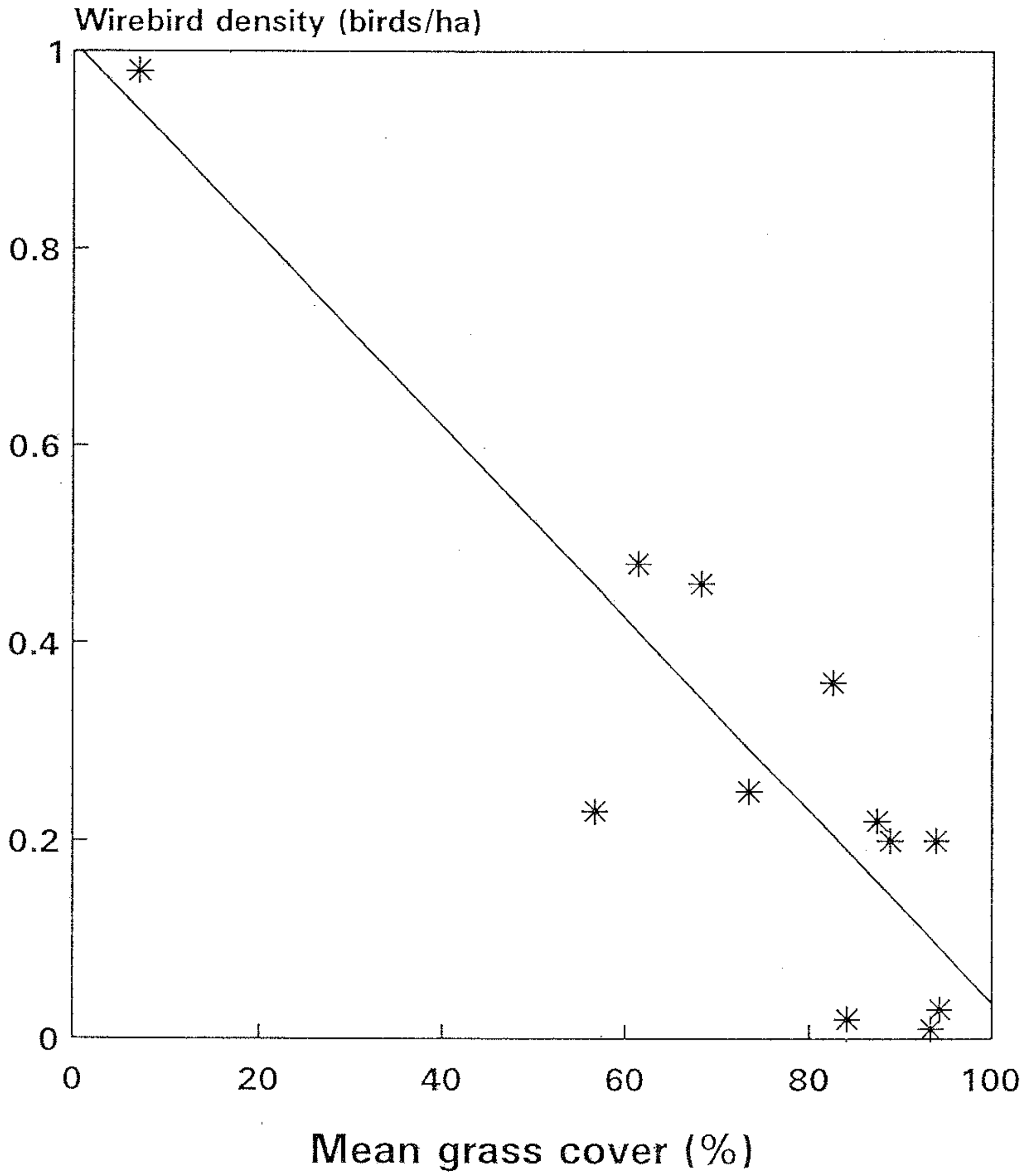


Figure 4.3 Relationship between Wirebird density (birds/ha) and percentage grass cover at 12 pastureland census areas.



5. FOOD AND FEEDING

5.1 DIET

The literature contains few references to the diet of the Wirebird. Layard (1867) examined the stomach contents of his specimens and found beetles (*Coleoptera*) and small snails (*Gastropoda*); Loveridge (1974) recorded a Wirebird taking various immobilized insects from a flat roof after heavy rain; Hartog (1984) was able to confirm that small snails were taken: and Alexander (1985) reported large beetles frequently being caught.

The prey of the closely-related Kittlitz's Sand Plover *Charadius pecuarius* in southern Africa has been more intensively studied. Beetles appear to predominate in the diet (Tree 1974) but crickets and grasshoppers (*Orthoptera*), earwigs (*Dermaptera*), bugs (*Hemiptera*), moth and butterfly caterpillars (*Lepidoptera*), flies (*Diptera*), ants (*Hymenoptera*), spiders (*Aranea*), mites (*Acarina*), earthworms (*Annelida*) and snails are also known to be taken (Cramp and Simmons 1983).

It is probable that a similar range of prey is taken by the Wirebird. During this study all identifiable organisms eaten by Wirebirds under observation were recorded, a total of 214 organisms (Figure 5.1). Beetles and caterpillars were the most frequently observed prey. Prey identification in the field is difficult, particularly as most smaller items are swallowed before the bird raises its head from the grass. Consequently the results are likely to be biased towards larger organisms. However, dissection of the gizzard (the stomach was missing) from a dead bird found on Longwood Golf Course supported the observational data. The gizzard contained eight beetles, tentatively identified as *Hopatrum hadroides* (*Hopatridae*) from a description in Melliss (1875), three caterpillars and three ants. "*Hopatrum*" is likely to be the single most important prey species as it is extremely abundant at all the major pastureland Wirebird sites. Most prey items are no more than 10mm in length but birds were seen to take a 40mm grasshopper and earthworms up to 120mm. In addition to those species listed, Wirebirds were seen to pick up a millipede (*Diplopoda*) and a carabid beetle and then drop them. As both these species secrete strong-smelling substances it is possible that they are distasteful.

5.2 PREY ABUNDANCE

The relative abundance of ground-living invertebrates at a number of Wirebird breeding sites was estimated by regular pit-fall trapping. At each trapping site a 4 x 3 grid of 12 pots spaced at 5m intervals was used. In the largest census areas up to three such grids were operated simultaneously. The pots were plastic drinking cups, 9cm deep and 7cm diameter, giving a total catching perimeter of 264cm for each grid. Trapping was carried out at 15 sites but regular sampling was confined to Barren Hill (2 grids), Deadwood Plain (3 grids), Bottomwoods, Horse Point Plain and Broad Bottom (2 grids), which were used every month in 1989, and Longwood Farm and Prosperous Bay Plain (3 grids) where trapping was bi-monthly. This analysis is confined to these seven sites. Within each month three consecutive 24-hour samples were taken, the mean being used in this analysis to reduce any effect of variation in catches between days caused by climatic conditions.

Pit-fall catches can be affected if the hole for each pot has to be re-dug after every sample is removed. To avoid this, the trapping pot was placed inside another, which formed a jacket into which the trap pot could be replaced without the soil being disturbed. All pots were removed between trapping periods and the positions of the holes were marked to aid relocation.

The composition of the total catch for the year at each of the sites sampled monthly is presented in Table 5.1 and the mean daily catch in Table 5.2. Collembola were excluded from the analysis as their occurrence in the traps was more heavily influenced by climatic conditions than any other species and their extremely small size (<1mm) makes them unlikely to be significant Wirebird prey.

The biomass of trapped samples was not measured directly but an indication of the relative mass of samples from different sites can be gained from the composition of the total catch in terms of body length (Table 5.3).

The effect of rainfall on invertebrate abundance was investigated by regression of the mean daily catch for each month on monthly rainfall at the nearest recording station. This was done for all monthly sampling sites, using data for the period January-November 1989. No significant correlations were found. Bottomwoods was the only site for which monthly temperature data were available but regression of mean daily catch on maximum temperature failed to reveal any relationship.

If there is an overall seasonal pattern of invertebrate abundance on St Helena then the relative size of monthly catches should show similarity between sites. This hypothesis was tested by ranking the monthly catches at each grid where trapping was carried out every month and using these ranks to calculate Kendall's coefficient of concordance (w).

This showed significant concordance between sites ($w = 0.28$, $X^2 = 24.8$, $P<0.001$, 11df). Figure 5.2 shows changes in relative abundance of invertebrates at monthly-sampled sites. In 1989 there were peaks from April to June, following the onset of the rains, and early in the dry season (November-December). The latter coincides with the breeding peak of the Wirebird. It is not known if this pattern is typical of all years however.

An index of relative invertebrate abundance was calculated by using the mean daily catch for the year at Deadwood Plain as a reference value and dividing the mean catches at other sites by this figure (Table 5.2). In calculating the mean catch for each site the data for all trap grids within the site were combined. An index of beetle abundance was calculated similarly. These indices were used to investigate the relationship between Wirebird density and prey abundance. Bird density was regressed on the indices for all species and for beetles from the seven regularly sampled sites. This produced significant positive correlations in both cases (all species: $r = 0.86$, $P<0.05$, 5 df; beetles: $r = 0.99$, $P<0.001$, 5df), indicating that Wirebird distribution corresponds well with prey abundance (Fig.5.3).

5.3 FEEDING METHODS

The feeding behaviour of the Wirebird is typical of small plovers as described by Pienkowski (1983). Prey are most commonly taken from the ground surface using a standard behaviour comprising three elements: a period of stationary scanning typified by an erect posture; a short run, usually not longer than six paces; and a peck, occasionally preceded by short-range scanning from a crouched position. Wirebirds occasionally probe for prey in loose substrates and may remove material covering prey with a sideways flick of the bill. Rarely, birds were seen to sweep their bill from side to side in dust or fine sand. Prey may be flushed from grass tussocks by "foot trembling": a foot is inserted into a tussock and vibrated rapidly. This behaviour was observed only three times in 14 months but has also been recorded in Kittlitz's Sand Plover (Tree 1974). Wirebirds occasionally pursued low-flying insects, especially moths, on foot and captured them by leaping into the air but they were rarely successful.

5.4 FEEDING RATE

If the results of pit-fall trapping reflect true prey availability, then the rate of prey intake should be correlated with the index of invertebrate abundance, though it is also likely to be influenced by the energetic value of the prey taken. During this study it was possible to determine the outcome (success or failure) of a peck only in a very small proportion of cases. Because of this, total "peck rate" (pecks/minute) was used as an estimate of true feeding rate.

Data were obtained from 10 sites between March and September 1989, during the wet season. Individual birds were observed for short periods, not usually exceeding five minutes, from a distance at which the presence of an observer did not affect their behaviour (normally around 30m-50m). The birds were observed through a 20-60 x 60 telescope or 10x40 binoculars. The number of pecks made and, if possible, their outcome and the identity of prey taken, were recorded. Peck rate was calculated as the total number of pecks divided by the total time spent foraging. Foraging time included stationary scanning, searching movements (runs) and time spent handling prey. The mean wet season peck rate for each site is presented in Table 5.4.

The observed peck rate during this period was highly correlated with the abundance indices for all species ($r = 0.99$, $P<0.001$; 3df) and for beetles ($r = 0.89$, $P<0.05$, 3df). This further suggested that the trapping data provided a valid indication of relative prey abundance.

Few observations were, however, made in semi-desert areas and the results from these were surprising in that the peck rates were higher than might be expected from the difference in mean invertebrate catches between grassland and semi-desert sites. For example, the mean daily invertebrate catch at Prosperous Bay Plain was only 25% of that at Deadwood Plain (despite the former being inflated by a large, but short-lived, caterpillar hatch) yet the mean peck rate was 70% of that at Deadwood. No observations of feeding rate were made at Prosperous Bay Plain during the caterpillar hatch.

This appears to contradict the assumption that the low Wirebird density at semi-desert sites is a response to food availability. It was therefore decided to carry out a comparative study of feeding behaviour in the two major habitat types to attempt to detect differences in diet or foraging effort that might counteract the relatively high peck rates observed in arid areas. Observations were carried out at two sites: Deadwood Plain (pasture) and Prosperous Bay Plain (semi-desert).

The methods employed were similar to those described above but additionally all observations were recorded directly onto audio tape, allowing timing of various aspects of behaviour to be timed and transcribed later. These included the time spent running in search of prey, the duration of non-foraging activities and, where possible peck success and prey identity. Observations were made from late November to mid December, during the dry season.

Mean values of peck rate per minute foraging, peck rate per second run-time, run duration, run time as a percentage of foraging time and number of large prey items (approx. 1cm and larger) taken per minute foraging were compared between sites by single-classification analysis of variance (Table 5.5). The duration of individual observations was variable, therefore means were weighted by foraging time since longer observations were assumed to more accurately reflect typical behaviour. A total of 247 observations, 158 from Deadwood Plain and 89 from Prosperous Bay Plain. Unfortunately some additional data were lost because of excessive wind noise on the tapes.

This analysis revealed the direction of the difference in peck rate to be the inverse of that found earlier in the year, the rate being slightly but significantly higher at Prosperous Bay Plain ($P < 0.01$). The percentage of foraging time spent running and mean run duration were also higher at Prosperous Bay Plain. No difference was found between sites in peck rate per unit run-time, however. No relationship between peck rate and time of day was evident at either site, though the total amount of feeding activity may vary with time (see Section 5.5). The most striking difference between sites was that the capture rate for large prey was approsximately nine time greater in pastureland than in semi-desert.

These results suggest that, although absolute rates of prey capture per unit effort may be similar in numerical terms in the major habitat types for at least part of the year (though it is uncertain how closely peck rate reflects true capture rate), it is probable that the greater abundance of large prey in pastureland allows greater feeding efficiency. Differences between sites in mean run-time suggest that birds in semi-desert areas are covering larger areas during feeding bouts, thus feeding territories may need to be larger in that habitat. This may at least partially account for lower Wirebird densities. Attempts were made to measure the distances covered by feeding Wirebirds by counting paces. This technique has been successfully applied to other plovers feeding on estuarine mudflats (e.g. Pienkowski 1983) but was found not to be feasible for Wirebirds because of their rapid rate of movement and because vegetation often obscured the legs. The general impression gained, however, was that speed of movement did not vary systematically between sites and therefore percentage run-time is probably a reasonable indicator of distance moved.

If Wirebirds in semi-desert areas are feeding on prey that is, on average, less energetically valuable than that available in pastureland, yet capture rates are similar in the two habitats, then it might be expected that individuals in the former would spend a greater proportion of the day feeding. No comparative data is available at present, however. This analysis also suggests that pit-fall catches of invertebrates at semi-desert sites may not be truly representative of prey available to Wirebirds. It may be that the three randomly placed trap grids at Prosperous Bay Plain were located in atypical areas but it seems more likely that the behaviour of some important prey species reduces the probability of their being trapped. It is possible that certain small moths may form a significant part of the diet of Wirebirds in semi-desert areas. These often formed a high proportion of organisms trapped at arid sites but are also amongst the most likely to escape and therefore probably substantially under-represented. These moths appear to spend much time on the soil surface where they may be vulnerable to Wirebirds.

