Biology of the Grey-headed Gull *Larus cirrocephalus* in South Africa

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for
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Preface

The work described in this dissertation was carried out at various field localities in KwaZulu-Natal, Gauteng and Northern Cape, South Africa, at the Durban Natural Science Museum, at the School of Biological and Conservation Sciences, University of KwaZulu-Natal, Pietermaritzburg and at the Avian Demography Unit, University of Cape Town from January 2004 to December 2005 under the supervision of Professor S.L. Piper (School of Biological and Conservation Sciences, University of KwaZulu-Natal, Pietermaritzburg), D.G. Allan (Durban Natural Science Museum) and Professor L.G. Underhill (Avian Demography Unit, University of Cape Town).

These studies, submitted for the degree of Master of Science in the School of Biological and Conservation Sciences, University of KwaZulu-Natal, Pietermaritzburg, represent the original work of the author and have not been submitted in any form to another university. Use of the work of others has been duly acknowledged in the text.

We certify that the above statement is correct

A.M. McInnes
August 2007

Professor S.E. Piper

D.G. Allan

Professor L.G. Underhill

Abstract

The biology of the Grey-headed Gull was studied between 2004 and 2005 in South Africa's Gauteng, KwaZulu-Natal and Northern Cape provinces.

Grey-headed Gulls have a widespread but patchy distribution in South Africa, occurring both inland and at the coast. Their largest population is centred on Gauteng, where the species appears to be a relatively recent colonizer and where the current breeding population is estimated at 2185 breeding pairs (the largest in South Africa). There is evidence that the species has also increased in other parts of South Africa, especially at Port Elizabeth in the Eastern Cape. The majority of coastal birds are found in KwaZulu-Natal and there is strong evidence for regular movements of adult birds between Durban and Lake St Lucia. By contrast, little evidence was found for a putative large-scale, regular movement between Gauteng and KwaZulu-Natal.

The breeding biology of the Grey-headed Gull was studied at four sites in Gauteng and at Lake St Lucia's Lane Island during 2004 and 2005. The distance between the Gauteng sites ranges from 1.7 km, between Lakefield Pan and Korsman's Bird Sanctuary, to 25.3 km, between Bonaero Park and Modderfontein Pan. The approximate distance between Gauteng and Lake St Lucia is 460 km. The mean clutch size at all sites was 2.42 eggs and the mean incubation period was 24.9 days. Parental investment in incubation was approximately equal between the sexes while males spent more time in attendance and participated in more aggressive encounters. Empirical growth curves are given for mass, wing, culmen, head and foot morphometrics of Grey-headed Gull chicks. Intraspecific variation in breeding parameters reveal significant differences between sites, including: highly synchronous laying at Lake St Lucia; the largest eggs and fastest growing chicks at Gauteng's Modderfontein Pan (a small, peripheral colony); and the smallest eggs and slowest growing chicks at Gauteng's Lakefield Pan (a large, 'core' colony). Possible reasons for these differences include the relative localities of each site in terms of feeding opportunities, high levels of predation by African Fish Eagle's at Lane Island, and density dependent factors operating on the large colonies within the core population on Gauteng's East Rand. Overall daily egg survival was comparatively high for all sites in Gauteng and low for Lane Island nests.

Morphometric, plumage and bare-parts data from a sample of trapped and resighted birds are used to age, sex and determine the timing and duration of moult in the Grey-headed Gull. Six age classes were identified and, for all measurements, males were significantly larger than females. The mean duration of primary moult was 136 days between October and January and there were two waves of secondary moult.