Wirebirds inhabiting semi-desert sites are in the minority but still comprise a substantial and important proportion of the population. Gathering information on the behaviour and ecology of these birds is more problematic than in pastureland sites because they occur at low density and are often difficult to observe continuously when foraging amongst low *Suaeda* scrub and

Carpobrotus mats. The limited data available requires the above interpretation of results to be largely speculative. There is, therfore, a need for better information on the composition and seasonal abundance of Wirebird prey and other factors potentially limiting numbers in arid areas of the island as such data may suggest ways in which some of these may be improved as Wirebird habitat, allowing higher breeding densities.

5.5 DIURNAL ACTIVITY PATTERN

A study of Kittlitz's Sand Plover has shown that non-breeding birds feed most intensively in early morning and evening (Tree 1974). To obtain comparative data for the Wirebird, birds at Barren Hill were observed throughout the day during October, November and December. Three periods of observation, each lasting one hour, were carried out each day between the hours of 06.00 and 19.00 GMT (approximately dawn to dusk). The starting times of the observation periods were randomized each day and a total of 10 observation periods were completed for each hour of the day. At the start of each period a target bird was chosen and the activity it was engaged in was recorded at 30 second intervals. If the target bird left the area during the observation period another was selected and observation continued.

Figure 5.4 shows feeding records as a percentage of the hourly total of registrations for all activities. The pattern of feeding that emerges is similar to that found in *C. pecuarius*, with highest intensity before 10.00hrs, lowest around mid-day and a resurgence in late afternoon. The birds were least active generally between 12.00hrs and 14.00hrs, spending a higher proportion of time either stationary or preening (Fig.5.6).

Feeding accounted for 57% of registrations for all hours combined. This is, however, probably an understimate of the proportion of time most Wirebirds spend feeding as most of the observations were of members of a pair about to nest and 16% of their time was accounted for by reproductive activity (courtship displays and mating) which peaked in late afternoon (Fig.5.5). Non-breeding birds may spend as much as 70% of their time foraging. It is not known how much feeding is done at night. At Man and Horse, Wirebirds were active three hours after sunset in February. Tree (1974) records that Kittlitz's Sand Plovers in Zimbabwe continued foraging till 23.00 hr on moonlit nights.

5.6 CONCLUSIONS

Wirebirds take a wide range of invertebrates as prey, amongst which beetles and caterpillars appear to be particularly important. Wirebird density and feeding rate are positively correlated with invertebrate abundance. Feeding rates at semi- desert sites were lower than those on pastureland during the wet season but were slightly higher in semi-desert during the dry period. Feeding in arid areas appears to be less energy efficient, however. Relatively large prey are taken more frequently in pastureland. Foraging accounts for at least 55% of diurnal activity and is most intensive in early morning and late afternoon.

Figure 5.1 Percentage composition of observed Wirebird prey 1988-89

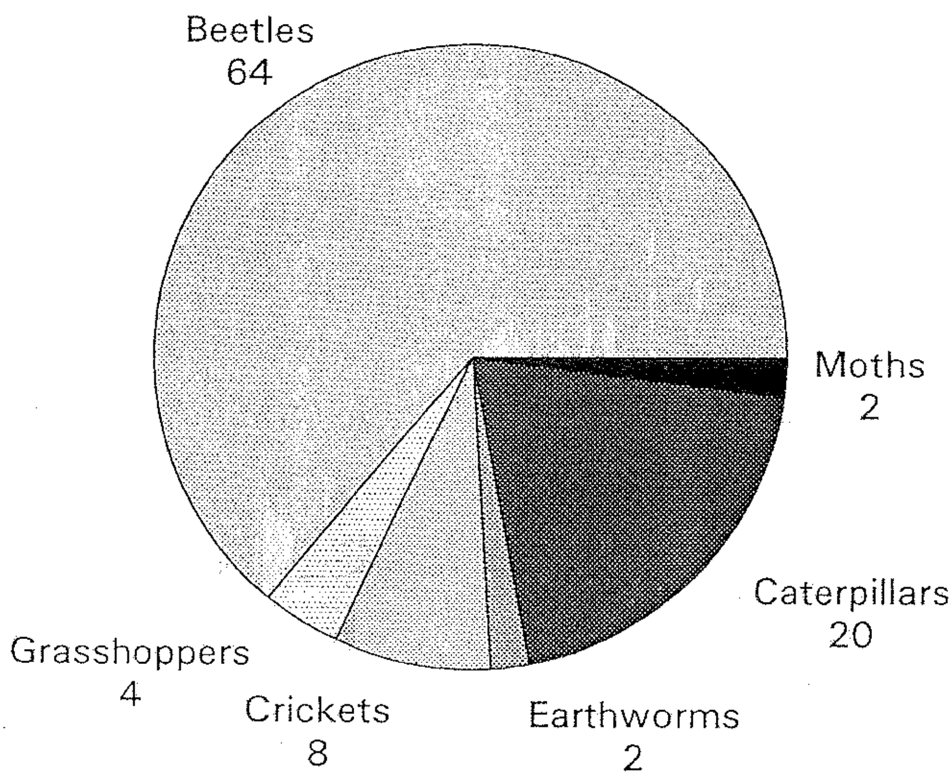


Table 5.1 Percentage composition of total invertebrate catch at monthly trapping sites

	BH 1	BH 2	DWP1	DWP2	DWP3	BW	HPP	BB 1	BB2
Platyhelminthes									
Turbellaria	0	0	0	0	0	0	0	0.2	*
Annelida									
Oligochaeta	0.4	*	*	0.1	0.4	*	0	*	0.1
Arthropoda: Insecta									
Thysanura	0	0	0	0	0	0	3.9	0	0
Orthoptera	1.8	0.3	0.4	0.1	*	0.2	1.0	0.2	0.3
Dictyoptera	0	*	0	0	0	0	0.1	0	0
Dermaptera	0.9	0.1	0.8	0.9	0.1	0.8	0	*	0.2
Hemiptera	0.2	*	0.9	0.1	*	0.1	0	1.4	1.0
Coleoptera (Adult)	7.4	3.0	14.4	17.8	9.4	12.6	4.5	5.2	6.0
Coleoptera (Larvae)	0	0.7	0.8	2.5	*	20.8	0	0.2	0.1
Lepidoptera (Adult)	0.8	*	0.5	0.9	0.3	1.7	33.7	0.2	*
Lepidoptera (Larvae)	0.3	*	0.6	0.3	1.1	0.4	0	0.2	0.3
Diptera	0.1	0	1.2	0.3	0	*	0.6	1.8	0.3
Hymenoptera	74.6	84.4	60.4	63.4	27.4	41.4	41.3	0.3	0.4
Chelicerata									
Aranea	1.9	0.3	3.1	0.8	1.7	0.9	6.6	4.9	2.2
Acarina	0.2	*	0.5	0.5	0.7	0.3	0.2	1.4	1.7
Crustacea									
Amphipoda	0.6	*	0	0	0	0	0	79.5	85.4
Isopoda	8.9	2.4	5.9	4.8	12.7	9.0	5.7	0	0.4
Myriapoda									
Chilopoda	0.3	*	0	*	*	0	0	0.8	0.6
Diplopoda	1.5	8.5	10.4	7.4	46.0	11.9	2.2	1.7	0.1
Mollusca									
Gastropoda	0.1	*	*	0	0	0	0	2.0	0.8
Total caught	1846	5790	2786	4457	3932	2920	863	2781	4434

* = less than 0.1%

Site key: BH = Barren Hill, DWP = Deadwood Plain, BW = Bottomwoods, HPP = Horse Point Plain, BB = Broad Bottom

Table 5.2 Mean daily catch of invertebrates and indices of relative abundance

				Indices**	
	mean	sd	n	all species	beetles
Barren Hill	106	106	72	1.0	0.3
Deadwood Plain	104	89	107	1.0	1.0
Bottomwoods	220	163	36	2.1	2.9
Horse Point Plain	24	24	36	0.2	0.1
Broad Bottom	109	123	66	1.1	0.4
Longwood Farm*	74	51	18	0.7	1.2
Prosperous Bay Plain*	26	50	54	0.3	0.2

* sampled bi-monthly

** see text

Figure 5.2 Seasonal variation in invertebrate abundance during 1989 based on mean ranks of monthly catches from eight trap sites.

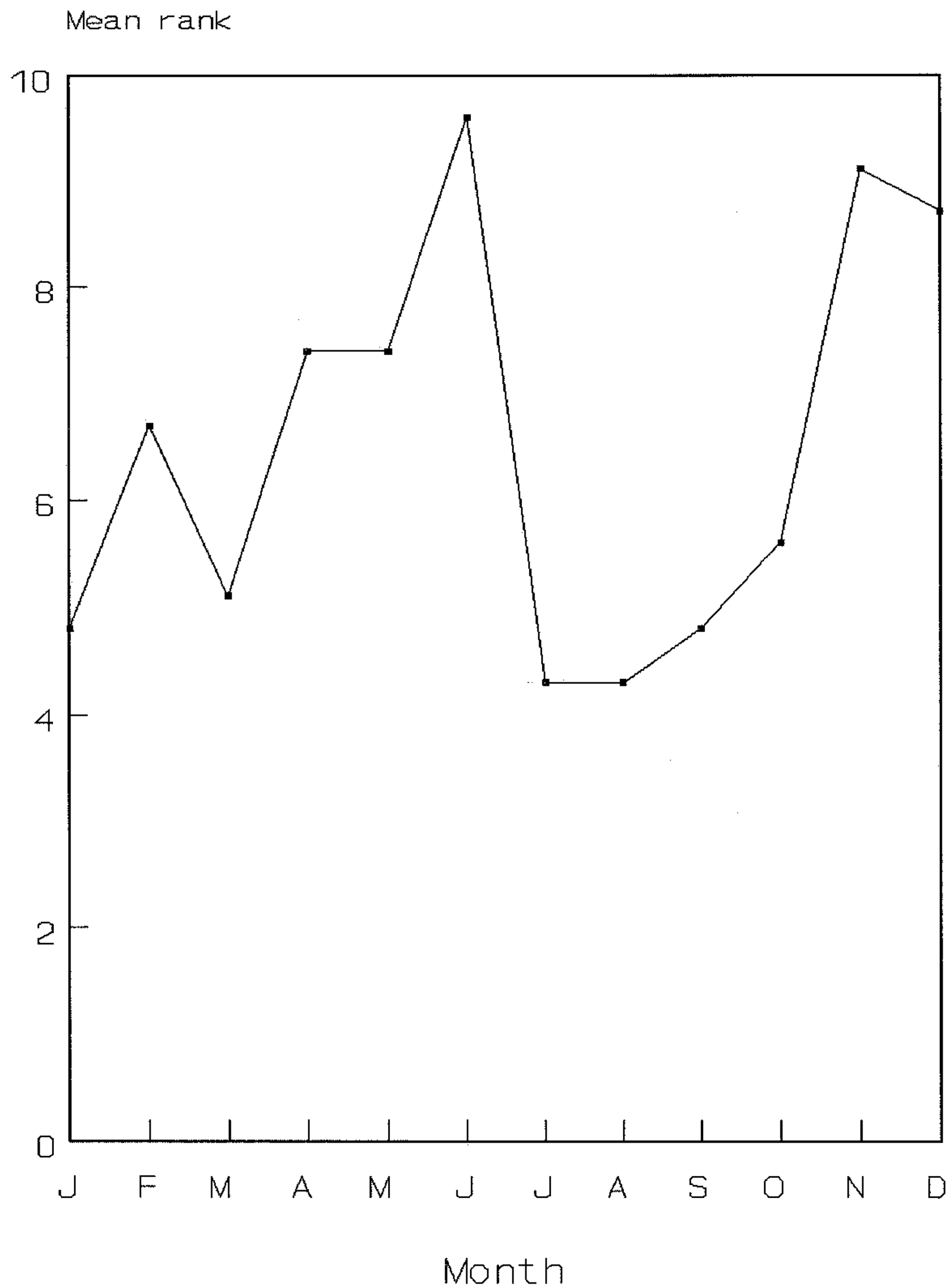
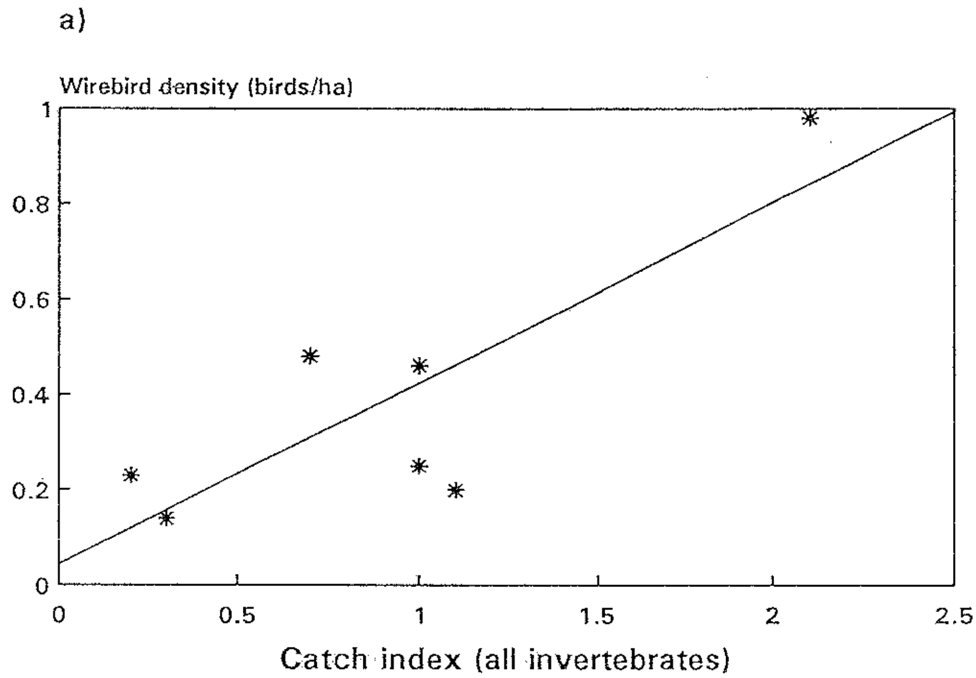


Table 5.3 Size distribution of trapped invertebrates expressed as percentages of total catch. Asterisks indicate frequencies of less than 1%