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Acknowledgments

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The most intensive field work, during the course of this study, was in Gauteng, both on the landfill sites, while trapping birds, and in the various wetlands where the breeding study was conducted. This work would not have been possible were it not for the help of the staff of Gauteng Nature Conservation, who contributed many hours to this project. In this regard I would like to convey a special thanks to the following: Craig Whittington-Jones, Sean West, Richard Koko, Job Motsamai, Jacob Makola, Andries Mputhi, Wilson Molaba and Aaron Matabane. I would like to thank the following bird-ringers and volunteers who contributed to the ringing effort in Gauteng and Durban and the field trips to Lake St Lucia: Pat Cochran, Joel Avni, Lynne Bingham, Terry Walls, Murray Christian, Fran de Jager, Richard White, Greg & Fiona Brown, Koos Stovold, Herman Bos, Guy Gibbon and Mathew Gibbon. For accommodating my needs in Kimberley, thanks go to Mark Anderson (Northern Cape Nature Conservation) and Eric Herman (Percy FitzPatrick Institute of Ornithology). The aerial survey conducted over the East Rand pans was made possible by the generous assistance of The Bateleurs, with pilot, Jay van Deventer providing the use of his motorglider and expertise for the job. Thanks to Mike Mostovsky, Curator of Entomology, Natal Museum, for identifying my Diptera specimens. Thanks also to BirdLife South Africa for providing funding for the project. Staff at the ADU (Avian Demography Unit), including Marius Wheeler and Dieter Oschadleus, are thanked for their assistance with the CWAC and SAFRING databases as well as with the issuing of the necessary ringing permit. I would like to thank Ezemvelo KZN Wildlife, and especially Ricky Taylor, for permission to access the Lane Island colony; thanks also to military staff at the Hell's Gate base for allowing us access through this area. Thanks to Dr York and the team at Molecular Diagnostic Services for sexing our blood samples.

I must thank my family, especially my mother for all her support over the years, and to my girlfriend, Michelle, for being by my side throughout the project, for all your help in the field and for your inspiration and support – I really appreciate it.

Chapter 1

Introduction

Gulls are a cosmopolitan group of birds that form a conspicuous component of many developed landscapes (del Hoyo *et al.* 1996). They are amongst the most studied of all bird groups (Chu 1998) and they have a long association with man (Southern 1987). A general increase in gull numbers in the latter half of the twentieth century brought the need for resource managers to determine what factors were driving this accelerated population growth (e.g. Coulson *et al.* 1982). In addition to this more practical component of gull research, breeding colonies of various species have presented scientists with the ideal opportunity to study more theoretical components of bird biology which have helped formulate many major biological concepts (Southern 1987). Despite the vast amount of research conducted on many gull species, there is a disproportionately large number of studies conducted on relatively few species with the result that northern hemisphere species and, to a lesser extent, Australasian species have received the most attention (Cramp & Simmons 1983; Higgins & Davies 1996). With a few exceptions, comparatively little is known of those species that reside in Africa and South America. The number of gull species the breeding ranges of which fall mostly within these continents is five and ten species for Africa and South America, respectively (del Hoyo *et al.* 1996). The Grey-headed Gull *Larus cirrocephalus* is unique in that it is the only small gull species resident in both continents. Together with Hartlaub's *Larus hartlaubii* and Kelp *Larus dominicanus* gulls this species is one of three that breed in South Africa (Hockey *et al.* 2005), and despite its widespread distribution and abundance in this developed part of Africa, it has somehow escaped the level of research that these other species have generated. In fact, most literature on the Grey-headed Gull is anecdotal and the scientific literature focused on this species alone is limited to one paper, that of Brooke *et al.* (1999), which gives a detailed account of the breeding distribution, population and conservation status of this species. The Grey-headed Gull, as a study species, presents itself as a good opportunity to initiate research into various aspects of its life history that can be compared with some of the more closely related and well-studied species.

Taxonomy

The group that comprises the gulls (tribe Larini) consists of 50 extant species which are closely related to their sister tribes: terns (tribe Sternini), skuas and jaegers (tribe Stercorariini) and skimmers (tribe Rynchopini), and which all make up the family Laridae of the order Ciconiiformes (Sibley & Monroe 1990). The morphological and genetic similarities between many gull species, as well as the high incidence of hybridization, have posed particular challenges to systematists when classifying this group (e.g. Collinson 2001; McGowan & Kitchener 2001). The different criteria used to classify gulls have resulted in different interpretations of groupings within these birds. Moynihan (1959), based on differences in behavioural traits, placed all extant gull species into a single genus. By contrast, (Dwight 1925),using morphometrics, divided extant species into nine genera.