Body length (mm)	0-5	6-10	11-15	16-20	21-25	26-30	>30
Barren Hill	84	6	2	*	*	2	5
Deadwood Plain	55	15	8	2	2	6	11
Bottomwoods	64	16	5	2	1	4	8
Horse Point Plain	76	13	8	1	*	*	2
Broad Bottom	29	66	3	1	*	*	*
Longwood Farm	42	22	10	1	2	8	15
Prosperous Bay Plain	43	25	10	9	6	6	1

Figure 5.3 Relationship between Wirebird density and index of relative abundance (see text) for a) all invertebrates; b) beetles



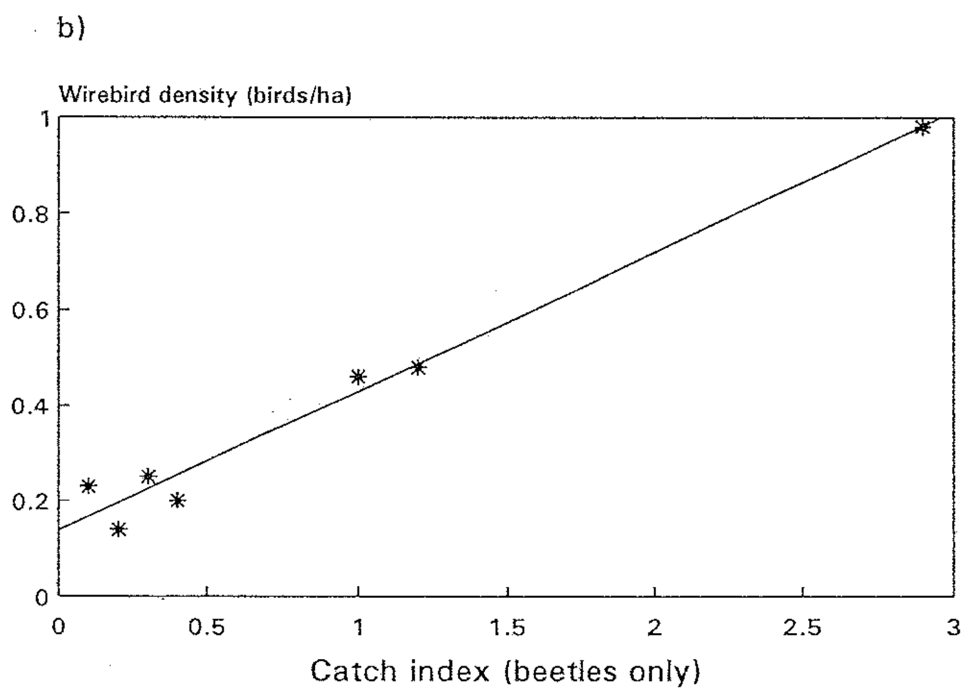


Table 5.4 Variation of mean peck rate (pecks/minute) between sites during the wet season (March - September)

	No. observations	Mean peck rate	s.d.
Barren Hill	30	5.5	1.7
Sane Valley	4	4.6	0.5
Deadwood Plain	36	5.1	1.7
Golf course	24	6.9	1.7
Bottomwoods	54	7.7	1.7
Horse Point Plain	6	3.2	0.7
Prosperous Bay Plain	9	3.6	1.6
Pounceys	10	4.9	1.7
Southern Pastures	4	4.7	1.0
Man and Horse	12	5.5	1.1

Table 5.5 Comparison of feeding behaviour of Wirebirds in intermediate pasture (Deadwood Plain) and semi-desert (Prosperous Bay Plain) habitats during November and December 1989.

PRATE	=	peck rate per minute of foraging time
PCRUN	=	percentage of foraging time spent running
MNRUN	=	mean duration of single run (sec.)
PKRUN	=	peck rate per second of run-time
LPREY	=	No. large prey captured per minute of foraging time

	Deadwood Plain (n=158)		Prosperous Bay Plain (n=89)			
	Mean	s.e.	Mean	s.e.	*df*	*F*
PRATE	3.33	0.24	4.07	0.34	1,245	10.26**
PCRUN	12.76	0.01	16.53	0.01	1,245	26.59***
MNRUN	0.65	0.02	0.87	0.06	1,245	43.33***
PKRUN	0.50	0.04	0.48	0.05	1,245	0.04
LPREY	0.10	0.02	0.02	0.01	1,245	8.95**

* = $P<0.05$; ** = $P<0.01$; *** = $P<0.001$

all means are weighted by foraging time

Figure 5.4 Diurnal variation in percentage of time spent feeding (observations from Barren Hill, October-December 1989)

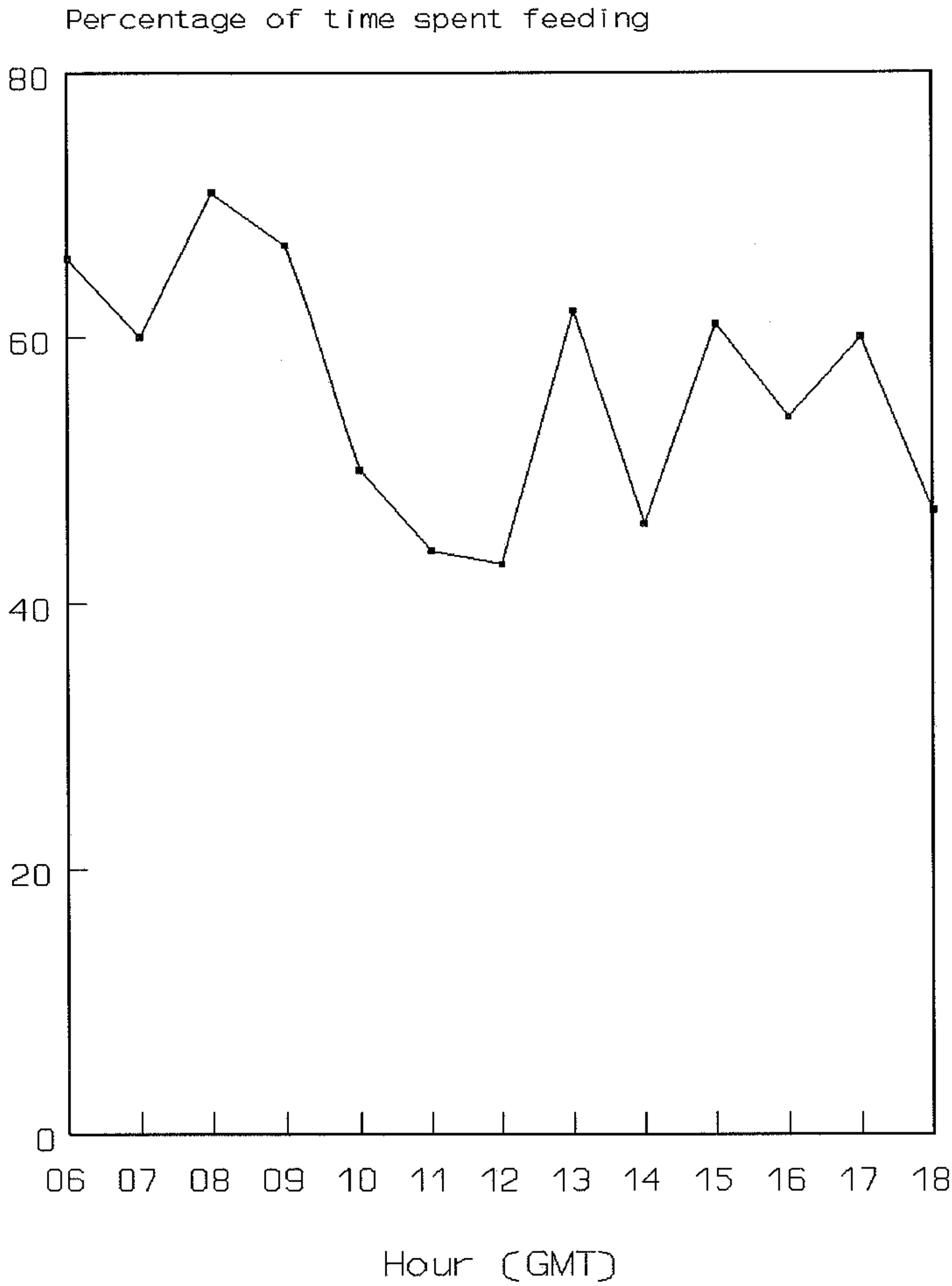
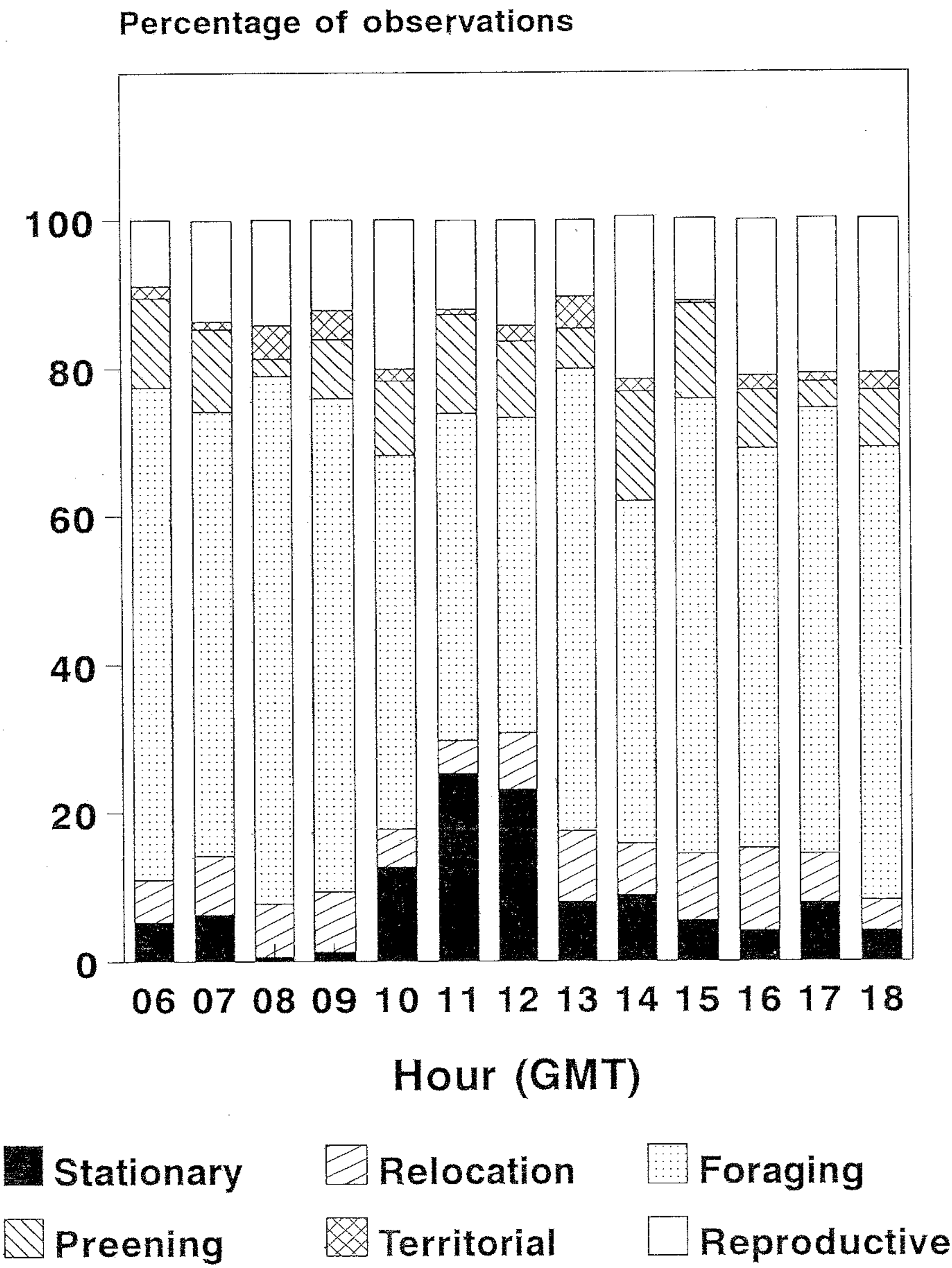


Figure 5.5 Temporal variation in diurnal activity pattern of Wirebirds at Barren Hill based on registrations at 30 second intervals (October-December 1989).



6. BREEDING BIOLOGY

6.1 TIMING OF BREEDING

Prior to this study egg-laying by Wirebirds had been recorded in every month of the year except June (Pitman 1965, Loveridge 1974, Alexander 1985) and in 1989 evidence of laying (eggs or chicks of the appropriate age) was found in all months. Previous authors have, however, concluded that there is a peak in nesting activity in the dry season, normally October - February. This is supported by the monthly distribution of nests and broods found during 1989 (Fig.6.1). In 1988 three nests and six broods were found in October, no nests but 16 broods in November and six nests and seven broods in December. All the major Wirebird sites except Man and Horse were visited every month.

Table 6.1 shows the frequencies of adults fledged juveniles and chicks recorded during the four census counts. Both counts in October - November contained higher proportions of chicks than those made at other times of the year but differed sufficiently from each other to suggest that the precise timing of the breeding peak varies between years, probably because of differences in rainfall patterns.

6.2 MATING AND TERRITORIALITY

6.2.1 PAIRING

Wirebirds appear to be monogamous, though too few adults were marked during this study for one to be certain. Identification of unringed individuals is usually impossible. I found that Wirebirds could only be sexed reliably in the field by observing the behaviour of breeding birds as differences in size and plumage are generally negligible; although males are, on average, probably slightly more brightly marked than females, there is considerable individual variation.

Little is known about the early stages of pair formation. In Kittlitz's Sand Plover this involves much nuptial chasing within flocks (Cramp and Simmons 1983) and this is probably true for the Wirebird. Adult Wirebirds rarely flock but juveniles do and intense bouts of chasing were frequently observed in groups of young birds. Although much of this chasing appears to be aggressive it seems likely that initial pairing does take place in sub-adult flocks. It is interesting to note that in October 1989, when an increase in sexual activity would be expected, a territorial dispute on Deadwood Plain stimulated a sustained period of chasing involving up to 14 neighbouring adult birds.

During September and October 1989 an aerial display which may be associated with courtship was observed at several sites. Between one and three birds would perform slow, ascending spiral flights while making a "rattle" call usually associated with antagonistic interactions. This often attracted other birds from the surrounding area. The birds would then chase each other in flight, calling, but without the speed and intensity of the typical pursuit flights that follow the expulsion of an intruder from a territory. During such displays birds often seemed to be associating in pairs. Usually the birds dispersed afterwards but on one occasion nine sub-adults landed together to forage as a flock. The significance of such displays remains unknown. Some elements bear resemblance to the "song flight" of the Kentish Plover *Charadrius alexandrinus* (Cramp and Simmons 1983), which advertises territory ownership, but the aggregative response of Wirebirds argues against this function.

There is little information on the duration of the pair-bond in Wirebirds. During this study one pair at Barren Hill remained together for at least two breeding attempts spanning one year. (The female was colour-ringed and the male had distinctive plumage markings facilitating identification). It is not known how typical such fidelity is of the population in general.

6.2.2 TERRITORY

Mating and nesting take place within a territory that is defended primarily by the male, though the female's participation increases as nesting approaches. No attempt at territory mapping was made in this study but the defended area ranged between 50m and 100m in diameter at regularly observed sites. Many pairs appeared to remain on territory throughout the year, particularly at small sites holding few birds, but the intensity of defence decreased outwith nesting periods and boundaries seemed to change frequently.

Usually intruding Wirebirds were driven off by the resident male, which would assume a hunched posture, with lowered head and ruffled feathers, and rush at the intruder while making the rattle call. In most cases the intruder would immediately take flight and was often pursued in the air by the resident for between 50m and 200m. Intruding juveniles provoked a particularly strong response.

Wirebirds use variants of the "parallel run" display common to several *Charadrius* plovers (Cramp and Simmons 1983, Bergstrom 1988b) in territorial disputes. The most frequently observed form of this display involved neighbouring males adopting the typical hunched threat posture and walking or running in parallel, about 1m apart, on the territory boundary. At intervals the birds would stop and face away from each other, then one would spin round and charge the other. A brief scuffle (usually less than 30 seconds) would ensue with both birds leaping into the air and striking at each other with wings and feet. Parallel running would then be resumed often in the opposite direction to before. Although females often chased intruders they were never seen to perform the parallel run display. Serious fighting is rare but can be intense. One fight lasted over 20 minutes with the combatants frequently rolling around on the ground, locked together.

6.2.3 COPULATION

Copulation is almost always preceeded by a "scrape ceremony" similar to that performed by Kittlitz Sand Plover (Hall 1958, Conway and Bell 1968, Clark 1982). The scrape ceremony is usually initiated by the male. A shallow scrape is made in the earth using exactly the same movements that are used in nest construction: The bird lowers its breast to the ground and pushes the substrate outwards, scraping with its feet until a circular depression is formed. This behaviour attracts the female, which investigates the scrape, settling in it if the male moves aside, as he usually does. Occasionally, the female may make her own scrape beside that of the male. If the female is receptive she leaves the scrape after a few seconds and performs a slow, crouched "invitation walk" of 1-5m. Sometimes, in the early stages of courtship, the male shows no interest and the female may repeat the "invitation walk" three or four times before giving up. Usually, however, the male follows immediately. The female then stops and crouches, whereupon the male stands behind her, making exaggerated "goose-stepping" movements. Frequently he strokes the female's back with a foot before mounting. Treading may last up to four minutes (mean = 2'18", sd = 37", n = 54). The act culminates with the male seizing the feathers of the female's nape with his bill and both birds falling backwards.

Copulation occurs at any time of day but in the intensively watched pair at Barren Hill was least frequently observed around mid-day and there was a suggestion of a peak of sexual activity in late afternoon (Figure 6.2).

The duration of this period of courtship and mating is not known. Copulation was first recorded between the Barren Hill pair 53 days before incubation was observed but I believe that there may have been an undetected nesting attempt that failed in the early stages during this period. Clark (1982) recorded copulation 11 days before egg-laying in Kittlitz's Sand Plover.

During courtship many scrapes may be made throughout the territory but as egg-laying approaches activity is concentrated in the area where the nest will be made. The last pre-laying copulations usually take place at the nest scrape.

6.3 LAYING AND INCUBATION

6.3.1 THE NEST

Nest-building behaviour is identical to that described above for the "scrape ceremony". The resulting scrape is 9-15cm in diameter. The amount of lining material varies between nests. In grassland it comprises mainly segments of dead grass stolons. In semi-desert areas *Carpobrotus* debris and twigs of *Suaeda helenae* are most frequently used.

Forty-three nests were found during this study. Their mean altitude was 472m a.s.l. (sd 73.8) and the nature of their sites is summarized in Table 6.2. Several *Charadrius* species tend to nest beside a prominent plant or object (Cramp and Simmons 1983, Bergstrom 1988a). This behaviour is not well developed in the Wirebird, though most nests in the Crown Wastes were on the leeward side of small shrubs, which may give some protection against drifting sand. The most frequently used sites were patches of bare earth, little larger than the scrape itself, amongst short grass. It is a commonly held belief on St Helena that Wirebirds usually nest amongst dry cattle dung but only two such nests were found.

6.3.2 EGGS

Wirebirds normally lay a clutch of two eggs. Five single-egg clutches were found during 1988-89 but at least some of these were probably incomplete or had lost one egg.

The eggs are of typical plover type, being distinctly pyriform and of an olive green colour with black or charcoal blotching (Pitman 1965). Freshly laid eggs have a paler, bluish cast and eggs from semi-desert areas were often paler, probably due to less staining by the soil under dryer conditions.

The eggs are relatively large, averaging 34.2mm long by 25.0mm broad (Table 6.3). Alexander (1985) found two clutches of particularly small eggs (mean: 25.3 x 14.4mm, sd 0.42, 0.44) which she attributed to the drought conditions prevailing in 1984. Nothing similar was found during this study (Fig.3). There was significant heterogeneity in egg size between females which suggests the prescence of a substantial genetic component in the variance of egg size (length: $F(29,33) = 4.9$, $P < 0.001$; breadth: $F(29,33) = 10.8$, $P < 0.001$).

6.3.3 INCUBATION

The eggs are incubated for around 28 days and incubation is shared by both parents. In Kittlitz's Sand Plover, daylight incubation is undertaken mainly by the female with the male predominating at night (Tree 1974) but observations of Wirebirds at the nest suggest that incubation during the day is shared approximately equally between the sexes. The mean duration of incubation between changeovers was 32.5 minutes (sd = 16.2, n=21). The mean incubation period for males was shorter than that for females but sample sizes were small and the difference was not statistically significant (males: mean= 25.9, sd = 8.0, n=9; females: mean= 35.8, sd = 15.4, n=9; $F(1,16) = 2.94$).

Changeovers at the nest rarely involve any sort of ritual. In most cases the incubating bird simply leaves as the relieving bird runs in. Occasionally the incubating bird remains sitting while the incoming parent approaches slowly, pecking at the ground and flicking plant debris into the air. The two birds then stand together over the nest for a few seconds with heads lowered and bills pointing downwards before the relieved parent moves away.

Tree (1974) recorded long parental absences from the nest (up to 7 hours) in Kittlitz's Sand Plover. This does not seem to occur in the Wirebird. At observed nests, eggs were never left unattended for longer than 10 minutes. On average, parents incubated for 94% of total observation time at 8 nests (sd=6.5).

6.3.4 EGG-COVERING

In common with Kittlitz's Sand Plover and several other species of the sand-plover group, the Wirebird covers its eggs with soil or other debris when disturbed at the nest by humans or potential predators (Hall 1959, Maclean 1974, Summers and Hockey 1981).

Covering usually takes place before an observer or predator approaches within 20m and is achieved by rapid inward scraping of the nest lining and soil with the feet as the bird rotates in the nest. It then slips unobtrusively away. The covered eggs are extremely difficult to find but when there is little lining material and the soil is baked hard adults may remain on the nest attempting to scrape together sufficient debris to cover the eggs until approached to within 5m thus revealing the exact position of the nest. Eggs may remain uncovered if the incubating bird is suddenly disturbed at close range.

When covering did occur at grassland sites it was rarely complete, between a quarter and a half of each egg remaining exposed. This may be related to the nature of the substrate as nests in the softer sandy soils of the Crown Wastes were usually completely covered.

Studies of sand-plovers in Southern Africa have produced evidence that the function of egg-covering is primarily concealment and has little thermoregulatory significance (Summers and Hockey 1981).

6.3.5 HATCHING

Hatching was observed only once during this study. As the first egg hatched the incubating male picked up a half shell and ran from the nest calling. In response, the female, which had been feeding nearby, immediately ran to the nest and began brooding the chick. The male deposited the shell about 7m from the nest and began pecking at it, appearing to eat some fragments; it then returned to the nest and removed the remainder of the shell. The other egg hatched within 15 minutes of the first and shell was again removed, broken up and deposited by the male between 6m and 10m from the nest. The female was still brooding 40 minutes later when observation was terminated because of failing light. At another nest a newly-hatched chick was brooded in the nest scrape for between 24 hrs and 30 hrs. Similar parental behaviour has been observed in Kittlitz's Sand Plover (Taylor 1959).

6.4 PARENTAL CARE

Chicks were reared mainly within the boundaries of the nesting territory, though not exclusively so. However, family movements similar to those of up to 750m from the nest site described by Tree (1974) for Kittlitz's Sand Plover in Zimbabwe were not observed. Parents defended an area of up to 30m diameter around the chicks against other Wirebirds and often against other bird species, ranging from small passerines to pigeons *Columba livia*.

Parents used a variety of distraction displays when chicks were approached by observers, potential predators (principally dogs) and occasionally, livestock. These displays included "mock- brooding",- the parent squatting with ruffled breast feathers well away from the chicks; "rodent run" - running in a croched posture with tail fanned downwards and loosely folded wings drooping and vibrating; "broken wing" - either running with one wing dragging or lying prone with both wings outstretched, tilted forward and fluttering (Cramp and Simmons 1983, Bergstrom 1988b).

During the first two weeks after hatching chicks, if pursued, quickly crouched and remained motionless until called up by their parents, relying on the camouflage pattern of their plumage to avoid detection. Older chicks usually attempted to outrun the pursuer.

6.4.2 BROODING

Chicks were brooded regularly, particularly during their first two weeks. No information was obtained on the partitioning of chick- care between male and female parents. Usually only one parent was in close attendance, but both sexes do brood chicks. Gathering information on undisturbed parental care was difficult as parents often became visibly agitated in the presence of even a distant observer, while at distances that minimized disturbance the chicks were frequently barely visible amongst vegetation. Only 12 observations of brooding patterns over periods of more than 30 minutes were made. Mean durations of brooding periods and between-brooding intervals are presented in Table 6.4. These data are insufficient to determine the relationship between brooding patterns and weather conditions. Observations on captive Kittlitz's Sand Plovers by Conway and Bell (1968) indicated that brooding was little influenced by variation in ambient temperature but my subjective impression was that the frequency of brooding increases during rain. In particularly hot weather the parent may remain standing during brooding. Such behaviour was also recorded by Conway and Bell (1968). The frequency of brooding decreases with the age of the chicks but may continue until fledging.

6.5 FLEDGING

Young Wirebirds fledge four to five weeks after hatching but may remain with their parents for some time after that. A juvenile at Barren Hill was at least eight weeks old before it left its parents territory, eventually being driven out by its father.

After fledging many juveniles aggregate in small, loose flocks of up to 15 birds. Juveniles are subject to frequent harassment by territorial adults and may wander widely around the island, but many spend much time loafing around permanent water, particularly at Cook's Bridge in Fisher's Valley. This site is especially heavily used after mid-day, the birds having presumably spent the morning feeding.

6.6 MULTIPLE AND REPLACEMENT CLUTCHES

Observations of marked birds during this study have shown that Wirebirds may lay more than one clutch in a year. Two females which were known to have successfully reared at least one chick from their previous clutch laid again after intervals of approximately 80 days and 230 days respectively. Another female re-laid after 320 days but is suspected to have attempted at least one other clutch in the intervening period. This last bird retained the same mate throughout but it is not known if there was any change of mate in the other two instances. A captive pair of Kittlitz's Sand Plovers at New York Zoo produced a second clutch before the chicks from the first had fledged (Conway and Bell 1968). In this case the male cared for the chicks while the female began incubation. In *Charadrius* species from temperate regions the female may leave the male to care for the first brood while she re-mates with a different partner (e.g. Lessells 1984). This may not occur in Wirebirds which are not subject to the same pressure to maximize reproductive output during a short breeding season but their reproductive strategy requires further investigation. Wirebirds will produce a replacement clutch if eggs or chicks are lost. A pair which lost eggs were observed performing a scrape ceremony at a new nest site within 24 hours. Another pair which lost chicks were seen copulating around 25 days later.

6.7 BREEDING SUCCESS

6.7.1 NEST SUCCESS

It was not possible to follow the progress of all nests found as closely as would have been desirable because of committments to other aspects of the study and lack of transport. Of the 43 nests recorded, 11 were successful (i.e. resulted in at least one hatched chick), 15 failed and the outcome of 17 was unknown. (Nests were assumed to have failed if the nest was found to be empty before the eggs could have hatched or if no chicks of appropriate age were found within 100m of the nest site and the parents failed to perform distraction displays on being approached).

In the absence of predation hatching success is high (95% in successful nests). It is impossible to give an accurate estimate of egg-loss due to predation because the age of most clutches at the time of finding was unknown. It was, therefore, not possible to know whether missing eggs had been taken or the chicks had died or been taken after hatching. The area around empty nests was searched for shell fragments but these are extremely difficult to find.

6.7.2 CHICK MORTALITY

Of the 78 broods found during this study only 46% were of two chicks. Assuming that all of these broods originally contained two chicks this gives an estimate of chick mortality of 34.6%. This, of course takes no account of broods which hatched but were not detected because both chicks were lost or any subsequent loss from recorded broods. The true mortality rate is therefore likely to be considerably higher than 35%.

As the body weight and growth rate of the Wirebird appear to be very similar to those of the Kentish Plover, the criteria devized by Lessells (1984) for the latter species could be used to allocate chicks to two age classes. Those that were completely down-covered or weighed less than 20g were assumed to be less than two weeks old; those which showed any feathering or weighed 20g or more were assumed to be older than two weeks. Estimation of the fledging success of colour-ringed chicks from both these classes suggested that the highest mortality occurred in the first two weeks after hatching. Of those chicks ringed when less than two weeks old 15.8% survived to independence whereas 34.6% of older chicks fledged successfully, though this difference was not statistically significant ($G = 3.01$, 1df). In all, 15 of 64 ringed chicks were re-sighted when fledged and independent of their parents giving a minimum fledging rate of 23.4%. Combining the estimated rates of nest success, hatching and fledging given above produces an estimate of survival from egg to independent juvenile of 19%. This figure is similar to the 0.5 chicks fledged per pair recorded by Tree (1974) for Kittlitz's Sand Plover in Zimbabwe but is almost certainly an overestimate.

6.8 MOVEMENTS

6.8.1 TRAPPING AND RINGING

As many Wirebirds as possible were marked with an individual combination of two or three plastic colour-rings (A.C. Hughes Ltd, Hampton Hill, Middlesex) to obtain information on the movement of birds around the island. All birds were also fitted with a standard British Trust for Ornithology metal ring (size B+, internal diameter 3.3mm) bearing an individual serial number. Normally two colour-rings were placed on the left leg and a metal ring, with a single colour above, on the right.