Recently, there has been a general consensus on the existence of a monophyletic masked gull group, based on morphology (Chu 1998) and genetics (Crochet *et al.* 2000). The species within this group are relatively small when compared to other gull species and usually possess a dark contrasting hood during the breeding season. The phylogeny within this sub-group has been studied in detail by Given *et al.* (2005) who describes the evolutionary relationships between ten masked gull species using sequencing data from four mitochondrial DNA genes (Figure 1.1). Two of these species occur and breed in South Africa, Hartlaub's Gull and the Grey-headed Gull, and together with the Palearctic Black-headed Gull *Larus ridibundus*, form a distinctive "southern clade" (Given *et al.* 2005). According to these authors, Grey-headed and Hartlaub's gulls diverged from Black-headed Gull approximately 380 000 years ago and from each other as recently as 70 000 years ago, this being the most modern split in masked gull phylogeny. The Grey-headed Gull is currently comprised of two subspecies: the nominate *L. c. cirrocephalus* from South America and *L.c. poiocephalus* from Africa (Given *et al.* 2005); the latter subspecies forms the central topic of this dissertation.

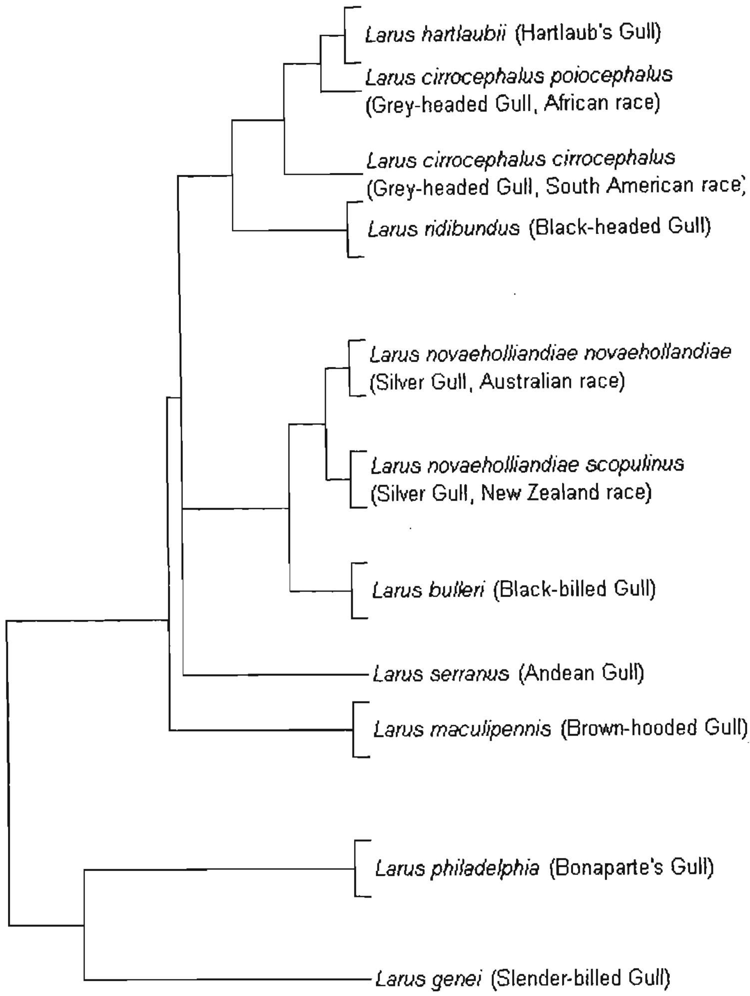


Figure 1.1. Phylogeny of the masked gull group as proposed by Given *et al.* (2005).