Most birds were caught by hand as chicks. Chicks are particularly easily caught during the first two weeks after hatching when their response to being approached is to lie down and remain motionless.

Adults were caught in a funnel trap on the nest. Trapping was only carried out under warm, dry conditions, to minimize the risk of the eggs becoming chilled. If a bird had not entered the trap after 20 minutes trapping was abandoned and not attempted again at the same nest for several days, to reduce the possibility of desertion. Most birds were caught within 10 minutes of the trap being set. All trapped birds were seen to return to the nest after release and there is no evidence that any nest failed as a result of disturbance during trapping.

6.8.2 PATTERNS OF MOVEMENT

Observations of marked birds indicated that adults, having once bred, tend to be sedentary. Only two out of 11 ringed adults were ever found at a census area other than that in which they were ringed and all re-sightings of others were within 200m of their previous nest sites. These sedentary birds were all seen regularly.

Juveniles were more likely to move than adults. Seven (47%) of the ringed juveniles that survived to become independent were found outside their natal areas, though one later returned to breed. Further evidence of the greater mobility of juveniles comes from several observations at various sites of small groups of young birds which stayed only a short time to feed before moving on; in contrast, the location of paired adults within sites was frequently predictable over long periods of time. All movements of at least 1km are presented in Table 6.5.

The only indications of any seasonal movement were found in the north-east of the island where the number of Wirebirds found at arid sites during the February 1989 census was only half that found in October 1988, suggesting an exodus in response to drought conditions. This interpretation was supported by a corresponding increase in Wirebird numbers at adjacent grassland sites (Table 6.6). By June, after the start of the wet season, numbers on the Crown Wastes had risen again, though they were probably inflated by the caterpillar hatch described in Section 3. There was a parallel reduction in numbers at grassland sites, though by an amount insufficient to explain all of the increase on the Crown Wastes. It is not known if such distributional changes occur annually but it has been suggested that similar movements took place during the drought of 1984 (L. Hepworth in Alexander 1985).

6.9 CONCLUSIONS

Wirebirds appear to be monogamous. Adults are territorial and highly sedentary. They can breed when 10 months old and nest throughout the year, with a dry-season peak from October to February. The clutch is almost invariably two eggs. More than one clutch may be laid in a year. Incubation is shared approximately equally between parents and appears to be more intensive than in Kittlitz's Sand Plover. Eggs are covered when an incubating bird is disturbed and distraction displays are used when chicks, but not usually eggs, are threatened. Less than half the clutches observed produced hatched chicks and chick mortality is estimated to be at least 65%. Survival from egg to independence is probably less than 20%. Nothing is known about the adult survival rate but, in the absence of heavy predation and severe seasonal climatic effects, this is likely to be high. Juveniles disperse widely and, in doing so, may form small flocks. The greater mobility of juveniles probably ensures interchange of birds between all populations on the island.

Figure 6.1 Number and percentage of nests and broods found in each month of 1989. Only first sightings of broods are included. (N.B. only three weeks observation in December)

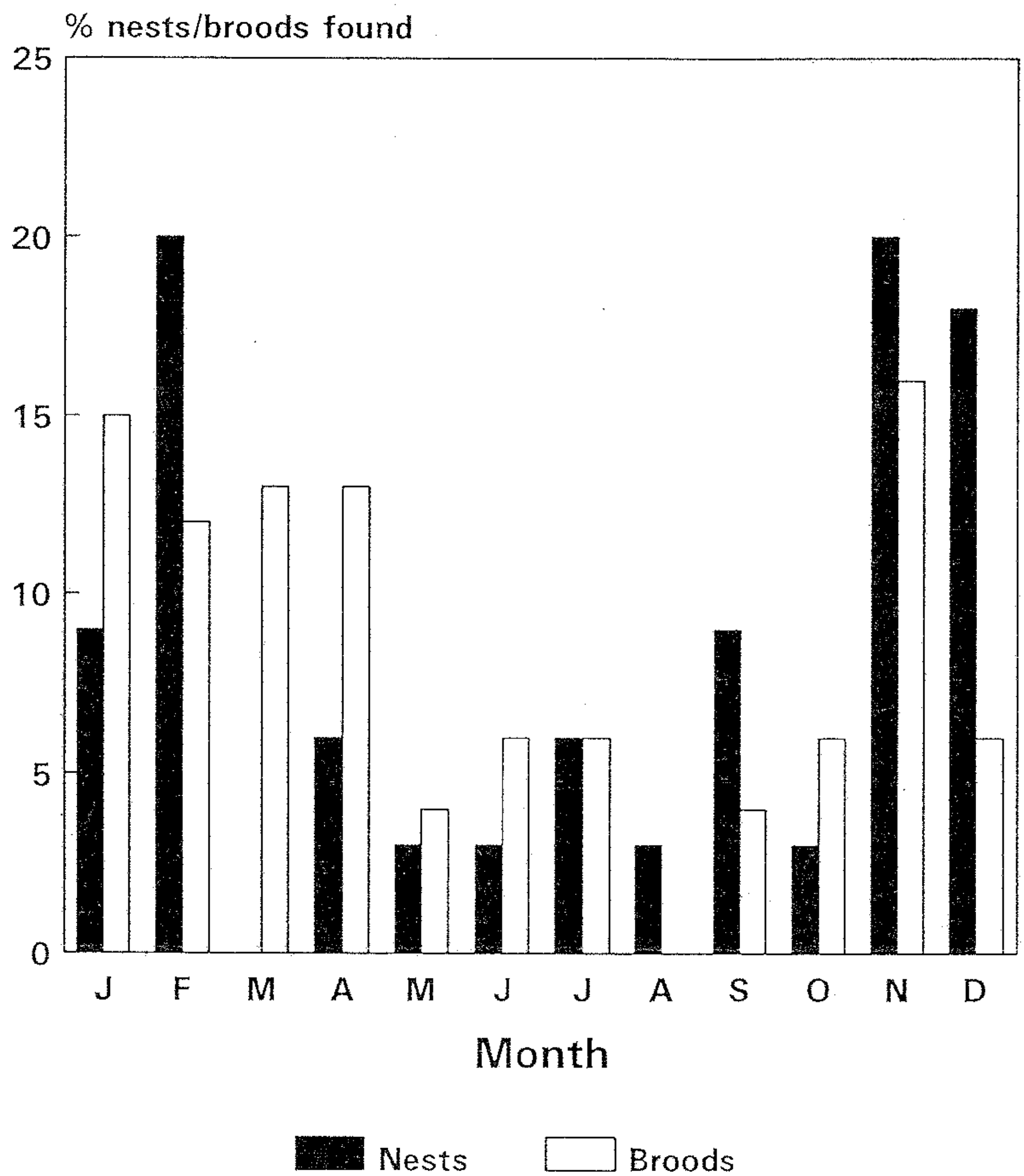


Table 6.1 Percentages of adults, fledged juveniles and chicks in census counts 1988-1989

		Adult	Juvenile	Chick	Total no.
October-November	1988	90.0	3.1	6.9	389
February-March	1989	88.1	9.6	2.3	427
June-July	1989	86.5	11.7	1.8	495
October-November	1989	91.6	4.8	3.6	475

Figure 6.2 Hourly distribution (percentage) of copulations by a pair of Wirebirds at Barren Hill, October-December 1989, based on 35 copulations observed.

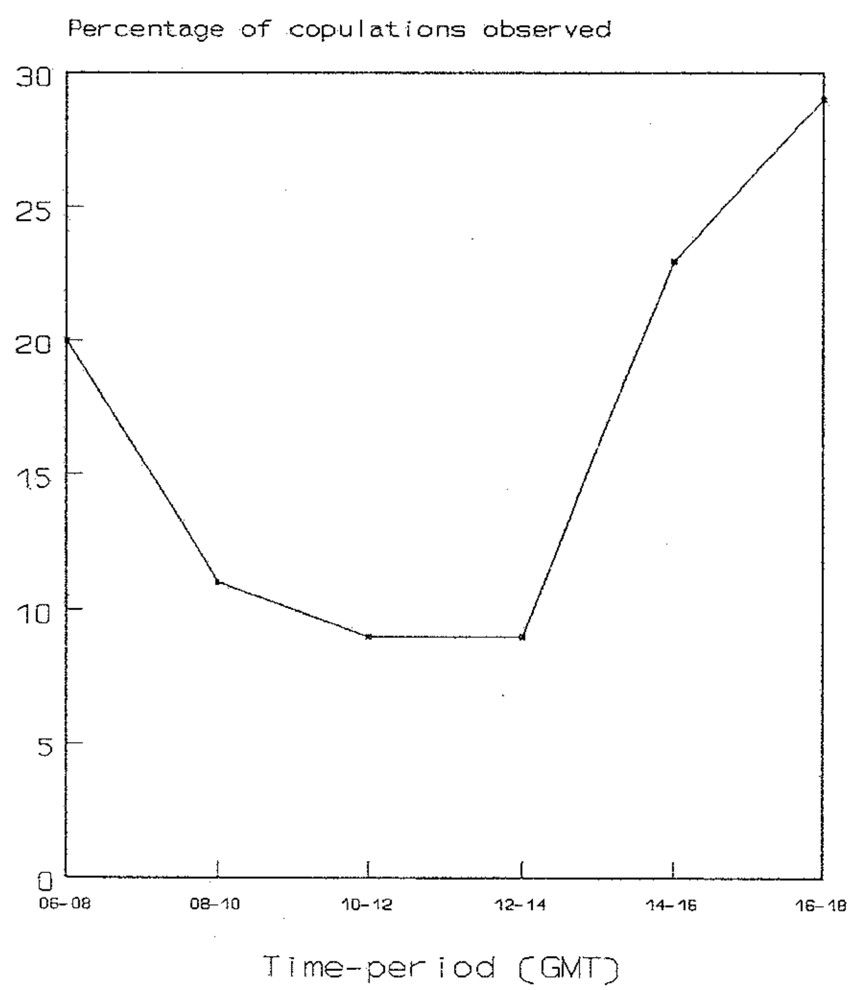


Table 6.2 Locations of 43 Wirebird nests found during 1988 and 1989, as percentage

Vegetation type	Nest location	Percentage
Semi-desert	*Carpobrotus* debris	7
" "	beside shrub	9
" "	gravel	2
Grassland	small bare area (under 30cm diam)	44
"	extensive bare area (over 1m diam)	7
"	mound	14
"	dry dung	5
"	beside grass tussock	7
"	*Carpobrotus* debris	2
other	potato crop	2

Table 6.3 Dimensions of Wirebird eggs (mm)

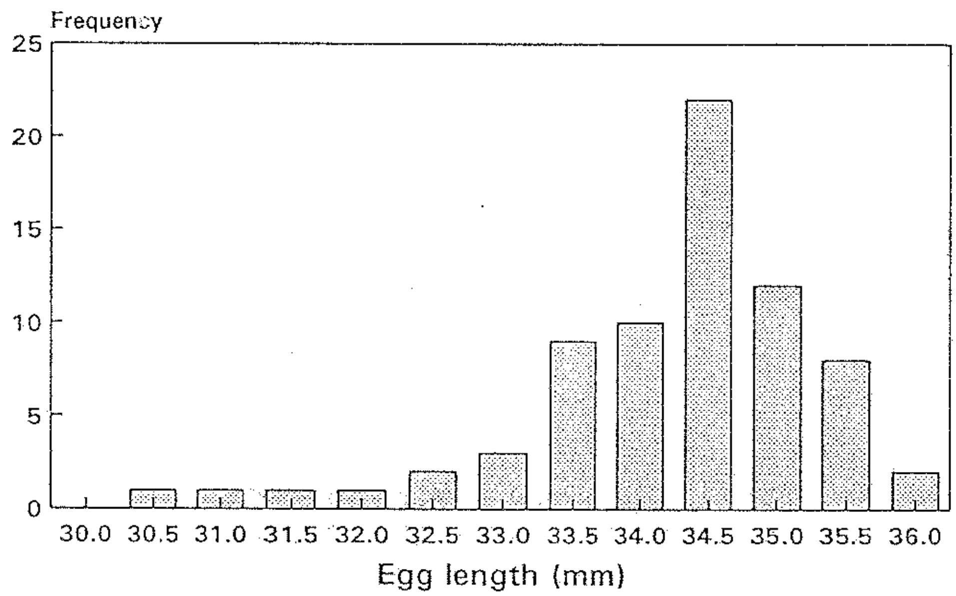
Source	n	length mean	sd	range	breadth mean	sd	range
Haydock (1954)	5	35.0	-	-	25.0	-	-
Pitman (1965)*	5	34.6	-	32.3-36.5	25.0	-	24.6-25.5
Loveridge (1974)	8	32.5	-	30.3-33.2	24.4	-	23.6-24.7
Alexander(1985)**	6	28.6	5.0	25.0-35.0	18.0	5.6	14.0-25.5
this study	72	34.2	1.1	30.5-35.9	25.0	0.7	22.1-26.1

* eggs in the British Museum (Natural History) collection dating from 1870 - 1911

** includes four unusually small eggs (see text)

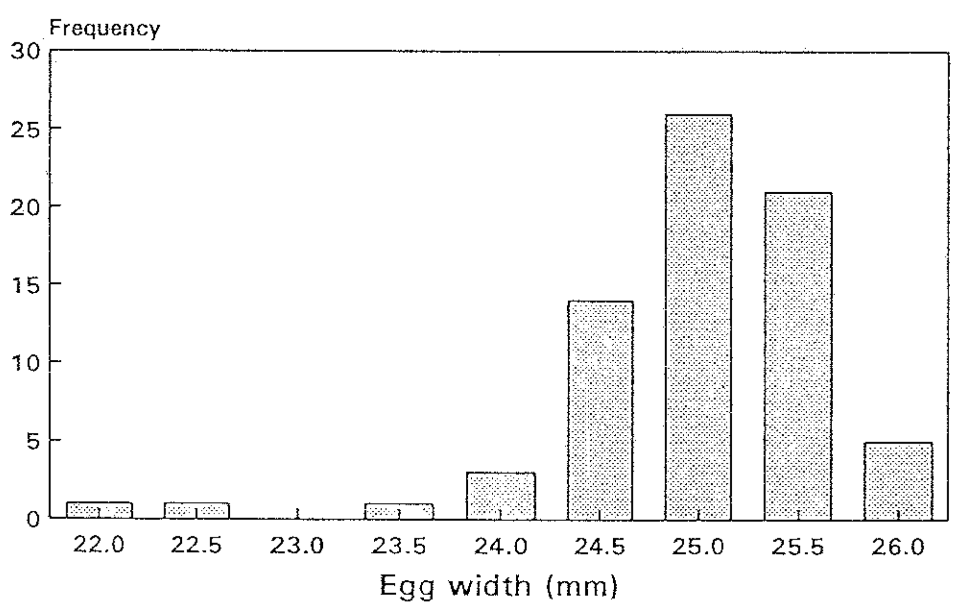
Figure 6.3 Variation in dimensions of Wirebird eggs found during 1988 - 1989

a) Distribution of egg length



n=72

b) Distribution of egg width



n=72

Table 6.4 Mean durations of brooding periods and between-brooding intervals observed during 1988 and 1989 (minutes and seconds)

No. chicks	Age of chicks	Weather	Brooding period Mean	sd	n	Interval Mean	sd	n
2	1st week	cold,windy	3'36"	47"	13	4'31"	45"	12
1	2nd week	hot,dry	2'33"	1'30"	4	9'51"	1'14"	3
2	2nd week	warm,dry	10'18"	12'23"	3	13'27"	2'12"	2
1	1st week	cool,rain	3'27"	1'24"	6	3'11"	1'10"	5
1	2nd week	cool,drizzle	4'04"	1'04"	11	4'48"	1'20"	10
1	3rd week	warm,dry	4'02"	45"	5	13'24"	4'07"	4
1	1st week	cool,windy	3'37"	38"	12	4'07"	57"	11
1	1st week	warm,dry	4'45"	56"	7	6'33"	1'59"	6
1	2nd week	warm,dry	4'46"	1'43"	6	7'07"	3'08"	5
2	1st week	cool,dry	4'53"	3'09"	10	5'16"	1'30"	9
2	2nd week	warm,dry	3'38"	1'09"	6	9'38"	2'48"	5
2	2nd week	cool,drizzle	8'23"	4'14"	5	5'23"	45"	4

Table 6.5 Movements of at least 1km by colour-ringed Wirebirds

a) **Adults**

From	To	Distance (km)
Sheep Pound Gut	Fisher's Valley	3.5
Barren Hill	Pounceys	1.5

b) **Juveniles**

From	To	Distance (km)
Horse Pasture	Deadwood Plain	6.6
Deadwood Plain	Fisher's Valley	4.0
Barren Hill	Prosperous Bay Plain	6.2
Fisher's Valley	Deadwood Plain	4.0
Longwood Golf Course	Prosperous Bay North	2.8
Deadwood Plain	Prosperous Bay Plain	4.7
Deadwood Plain	Flagstaff Hill	1.4
Deadwood Plain	Longwood Golf Course	2.5
Longwood Golf Course	Fisher's Valley	2.1
Prosperous Bay Plain	Fisher's Valley	1.0
Prosperous Bay Plain	Fisher's Valley	1.0

Table 6.6 Seasonal changes in Wirebird numbers at major arid and grassland sites in north-east St Helena 1988 - 1989

a) Arid sites

	October 88	February 89	June 89	October 89
Horse Point Plain	20	13	20	21
Prosperous Bay North	24	6	17	19
Prosperous Bay Plain	14	9	43	20
Upper Prosperous Bay	15	10	26	29
total	73	38	106	89
percentage change	-	-48	+179	-16

b) Grassland sites

	October 88	February 89	June 89	October 89
Deadwood Plain	129	147	150	121
Longwood Farm	13	22	15	17
Bottomwoods	37	53	40	47
total	179	222	205	185
percentage change	-	+24	-8	-10

7. PREDATION AND DISTURBANCE

7.1 PREDATION

The previous section showed that pre-fledging mortality in the Wirebird is high. Predators certainly cause some loss of eggs and chicks but the exact proportion is not known: no clues to the cause of failure were ever found at nests. The may also be some predation of fully-grown birds but again the scale of this is unclear and only circumstantial evidence was found during my study. Three Wirebirds with injured legs and another with a broken wing were encountered on Longwood Golf Course, the Wire- bird site most frequented by cats and dogs, during the 14 months of field-work. A further injured bird was found at Bank's Ridge. All but one of these casualties were juveniles, which might be more vulnerable to predators than experienced adults.

The potential predators of the Wirebird and its eggs are as follows:

7.1.1 CATS

Cats became established on St Helena within 150 years of the island's discovery and were found to be numerous by Peter Mundy in 1634 (Temple 1914). They are now widespread, the greatest numbers occurring around the larger settlements. There are probably relatively few truly feral cats, though these were encountered at Flagstaff Hill and Man and Horse, but large numbers of domestic pets that wander freely.

Cats probably have their greatest impact on the Wirebird in the areas surrounding Longwood, Deadwood and Bottomwoods settlements, where a large number of domestic cats live near substantial Wirebird populations.

Cats are probably the only predator of fledged Wirebirds. A corpse found on the golf course had injuries consistent with its having been killed by a cat. If, however, predation of full-grown birds was severe one would expect to find corpses more often. It is probable that cats take significant numbers of chicks in some areas and I received one report from a usually reliable source that a cat had been seen to take Wirebird eggs.

The Public Health Department occasionally traps cats but the effort is centred on Jamestown and Half Tree Hollow and so is of little significance to Wirebird protection. Some trapping is done at Longwood but financial constraints prevent this being carried out more regularly. Only cats without any mark of ownership are destroyed and it is unlikely that numbers are much reduced. Information on the number of cats trapped in specific areas is not available.

7.1.2 DOGS

Dogs have been present on St Helena for a similar length of time to cats and are numerous throughout the island, especially around settlements. Intensive shooting campaigns in recent years have greatly reduced the number of feral dogs on the island but some still exist and were seen regularly around Turk's Cap Valley during this study and also at Prosperous Bay Valley. Little control is exercised over a large proportion of domestic pets, however, and these roam widely. Small packs were often encountered in various parts of the island.

Predation by dogs on Wirebirds is likely to be confined to chicks and eggs. No direct evidence was found but dogs were seen to chase adult Wirebirds on the golf course and the consumption of eggs has been reported.

7.1.3 RATS

Two species of rat occur on St Helena. The Black Rat *Rattus rattus* was possibly the earliest mammalian colonist of the island after its discovery by man in 1502 but as much as 200 years may have elapsed before it was joined by the larger Brown Rat *R. norvegicus* (Atkinson 1985).

The numbers of rats on St Helena have occasionally reached plague proportions. This seems to have occurred frequently in the hundred years after 1650 (Gosse 1938) but in more recent times continuous poisoning appears to have suppressed the population to some degree. Rats are still widespread and common, however. The greatest numbers encountered outwith the settlements were found in densely vegetated road verges and around the margins of flax plantations. Rats appeared to be scarce at most grassland Wirebird sites and absent from the most arid areas but the true situation is unknown. Sightings or other evidence of rats (e.g. droppings) on pastureland were obtained at Deadwood Plain, Broad Bottom, The Dungeon, Barren Hill and Blue Hill. Two Wirebird sites, Horse Point Plain and Donkey Plain, are adjacent to rubbish dumps, which are likely to harbour large numbers of rats.

Because of its more terrestrial lifestyle, the Brown Rat is likely to pose the greater threat to Wirebirds (Atkinson 1985). It is highly probable that rats take eggs and are certainly capable of killing chicks, though evidence is lacking.

7.1.4 MICE

The House Mouse *Mus musculus* is another long-established colonist of St Helena. Mice are extremely abundant at all Wirebird sites and, in the absence of significant predation, are active throughout the daylight hours. In other parts of the world mice have been found to eat the eggs of ground-nesting birds (Maxson and Oring 1978). No evidence of this was found at any of the failed nests recorded during this study but the possibility remains. As a testimony to their omnivory, mice have been implicated in the decline of endemic snails *Succinea* spp. and the Giant Earwig *Labidura herculeana* on St Helena (Clarke 1990).

7.1.5 MYNAHS

The Common Mynah *Acridotheres tristis* is a relatively recent addition to the fauna of St Helena, though the exact date of its introduction is uncertain as there may be some confusion with the Hill Mynah *Eulabes religiosa* in the early literature. The latter species was introduced to the island in the early 19th century but failed to become established (Mellis 1871) and the present Mynah population is probably descended from a number of birds released at the Briars in 1885 (Basilewsky 1970). Mynahs were originally introduced with the intention of controlling cattle ticks. The population has increased rapidly and the Mynah is now amongst the commonest birds on the island. It is an omnivorous opportunist and any small success its introduction has achieved in controlling pests of cattle is probably at least balanced by its depredations on fruit trees and other crops.

Mynahs are known to raid the nests of other small birds and, occasionally, of their own species (Loveridge 1974). It is likely, therefore, that they will take the eggs of Wirebirds, should the opportunity present itself. The reaction of Wirebirds at the nest or with chicks towards Mynahs in the vicinity is stronger than that towards any other birds, suggesting that Mynahs are perceived as a threat by Wirebirds.

During this study Mynahs were seen to approach five nests and seven broods. In all cases the parents either performed distraction displays or attacked. The response of individual Wirebirds varied in intensity. Some would simply follow any Mynahs within 10m of the nest or position themselves between the Mynahs and the nest but any approach within 5m of the nest would provoke display or aggression. Alexander (1985) observed similar behaviour. On one occasion a Wirebird which was guarding a chick flew up to chase a pair of Mynahs passing overhead. If a nest was left unoccupied during interactions with Mynahs the eggs were always covered - the usual reaction to potential predators. Despite these observations no positive proof of nest robbery by Mynahs was found. I suspect that this may be relatively common, however. Further investigation is required.

The Mynah population of St Helena now numbers several thousands. No attempt was made to census Mynahs as the birds are highly mobile, making direct counts of limited value. To obtain some indication of predation risk, the relative abundance of Mynahs at various Wirebirds sites was estimated by calculating an index based on numbers of Mynahs observed per unit time spent at a particular site. This avoided problems in sampling arising from the large differences in area between sites. To calculate the index, the total number of Mynahs seen during a visit was divided by the time (hours) spent at the site. These counts were carried out simultaneously with the second, third and fourth Wirebird censuses. A mean index was calculated from the three figures obtained (Table 7.1).

Mynah numbers can vary dramatically between visits to particular sites and are strongly influenced by the presence of transient food sources such as the fruits of Prickly Pear (*Opuntia* spp.) and insects attracted to, or disturbed by grazing cattle. Indices at particular sites were fairly consistent, however. When mean indices were compared between the three major vegetation types (intermediate pasture, upland pasture and semi-desert) by single-classification analysis of variance no difference was found between the two pasture types but both intermediate and upland pastures had significantly higher indices that semi-desert ($F(1,14) = 11.69$, $P<0.01$ and $F(1,13) = 11.27$, $P<0.01$). Thus Wirebirds and Mynahs are commonest in the same habitats, suggesting that competition and predation are both greatest in the Wirebird's preferred habitat.

The Mynah is the Wirebird's only avian competitor for terrestrial invertebrate prey but the extent of this competition has yet to be quantified and more information on the dynamics of the Mynah population is required.

7.2 DISTURBANCE

7.2.1 DISTURBANCE BY HUMANS

Regular disturbance of breeding birds by humans has been shown to result in reduced fledging success in some plover species by reducing the feeding and brooding time available to the chicks (e.g. Flemming et al 1988). Disturbance of Wirebirds can arise from the use of breeding areas by walkers, passage of motor vehicles (though Wirebirds are considerably more tolerant of vehicles than of persons on foot), and from crop husbandry. The last only affects birds at Broad Bottom, Longwood Farm and, to a lesser extent, Woody Ridge and Rosemary Plain.

It was not possible to carry out a detailed investigation of the effects of disturbance in the time available but a subjective assessment of the average level of disturbance at each Wirebird site, based on personal experience, was made. This is presented in table 7.2.

Despite St Helena's small size and relatively large human population, few Wirebird sites are subject to serious disturbance. The worst affected are Francis Plain, Longwood Golf Course, the lower parts of Deadwood Plain around Deadwood village, and Horse Pasture. The playing fields at Francis Plain are intensively used almost every day. The golf course is crossed daily by large numbers of pedestrians in addition to golfers. On lower Deadwood Plain most pedestrian and vehicular disturbance is associated with the daily movement of cattle to and from the common grazings and feeding of resident stock. The upper part of the Horse Pasture census area is a public picnic site which is heavily used at weekends though usually much less on weekdays. Recently moto-cross competitions have been held over tracks in the scrub at Horse Pasture. These events are infrequent, however, and do not impinge upon areas regularly used by Wirebirds but the disturbance caused by spectators and their vehicles throughout the area is considerable. During grass-cutting operations at Francis Plain and the golf course, known Wirebird nests are usually marked and the eggs replaced after cutting.

The high levels of disturbance described above affect less that 5% of the breeding population and successful fledging is known to have occurred at all the worst affected sites except Francis Plain during 1988-89.

7.2.2 DISTURBANCE BY LIVESTOCK

Wirebirds generally show no fear of cattle or other grazing animals, often allowing them to approach within 2m without any sign of alarm, they rarely forage where livestock are concentrated, however. Adult Wirebirds were occasionally seen to perform distraction displays when cattle came very close to nests or chicks, though with little effect. Egg-covering in response to the approach of livestock was never observed.

The major threat posed to ground-nesting birds by livestock is that of nest-trampling. None of the failed nests that were examined showed discernible signs of this, but studies of nesting waders in Holland and England have shown that trampling by cattle, at a grazing density of one cow per acre, can destroy 40% to 60% of nests (Beintema 1982, O'Connor and Shrubb 1986). During the 1988-89 dry season grazing densities within individual paddocks at Deadwood Plain occasionally exceeded 12 cattle per acre. However on such occasions the entire Deadwood herd (c.90 head) were confined to one paddock and around 90% of the Plain remained ungrazed.

7.3 CONCLUSIONS

It is not possible to quantify the effects on the Wirebird of predation and disturbance from data gathered during this study but only a small proportion of the Wirebird population is subject to severe disturbance. Predation in general and competition for food between the Wirebird and the common Mynah require futher investigation.

Table 7.1 Indices of the relative abundance of Common Mynahs *Acridotheres tristis* in Wirebird census areas during 1989.