Aims of dissertation

The aim of the following chapters is to elucidate the biology of the Grey-headed Gull in areas that have not been previously investigated. The second chapter is an exception in that it provides a review of what is currently known on the distribution, abundance and movements of this species. Some of these aspects, however, are examined in more detail than previously in the light of new data collected during this study. The third and fourth chapters concentrate on the breeding biology of this species, beginning with the nest and egg stages and progressing to the chick stage. In these two sections, the results of certain breeding parameters are used to compare intraspecific differences between breeding colonies in Gauteng and at Lake St Lucia's Lane Island. The fifth chapter looks at age classes, sexing and moult of post-fledgling Grey-headed Gulls. All research presented concerns South African populations.

Distribution, abundance and movements

This section of the dissertation provides a review of what is currently known on the distribution of the Grey-headed Gull, both currently and historically, and relies heavily on Brooke *et al.* (1997). Abundance data, extracted from the CWAC (Coordinated Waterbird Counts Project, Avian Demography Unit, University of Cape Town) database, together with results of count data conducted during the course of this study, are used to analyze and interpret the relative abundance and seasonality of Grey-headed Gulls in South Africa. A review of the movements of this species is also provided and is supplemented with ring-resighting information, especially of adult birds, trapped by my team on Gauteng's landfill sites and on Durban's beachfront. The results of these seasonality and movements data are then interpreted to test the hypothesis of regular movements between Gauteng and KwaZulu-Natal, as proposed by Cyrus & Robson (1980).

Breeding biology

Various life history traits of the Grey-headed Gull's breeding biology are investigated in these sections. This begins with the nest and egg stage (Chapter 3) that describes the clutch size, laying synchrony, oometrics, incubation period and parental investment during the incubation phase. Information related to oometric data and clutch size is then compared between different subpopulations. Data coming from four sites in Gauteng, as well as Lake St Lucia's Lane Island in KwaZulu-Natal, studied during the winter months of 2004 and 2005, are used for this purpose and are interpreted in light of their relative locations and associated environmental conditions. A model is produced to determine the daily egg survival rates for all these sub-populations taking into consideration the effects of both intrinsic and extrinsic variables. The dissertation then progresses to the chick stage (Chapter 4), i.e. the period between hatching and fledging. This chapter provides details of the growth rates of different areas of the anatomy of the Grey-headed Gull, facilitated by the use of empirical growth curves. Standardized growth rate values are used to compare differences between three sub-populations in Gauteng in an attempt to identify those ecological factors that limit and benefit different breeding colonies at a local scale.

Ageing, sexing and moult

In this section, morphometric and plumage data, recorded both from trapped and re-sighted known-age individuals, are used to formulate an updated age classification of Grey-headed Gulls. Morphometric information coming from a small sample of sexed individuals is used to generate a discriminant function for sexing of this species. Morphometrics are then compared between different age groups and between the results of different studies. Finally, the moult of the Grey-headed Gull is described. This includes the duration and timing of primary moult, as well as details of secondary, tail and head moult.

Comparison with closely related species

Where possible, all results coming from this dissertation are compared with what is currently known on other closely related species, especially those species that comprise the masked gull complex (Figure 1.1).

Chapter 2

Distribution, abundance and movements of the Grey-headed Gull *Larus cirrocephalus* in South Africa

Summary

The current and historical distribution, abundance and patterns of movements of the Grey-headed Gull *Larus cirrocephalus* in South Africa are reviewed. This includes results of CWAC (Coordinated Waterbird Counts Project) data, count information from this study, resightings of birds colour ringed in Gauteng and Durban during 2004 and 2005, and results of published and unpublished SAFRING ring recoveries. Grey-headed Gulls currently are widely but patchily distributed in South Africa, with their largest population centred on Gauteng, which supported *ca* 2409 breeding pairs in 2004 and *ca* 2185 breeding pairs in 2005. Along the coast, they are more numerous in the northeast and become less abundant and more scattered further south. Their abundance along the KwaZulu-Natal coast is highest at the large wetland systems in Durban, Richards Bay and Lake St Lucia; the last-mentioned site is a long-established breeding locality of the species. Grey-headed Gulls have become more abundant in Gauteng, the Eastern Cape, and, to a lesser extent, the Western Cape during the last half of the twentieth century and this seems to be due to anthropogenic modifications of the landscape. Ring-resighting information from this study provides little evidence for regular migration of significant numbers of birds between Gauteng and the KwaZulu-Natal coast but does show convincing evidence of regular movements of adult birds between St Lucia and Durban.

Introduction

Grey-headed Gulls are mostly limited to the tropical and sub-tropical regions of Africa and South America where they are commonly associated with a variety of wetlands both inland and coastal (del Hoyo *et al.* 1996; Olsen & Larsson 2003). Their range also extends to Madagascar where they are localised and uncommon (Sinclair &

Langrand 1998). In western and central Africa, Grey-headed Gulls are common at various localities at wetlands along the Niger River and are found from Gambia to Ghana, Lake Chad and the eastern and southern Congo (Mackworth-Praed & Grant 1970; Borrow & Demey 2001; Olsen & Larsson 2003). In eastern Africa the majority of birds reside in the large lakes and wetlands associated with the Rift Valley (Zimmerman *et al.* 1996). The distribution of Grey-headed Gulls in southern Africa is widespread but patchy and they are largely absent from the drier interior regions of Namibia and Botswana (Brooke 1997). In Mozambique they are mostly limited to the coast and along the Zambezi River (Brooke 1997; Parker 1999, 2005). Their population in eastern and southern Africa is estimated at 200 000 to 400 000 birds, and in West Africa their population is estimated at 30 000 birds (Wetlands International 2002).

Grey-headed Gull movements in southern Africa have been summarised by Underhill (1999) mostly from birds ringed as chicks at breeding colonies in Gauteng. There appears to be a high level of dispersion to all provinces of South Africa as well as long-distance movements to other countries in Africa, e.g. Angola, Zambia, Botswana, Zimbabwe and Mozambique. Despite these recorded movements, and owing to a paucity of birds both ringed and recovered as adults, there is little evidence for regular migration of the Grey-headed Gull in South Africa (e.g. Brooke 1997).

This chapter provides a review of the current and historical distribution and abundance of the Grey-headed Gull in South Africa. It is supplemented with count information coming from: the author during the course of this study at Gauteng, KwaZulu-Natal and Kimberley, Northern Cape; and the Coordinated Waterbird Counts (CWAC) database housed at the Avian Demography Unit, University of Cape Town. I also look at movements of the Grey-headed Gull in South Africa based on seasonal patterns of abundance and re-sighting information of birds ringed as adults during this study, as well as recovery data from the SAFRING database. One of the aims of this chapter is to test the hypothesis that Grey-headed Gulls have regular movements between breeding and non-breeding localities, as has been suggested by Cyrus & Robson (1980) for movements between Gauteng and KwaZulu-Natal.

Methods

Distribution

Brooke (1997) was used as a basis for the review on current distribution. Information on the distribution of breeding localities within South Africa largely came from Brooke *et al.* (1999), CWAC-count confirmed breeding localities and field work coming from this study.

A reference list extracted from the Percy Fitzpatrick Institute of Ornithology's reference database was the main source for the literature reviewed on historical distribution.

Abundance

This study

All Grey-headed Gulls counted at all sites, other than Gauteng, were classed into either adults or non-adults (for descriptions of age characteristics see Chapter 5).

Counts during the breeding season

Grey-headed Gulls were counted during the 2004 breeding seasons in Gauteng and Lake St Lucia and again in Gauteng during 2005. The location of breeding colonies in Gauteng during 2004 took place within an area where Grey-headed Gulls had previously been recorded breeding (CWAC data; Whittington-Jones pers. comm.) and the extent of this area is illustrated in Figure 2.1. During 2005 in Gauteng, in addition to the ground covered during 2004, an aerial census using a motor-glider was conducted over the extensive network of pans in the agricultural areas east of their known breeding range (flight route illustrated in Figure 2.1). All sites observed with Grey-headed Gulls were noted and their co-ordinates were recorded with a Geographic Positioning System; these sites were re-visited by vehicle between two and five days later to establish if the birds were breeding there. All breeding localities found in both years are illustrated in Figure 2.1. I used a 27X spotting scope and 10 X 40 binoculars to count all Grey-headed Gulls present at confirmed breeding localities.