	Feb/ March	June/ July	Oct/ Nov	Mean	s.d.
Intermediate Pasture					
Longwood Golf Course	101	102	117	107	9
Woody Ridge	19	26	233	93	122
Francis Plain	62	75	114	84	27
Man and Horse	35	29	102	53	41
Longwood Farm	61	21	40	41	20
Sane Valley	53	21	36	37	16
Southern Pastures	28	23	52	34	16
Deadwood Plain	37	33	29	33	4
Bottomwoods	14	23	45	27	16
			overall	57	30
Upland Pasture					
Prospect Pastures	81	97	181	120	54
Broad Bottom	80	80	97	86	10
Oaklands Pastures	97	85	64	82	17
Pounceys	56	34	87	59	27
Blue Hill-Head O'Wain	41	31	40	37	6
Central Pastures	42	54	16	37	19
Barren Hill	17	32	42	30	13
The Dungeon	18	26	41	28	12
			overall	60	33
Semi-Desert					
Weather Station Ridge	32	19	30	27	7
Horse Point Plain	30	9	22	20	11
Longwood Erosion Zone	17	28	16	20	7
Prosperous Bay Plain	21	18	10	16	6
Prosperous Bay North	14	15	16	15	1
Upper Prosperous Bay	14	6	15	12	5
Bank's Ridge	11	4	10	8	4
			overall	17	6
Others					
Fisher's Valley	127	158	108	131	25
Rosemary Plain	44	60	112	72	36
Horse Pasture	21	87	76	61	35
Donkey Plain	50	37	17	35	17
			overall	75	41

Table 7.2 Estimated human disturbance in Wirebird Census areas.

	Pedestrians	Vehicles	Crop Husbandry
High Knoll/Cowpath	4	B	
Donkey Plain	2-4	B	
Rosemary Plain	2-4	B	*
Francis Plain	4	A	
Barren Hill	2		
Prospect pastures	2		
The Dungeon	2		
Sane valley	3		
Deadwood Plain (lower)	4	B	
Deadwood Plain (upper)	1-2	A	
Banks' Ridge	1	A	
Longwood Farm	2	A	*
Longwood Golf Course	4		
Bottomwoods	3	A	
Longwood Erosion Zone	1		
Weather Station Ridge	2		
Horse Point Plain	2	A	
Prosperous Bay North	1		
Fisher's Valley	3	A	
Prosperous Bay Plain	2	A	
Upper Prosperous Bay	1		
Woody Ridge	3	A	*
Stone Top Ridge	1		
Central Pastures	2-3		
Pounceys	4	A	
Oaklands Pastures	2		
Broad Bottom	1-3	B	*
Horse Pasture	1-4	B	
Blue Hill-Head O'Wain	2		
Southern Pastures	1-3	B	
Man and Horse	1	A	

Key: 1 = <1 person per day   A = < daily, but regular
2 = 1-5 persons per day   B = daily
3 = 6-10 persons per day
4 = >10 persons per day   * = regular

8. CONSERVATION

The counts made during this study indicate that the current Wirebird population is considerably larger than the most recent previous estimate (Alexander 1985). It is only possible to speculate about recent trends in numbers, however. It is likely that the population has declined since last century because of habitat lost to flax, forestry and housing but it is not known if any significant changes have occurred during the last 50 years. Enquiries amongst the older members of the island's population produced conflicting views. Approximately half of those asked thought that the Wirebird population had declined significantly during their lifetime, whereas the others thought the species was now commoner than ever. Such observations suggest that there may have been some change in distribution but the information received was generally too vague to allow reliable conclusions to be drawn. Loveridge (1974) reported a decline in numbers around upper Deadwood Plain and Flagstaff Hill in the early 1960's, which he attributed to loss of cover as scrub was cleared to improve and extend grazing. The population appears to have recovered, however, as I found similar numbers of breeding birds in the Flagstaff area to those recorded by Loveridge in 1957 (Loveridge 1974). This study provides a baseline estimate of the size of the Wirebird population but comparative census work will be required in the future to determine whether the population is stable.

The Wirebird suffers no direct human persecution. It is fully protected by law and is regarded with considerable affection by the islanders. However, any species with a total population of only around 500 individuals must be vulnerable to any major change of land-use within its habitat. The future of the Wirebird on St Helena is therefore inextricably linked with that of the pastures as these areas hold approximately 80% of all Wirebirds. It is therefore essential that the pastures, especially those below 600m, are maintained as grazing land and are managed in a manner sensitive to the needs of the Wirebird.

Possible conservation measures and assessment of the impact of proposed agricultural, forestry and amenity developments are discussed below.

8.1 AGRICULTURE

It is unlikely that there will be any large-scale loss of pastureland to other land-use in the foreseeable future. The present pastures are a valuable resource for meat production on an island which has to import most of its foodstuffs and, as current agricultural policy is directed towards increased self- sufficiency, pastureland is likely to be protected from development. There is, however, a desire to increase the area of land under cultivation and this could lead to the conversion of some pastureland. Any expansion of arable land would require the use of irrigation and would therefore be dependent on major improvements to the current water supply which is inadequate, in most areas, to meet such needs.

It is, however, proposed to use effluent from a new sewage treatment plant currently under construction to provide irrigation for the Bottomwoods pasture. This would allow some 25ha to be used for arable production. During this study Bottomwoods held, on average, 44 Wirebirds; a significant population. The mean Wirebird density (0.98/ha) was the highest of any census area, indicating that the habitat is currently of very high quality. Any environmental modification is, therefore, likely to be detrimental to the Wirebird population to some degree.

Observations at other cultivated sites, however, suggest that it is unlikely that Bottomwoods would be abandoned by Wirebirds after development. Less than 50% of the total pasture area would be taken into cultivation, of which only some 40% would be in production at any one time. This regime should allow ample opportunity for Wirebirds to forage. The effects of cultivation on the abundance of prey species is unpredictable but would seem unlikely to be beneficial, however. It is also likely that increased disturbance associated with crop husbandry would reduce the breeding success of Wirebirds attempting to nest within the developed area.

If the development goes ahead, it would be advisable to monitor its effect on habitat quality and usage of the site by Wirebirds as it might be possible to ameliorate any deleterious consequences by habitat management in adjacent areas.

There is also a possibility of some future expansion of existing arable land at Broad Bottom and Woody Ridge.

Economic circumstances may change. For that reason it is important that the dependence on the pasturelands of the greater part of the Wirebird population is taken into account in the formulation of development policy. Around 25% of all Wirebirds inhabit Deadwood Plain and statutory protection of this most important breeding area would make a substantial contribution towards ensuring the survival of the species. This would require the drawing-up of a formal management policy taking into account the needs of the Wirebird and a long-term commitment to the area being used exclusively for grazing.

A management policy would cover such aspects as stocking density, grazing rotation, pasture improvement (including the use of fertilizers and the use of pesticides. Stocking density and rotation period may be of considerable importance during the peak breeding months because of the risk of nests being trampled (see section 7.2.2). Any use of strip-grazing during the dry season is likely to cause a high rate of nest failure. However, given the poor growth of grass during this period it highly unlikely that such a grazing regime would be feasible in the absence of irrigation.

The St Helena National Development Plan (ODA 1989) identifies pasture improvement by establishment of alternative grass species and legumes as an important component of agricultural development on the island. It was shown in Section 4 that Wirebirds prefer short grass and there is some indication that relatively dense swards are less favoured, therefore any improvements that produced a substantial increase in vegetation height and density over large areas at major pastureland Wirebird sites might be detrimental to the birds by reducing both feeding efficiency and chick survival. Other waders breeding in grassland and cereals have been shown to be sensitive to changes in vegetation height: for example, Lapwings tend not to nest in sites with a crop height greater that 9cm if growth is dense (Cramp and Simmons 1983). The survival of Lapwing chicks has aso been shown to decline with increasing vegetation height in the vicinity of the nest (Galbraith 1988). Again it is improbable that such conditions would prevail, even in improved pastures, during the dry season on St Helena.

Inorganic fertilizers are not extensively used on St Helena at present, though they have been applied to some areas of Deadwood Plain. It would be wise to exercise caution before substantially increasing the application of nitrogenous compounds at important Wirebird sites, not only because of potential effects on plant growth but also because evidence is beginning to emerge that regular treatment may reduce the numbers of soil invertebrates such as form the prey of the Wirebird (Edwards 1984). As so little is currently known about the effects of pasture management practices on Wirebirds it would be highly desirable to monitor the reaction of the birds to pasture improvement trials.

The limited use of pesticides on St Helena is unlikely to be a threat to the Wirebird and its prey as these are only applied to vegetable crops and fruit trees. However, as Wirebirds do forage amongst crops in a few areas, particularly at Broad Bottom, any pesticides used should be of low avian toxicity and environmental persistence to avoid the risks of poisoning and reduced fertility that have occurred in other bird species world-wide as a result of the consumption of contaminated prey.

8.2 FORESTRY

Wirebirds avoid dense woodland, so the afforestation of current Wirebird habitat would eliminate the birds. Most expansion of forestry on St Helena is likely to take place on the fringes of the Crown Wastes to assist soil conservation. It will be constrained by rainfall and soil conditions and most of the currently barren areas inhabited by Wirebirds are classified as unsuitable for forestry, though Sane Valley, Netley Gut and Sheep Pound Gut are possible forestry sites, (Brown 1981, vol.3). Any such developments would result in significant loss of Wirebird habitat.

The Agricultural and Forestry Department is establishing plantations of threatened endemic tree species throughout the island. One of these, consisting mainly of Gumwood *Commidendrum robustum*, is at Horse Point Plain. At present it covers less than 5ha. It is at an early stage of growth and is still used by Wirebirds. It has been suggested that this plantation be extended over the entire Plain (A.Barlow pers. comm.). This would achieve the laudable result of restoring the area's natural vegetation, as it known that Horse Point Plain was covered by Gumwood woodland until at least 1700, but the effect on the population of around 10 pairs of Wirebirds would seem likely to be detrimental, although there is some controversy surrounding the Wirebird's relationship with the Gumwood. The Wirebird's present range, particularly on pastureland, seems to have been largely occupied by Gumwood forest prior to human colonization of the island and it has been suggested that the Wirebird may have originally inhabited the woodland floor which, under Gumwoods, is sparsely vegetated (Cronk 1989). This would, however, be aberrant behaviour for a plover and the present Wirebird population shows no inclination to enter even the most open woodland. It would, therefore, seem inadvisable to greatly increase the present area of Gumwoods at Horse Point, particularly as the plain may become more important in the future as a "buffer zone" able to absorb Wirebirds displaced by agricultural development at Bottomwoods (see section 8.1). Low- density planting of Scrubwood would seem to offer greater compatibility between the conservation of St Helena's endemic flora and that of its fauna. Some organic enrichment of the site by additional leaf-litter might well improve it for Wirebirds by increasing the abundance of invertebrates but, again, the impact of planting would require monitoring.

8.3 CONSTRUCTION

Wirebird habitat is unlikely to be significantly threatened by new housing development in the future as environmental conservation is now given high priority in planning by the St Helena Government. Pastureland sites are too valuable to the island's economy to be developed and it is improbable that any residential development in the crown wastes would be contemplated. There is a shortage of housing throughout the island but it is now government policy to concentrate new construction in the Half Tree Hollow area. As a result it is certain that the little remaining Wirebird habitat along the north-west coast of the island, between Lemon Valley and Jamestown, will suffer further attrition but less than 20 birds now inhabit the area and the effect on the population as a whole would not be great.

Studies of the feasibility of constructing an airfield on St Helena are currently underway. It is proposed to site this on Prosperous Bay Plain where a tarmac runway lkm long would be built on Wirebird breeding habitat. The long-term impact of this might not be particularly serious, however, as the Wirebird density at this site is low. The birds in other parts of the island have also shown themselves to be adaptable to human disturbance. Given the propensity of its close relative, Kittlitz's Sand Plover, for nesting on airfields and similar sites in Africa it would seem reasonable to expect that, after the disturbance of the construction phase, Wirebirds would return to nest within the airfield perimeter. Subsequent disturbance would not be high as only two flights per week are projected. It is, however, by no means definite that the airfield will be built in the near future as the air service would be dependent on private capital and the commercial viability of the project is uncertain.

Bottomwoods has also been mentioned as a possible airport site. This is major Wirebird breeding area with the highest density of Wirebirds on the island. Because of the large number of birds affected major developments at this site should be opposed. At present a small sewage treatment plant is under construction at Bottomwoods but this is sited in an area not especially favoured by Wirebirds.

It is probable that a wind-powered generator will be sited at Deadwood Plain in the near future. Some concern was expressed to me by those in favour of the scheme about its possible effect on Wirebirds but, although there will undoubtedly be disturbance during construction, studies of similar machines in Holland and the United Kingdom have shown that they are unlikely to endanger or disturb birds to a significant degree (Winkelman 1985; C.J.Mead pers.comm.). This would apply particularly to species like the Wirebird which is so predominantly terrestrial.

8.4 PREDATION

Most potential predators (dogs, cats, and rodents) have existed on St Helena for several hundred years and records suggest that all have been more numerous in the past. Despite this the Wirebird population is still substantial and it may be that the species had adapted to the presence of these long-established threats, though complacency should be avoided.

The current rodent control programme should be continued at least at its present level but, despite the attractiveness of the idea, no predatory animal should be introduced to St Helena to control rodents. On other islands throughout the world such introductions have had disastrous consequences for the native fauna. Any new vertebrate predator would be a threat to Wirebirds, particularly to chicks.

An increase in cat-trapping in the Longwood area would be of some benefit to the Wirebird, as would stricter legislation on the control of dogs throughout the island.

The Common Mynah is the most recently introduced potential predator on St Helena. Their numbers have increased rapidly and there may be a need for them to be controlled but more information about their population dynamics and their impact on the Wirebird population through predation and competition is needed.

Some islanders occasionally take Wirebird eggs and chicks with the intention of rearing them as pets although this is illegal. Rearing is usually unsuccessful but attempts are rare and unlikely to have any significant impact on the population. Raising public awareness of the uniqueness and rarity of the Wirebird might help to eradicate the practice.

8.5 EDUCATION

Although there is little conflict at present between the requirements of the indigenous fauna and flora and those of the people of St Helena, knowledge of and interest in local natural history is low and the aims of conservation in the long-term would be assisted by making the local population more aware of their natural heritage and of wider environmental issues. It is particularly important that children are given the opportunity to develop an interest in their environment. Environmental subjects will be given a higher profile at the recently opened Prince Andrew (senior) School but there is a need for pupils to be introduced to these at junior and middle school levels.

A major problem confronting environmental education on St Helena is the paucity of literature available on local wildlife. Most of what there is comprises long out of print and out of date books or papers in scientific journals, neither of which is readily accessible or attractive to the average islander. Recently the Agriculture and Forestry Department produced a successful booklet on the endemic plants of St Helena and a book covering all aspects of the island's natural history is planned. While on St Helena I found there was a demand for a simple identification guide to the local birds and I believe the production of such a publication would be a small but significant step in promoting bird conservation on the island.

During my stay on the island I was able to publicize the Wirebird and other island species in two radio interviews, newspaper articles, a poster display at the island's agricultural show, and lectures to the St Helena Heritage Society and to biology and agriculture students at the Prince Andrew School. All of this appeared to stimulate genuine interest.