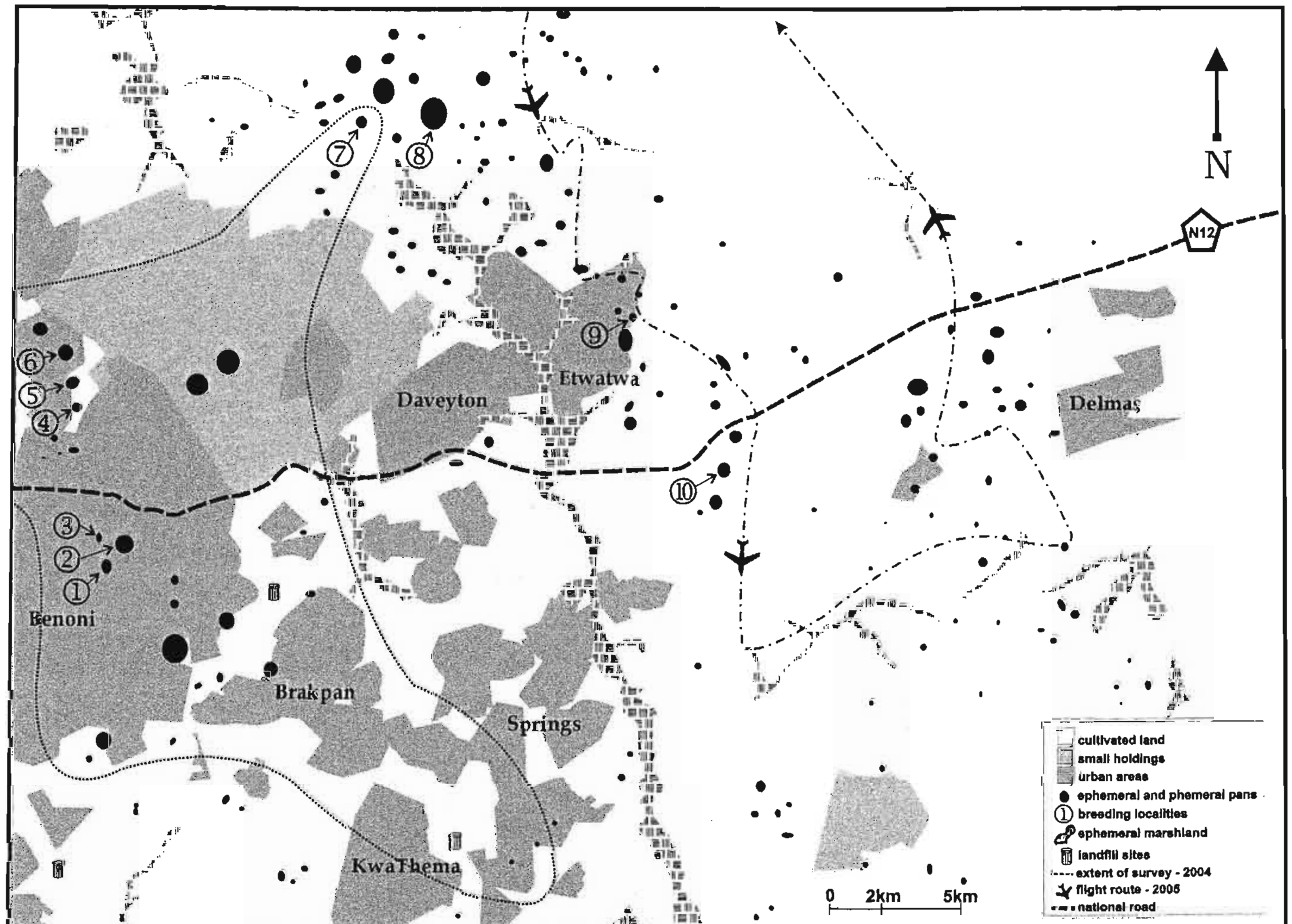


Figure 2.1. Study area, eastern Gauteng, showing extent of Grey-headed Gull breeding surveys during 2004 and 2005 and confirmed breeding localities. Numbered breeding localities: 1. Stewards Pan, 2. Korsman's Bird Sanctuary, 3. Lakefield Pan, 4. Parkhaven South, 5. Parkhaven North, 6. Bonaero Park, 7. Varkfontein Pan, 8. Loch Ness Pan, 9. Etwatwa Pan, and 10. Modderfontein Pan. Locality co-ordinates are given in Table 2.1.