8.6 CONCLUSIONS

The Wirebird does not appear to be threatened at present. However, there may be substantial changes in agricultural practices on St Helena in the future, the impact of which cannot be fully predicted on the basis of the limited data gathered during this study. Future monitoring of Wirebird numbers is essential. More information is needed on effects of pasture management on Wirebirds and on the causes of nest-failure and pre-fledging mortality. The role of the Mynah as a competitor of the Wirebird also needs be clarified.

The following points are suggested as the basis for a conservation strategy for the Wirebird:

1) Designation of Deadwood Plain/Flagstaff as a special protected area within which land-use is restricted to grazing and management practices are compatible with the requirements of the Wirebird.

2) Maintenance of the other present areas of pasture as grazing land, especially those at Man and Horse, Botleys Lay, Broad Bottom, Sane Valley, Middle Point and as large an area as possible at Bottomwoods.

3) Livestock densities at important sites to be held at, or preferably below, present levels during the main Wirebird breeding season (October - March).

4) Restrictions on the use of pesticides and herbicides in Wirebird breeding areas. Where the use of the above is essential, only non-persistent compounds of low avian toxicity should be applied.

5) Intensification of control measures against feral cats in rural areas, particularly around Longwood.

6) Maintenance of the current rodent control programme.

7) Maintenance of stringent measures against the importation of avian diseases.

8) Establishment of long-term monitoring of Wirebird numbers. This should be carried out by experienced personnel at intervals of not more than five years. An annual census project in conjunction with the schools might be possible but would require adherence to standardized methods to give meaningful results.

9) Further research into factors affecting Wirebird breeding success and into utilization of cultivated land by Wirebirds.

10) Investigation of the diet and population dynamics of the Common Mynah with a view to establishing its significance as a competitor and predator of the Wirebird.

11) Increasing the awareness of St Helena's unique natural heritage amongst islanders, particularly children, through the schools (especially at Junior and Middle levels) and the local media. This should be supported by the production of introductory literature of a style and price appropriate to island readership.

NOTE: NEED FOR A RESEARCH VEHICLE ON ST HELENA

Should further studies of the Wirebird be undertaken, experience shows that four-wheeled transport is essential to maximize the efficient use of time spent on the island, where the terrain is so difficult. A vehicle would increase the area possible to cover in a day, would enable much more equipment to be carried, and, not least, could be used as a mobile hide to facilitate close approach to feeding and nesting birds.

ACKNOWLEDGEMENTS

Fieldwork on St Helena was funded by the Worldwide Fund for Nature (UK), the International Council for Bird Preservation (UK) and the Peter Scott Trust for Education and Research in Conservation. Additional financial support was received from the Iris Darnton Foundation, the Peter Nathan Charitable Trust and the International Trust for Nature Conservation. The project was administered by the British Trust for Ornithology and supervised by Dr J.J.D. Greenwood, for whose advice and encouragement I am extremely grateful.

I am indebted to Mr A. Dunthorn who assisted me in the final stages of fieldwork. He most generously volunteered to travel to St Helena at considerable personal expense and was able to collect data on aspects of wirebird social behaviour which, without his help, could not have been covered.

I thank their Excellencies Governors F.E. Baker and R.F. Stimson for permission to carry out fieldwork on St Helena, and Mr. V. Hart, Agriculture and Forestry officer, for the generous assistance given by himself and many of his staff. Mr I.K. Mathieson provided much useful climatic data and Mr G. Benjamin gave invaluable assistance in identifying plant specimens. Mr. A. Rennie, Director of Works, and Mr. D. Tonge, Environmental Health Officer, also provided valuable information.

Mrs G. Denbow (UK representative of the St Helena Government), Mr D. Clarke, Mr P. Pearce-Kelly and Mr. R. Veal of the Zoological Society of London, Dr Q.C.B.Cronk, Dr M.W.Pienkowski and Ms C. Alexander all gave advice and assistance at the planning stage. At ICBP Dr.N.Collar made valuable comments on parts of the manuscript and Dr M.Rands was a constant source of encouragement throughout the project. Susan Waghorn, Sophie Foulger and Tracey Brookes provided invaluable secretarial support.

I am extremely grateful to Mr and Mrs N. Thorpe for providing excellent accommodation at very short notice to numerous friends on St Helena who assisted me with transport and to the islanders of St Helena in general for their hospitality and unfailing co-operation.

REFERENCES

ALEXANDER, C. (1985). The St Helena Wirebird: its status and distribution. Unpublished.

ASHMOLE, N.P. (1963). The extinct avifauna of St Helena island. *Ibis* 103b: 390-408.

ATKINSON, I.A.E. (1985). The spread of commensal species of *Rattus* to oceanic islands and their effect on island avifaunas. In "Conservation of Island Birds" (ed. P.J. Moors). I.C.B.P., Cambridge.

BAKER, E. (1868). The birds of St Helena. *Zoologist* (2) 3: 1472-1476.

BAKER, I. (1970). Geological history of Saint Helena in relation to its floral and faunal colonization. In "La faune terrestre de l'ile Sainte-Helene (premiere partie)". *Annales de la Musee Royale de L'Afrique Centrale, Tervuren* Serie 8, Sci.Zool. 181: 25-35.

BAKER, I., GALE, N.H. and SIMONS, J. (1967). Geochronology of the St Helena volcanoes. *Nature* 215: 1451-1456.

BASILEWSKY, P. (1970). La faune terrestre d l'ile de Sainte-Helene, 1 - Vertebres. *Annales de la Musee Royale de L'Afrique Centrale, Tervuren* Serie 8, Sci.Zool. 181: 77-130.

BEATSON, A. (1816). "Tracts Relative to the Island of St Helena". Jamestown, St Helena.

BEINTEMA, A.J. (1982). Meadow birds in The Netherlands. Rijksinstituut voor Natuurbeheer - Rapport 1981: 86-93.

BENSON, C.W. (1950). A contribution to the ornithology of St Helena, and other notes from a sea voyage. *Ibis* 92: 75-83.

BERGSTROM, P.W. (1988a). Breeding biology of Wilson's Plovers. *Wilson Bulletin* 100: 23-35.

BERGSTROM, P.W. (1988b). Breeding displays and vocalisations of Wilson's Plovers. *Wilson Bulletin* 100: 36-49.

BOCK, W.J. (1958). A generic review of the plovers *(Charadriinae, Aves)*. *Bulletin of the Museum of Comparative Zoology*, Cambridge, Mass., U.S.A., 118: 27-97.

BROWN, L.C. (1978). Agronomic studies on St Helena 1973-1977: a summary report. Ministry of Overseas Development Project Report 58, Tolworth.

BROWN, L.C. (1981). The land resources and agro-forestal development of St Helena (3 volumes). Ministry of Overseas Development Land Resource Study 32. Tolworth.

BROWN, L.C. (1982). The flora and fauna of St Helena. Ministry of Overseas Development Project Report 59, Tolworth.

CLARK, A. (1982). Some observations on the breeding behaviour of Kittlitz's Sandplover. *Ostrich* 53: 120-122.

CLARKE, D. (1990). Invertebrates - The "Project Hercules" expedition. In: St Helena, Natural Treasury. Proceedings of a symposium held at the Zoological Society of London, 9th September 1988 (P. Pearce-Kelly & Q.C.B. Cronk eds.), Zoological Society of London.

COLLAR, N.J. and STUART, S.N. (1985). "Threatened Birds of Africa and Related Islands". I.C.B.P./I.U.C.N., Cambridge.

CONWAY, W.G. and BELL, J. (1968). Observations on the behaviour of Kittlitz's Sandplovers at the New York Zoological Park. *Living Bird* 7: 57-70.

CRAMP, S. and SIMMONS, K.E.L. (eds.) (1983). "The Birds of the Western Palearctic". Vol.3. Oxford University Press, Oxford.

CRONK, Q.C.B. (1983). The decline of the redwood *Trochetiopsis erythroxylon* on St Helena. *Biological Conservation* 26: 163-174.

CRONK, Q.C.B. (1986a). The decline of the St Helena ebony *Trochetiopsis melanoxylon*. *Biological Conservation* 35: 159-172.

CRONK, Q.C.B. (1986b). The decline of the St Helena Gumwood *Commidendron robustum*. *Biological Conservation* 35: 173-186.

CRONK, Q.C.B. (1987). The history of endemic flora of St Helena: A relictual series. *New Phytologist* 105: 509-520.

CRONK, Q.C.B. (1989). The past and present vegetation of St Helena. *Journal of Biogeography* 16: 47-64.

DALY, R.A. (1927). The geology of St Helena Island. *Proceedings of the American Academy of Arts and Sciences* 62: 31-92.

EDWARDS, C.A. (1984). Changes in agricultural practice and their impact on soil organisms. In "Agriculture and the Environment" (ed. D. Jenkins) pp. 56-65. Institute of Terrestrial Ecology, Cambridge.

FLEMMING, S.P., CHIASSON, R.D., SMITH, P.C., AUSTIN-SMITH, P.J. and BANCROFT, R.P. (1988). Piping Plover status in Nova Scotia related to its reproductive and behavioral responses to human disturbance. *Journal of Field Ornithology* 59: 321-330.

GALBRAITH, H. (1988). Effects of agriculture on the breeding ecology of Lapwings *Vanellus vanellus*. *Journal of Applied Ecology* 25: 487-503.

GOSSE, P. (1938). "St Helena, 1502-1938". Cassell and Company, London.

HALL, K.R.L. (1958). Observations on the nesting sites and nesting behaviour of the Kittlitz's Sandplover *Charadrius pecuarius*. *Ostrich* 29: 113-125.

HALL, K.R.L. (1959). Nest records and additional behaviour notes for Kittlitz's Sandplover *Charadrius pecuarius* in the S.W. Cape Province. *Ostrich* 30: 33-38.

HARTING, J.E. (1873). On rare or little known Limocolae. *Ibis* Series 3, 3: 260-269.

HARTOG, J.C. den (1984). A note on the avifauna of St Helena, South Atlantic Ocean. *Bulletin of the British Ornithologists' Club* 104: 91-95.

HAYDOCK, E.L. (1954). A survey of the birds of St Helena island. *Ostrich* 25: 62-75.

HUCKLE, C.H. (1924). Birds of Ascension and St Helena. *Ibis* 11: 818-821.

HUMPHREY, N. (1957). A Review of Agriculture and Forestry in the Island of St Helena. Crown Agents, London.

LAYARD, E.L. (1867). Letter. *Ibis* (2) 3: 248-252.

LESSELLS, C.M. (1984). The mating system of Kentish Plovers *Charadrius alexandrinus*. *Ibis* 126: 474-483.

LLEWELLYN, D.G. (1982). Aspects of the water supply of St Helena. In: University College London, Dept. of Geography. St Helena Expedition: Final Report (ed. P.D. Nunn) pp. 45-96.

LOVERIDGE, A. (1974). Notes on the vertebrates of St Helena Island. Unpublished.

LYNN, C.W. (1966). Review of Agriculture and Forestry in the Island of St Helena. Government Printer, St Helena.

MARKHAM, C.R. (ed.) (1911). "Early Spanish Voyages to the Straits of Magellan". Hakluyt Society, Series II, No.38, London.

MATHIESON, I.K. (1990a) End of tour report. Agriculture and Forestry Department, St Helena.

MATHIESON, I.K. (1990b). The Agricultural Climate of St Helena (with reference to Ascension). Overseas Development Administration, London and Agriculture and Forestry Department, St Helena.

MAXSON, S. and ORING, L. (1978). Mice as a source of egg loss among ground-nesting birds. *Auk* 95: 582-584.

MELLISS, J.C. (1871). Notes on the birds of the island of St Helena. *Ibis* Series 3, 6: 97-107.

MELLISS, J.C. (1875). "St Helena: A Physical, Historical and Topographical Description of the Island Including Its Geology, Fauna, Flora and Meteorology". Reeve and Company, London.

MACLEAN, G.L. (1974). Egg-covering in the Charadrii. *Ostrich* 45: 167-174.

MOREAU, R.E. (1931). Some birds on a voyage. *Ibis* 13: 778-781.

MORRIS, D. (1884). Report upon the present conditions and prospects of the agricultural resources of the island of St Helena. Miscellaneous Colonial Report No.38, London.

NICHOLSON, A.J. (1982). The Geology of St Helena. In: University College London, Dept. of Geography. St Helena Expedition: Final Report (ed. P.D.Nunn).

NUNN, P.D. (1982). The Geomorphology of St Helena. In: University College London, Dept. of Geography. St Helena Expedition: Final Report (ed. P.D.Nunn).

O'CONNOR, R.J. and SHRUBB, M. (1986). "Farming and Birds". Cambridge University Press, Cambridge.

OLSON, S.L. (1975). The palaeornithology of St Helena Island, South Atlantic Ocean. *Smithsonian Contributions to Paleobiology* No.23.

OVERSEAS DEVELOPMENT ADMINISTRATION (ODA) (1989). St Helena National Development Plan. London.

PIENKOWSKI, M.W. (1983). Changes in the foraging pattern of plovers in relation to environmental factors. *Animal Behaviour* 31: 244-264.

PITMAN, C.R.S. (1965). The eggs and nesting habits of the St Helena Sand-Plover or Wirebird *Charadrius pecuarius sanctae-helenae* (Harting). *Bulletin of the British Ornithologists' Club* 85: 121-129.

SCLATER, W.L. (1924). Systema Avium Aethiopicarum. British Ornithologists' Union, London.

SIMMONS, G.F. (1927). Sinbads of science. *National Geographic Magazine* 52: 1-75.

STOCKDALE, F. (1939). Agriculture in St Helena. Colonial Office Report No.30, London.

SUMMERS, R.W. and HOCKEY, P.A.R. (1981). Egg covering behaviour of the White-fronted Plover *Charadrius marginatus*. *Ornis Scandinavica* 12: 240-243.

TAYLOR, I. (1959). Hatching of Kittlitz's Sandplover. *Ostrich* 30: 98-90.

TEMPLE, R.C. (ed.) (1914). "The Travels of Peter Mundy in Europe and Asia, 1608-1667". Hakluyt Society, Series II, No.35, Vol.2, London.

TEMPLE, R.C. (ed.) (1919). "The Travels of Peter Mundy in Europe and Asia, 1608-1667". Hakluyt Society, Series II, No.46, Vol.3, London.

TEMPLE, R.C. and ANSTEY, L.M. (eds.) (1936). "The Travels of Peter Mundy in Europe and Asia, 1608-1667". Hakluyt Society, Series II, No. 78, Vol.5. London.

TREE, A.J. (1974). A comparative ecological study of the Kittlitz Plover and Treble-banded Plover at Lake McIlwaine. M.Sc. thesis, University of Rhodesia, Salisbury. Unpublished.

WINKELMAN, J.E. (1985). Impact of medium-sized wind turbines on birds: a survey on flight behaviour, victims and disturbance. *Netherlands Journal of Agricultural Science* 33: 75-78.