The total number of breeding pairs was estimated by counting all nests attended by incubating adults or adults with chicks, as well as breeding adults that were accompanied by chicks away from the nest.

Lane Island, the breeding colony at St Lucia, was visited on six occasions: five visits during the breeding season of 2004 and on one occasion during the pre-breeding season of 2005. An inflatable boat with a 5Hp motor or a two-man canoe was used to access the island from Hell's Gate. Between 26 July and 10 September 2004 while Grey-headed Gulls were actively breeding on the island, between two and seven observers counted all nests on the island and an estimate of the total number of breeding adults was recorded. Lane Island was visited again on 20 March 2005, at the end of the non-breeding season, and all Grey-headed Gulls were counted.

Counts during the non-breeding season

Kimberley was visited during March 2005 and all Grey-headed Gulls were counted at the local landfill site, a well-known feeding locality for this species (M. Anderson, pers. comm.).

Total monthly counts of all waterbirds in Durban Bay, including Grey-headed Gulls were conducted in all months between July 1999 and August 2006 (McInnes *et al.* 2005a). A South African Navy Namakuru patrol boat was used to transport between three and six observers around the entire periphery of the bay at spring low tide. To estimate the total Grey-headed Gull population in Durban, all birds were counted along Durban's beachfront, from Vetjie's Beach to Umgeni River, as well as at the Umgeni River estuary. Only counts from January 2005 during low tide were used, as this was the only period when counts at all three localities, including Durban Bay, were conducted; this time of year is also the period when Grey-headed Gulls are most abundant in Durban (Allan *et al.* 2002).

CWAC data

Count information on Grey-headed Gulls at all sites visited by CWAC count volunteers between 1992 and 2004 during winter and summer was analysed. In order to establish the current status of Grey-headed Gull abundance in South Africa, only the 2004 counts were used. Count localities that only had data for one season were discarded from this analysis. For the purpose of establishing long-term trends in abundance, only those sites that had a minimum of ten years of counts during winter were used. Winter is the known breeding season for Grey-headed Gulls (Crawford & Hockey 2005) and they were expected to be more sedentary during this period.

Literature review

As with distribution, a reference list extracted from the Percy Fitzpatrick Institute of Ornithology's reference database was the basis for the literature reviewed on historical abundance. Historical trends in Grey-headed Gull numbers in Durban Bay were taken from Allan *et al.* (1999) and additional unpublished data.

Movements

This study

Grey-headed Gulls were trapped at landfill sites at Gauteng and at Durban's Blue Lagoon beach during 2004 and 2005 (for information on trapping techniques see Chapter 5). Birds were aged (Chapter 5) and fitted with engraved colour Canada rings. Colour-ringed birds were searched for with 10 X 40 binoculars and a spotting scope at all localities visited and re-sighting information (unique character combinations, locality and date) was recorded.

SAFRING data

Information on ring recoveries of Grey-headed Gulls was extracted from the SAFRING database, Avian Demography Unit, University of Cape Town.

Results

Distribution

Southern African Bird Atlas

The distribution of the Grey-headed Gull in South Africa is illustrated in Figure 2.2. The Grey-headed Gull has a widespread but patchy distribution in South Africa with birds being more prevalent in the eastern half of the country. Inland birds have a large concentration centred on Gauteng that extends into the southwestern regions of Mpumalanga. They are relatively densely distributed west of this core in the Free State and the North West Province around the Barberspan area. As one moves west from this concentration into the drier parts of the country, their distribution becomes

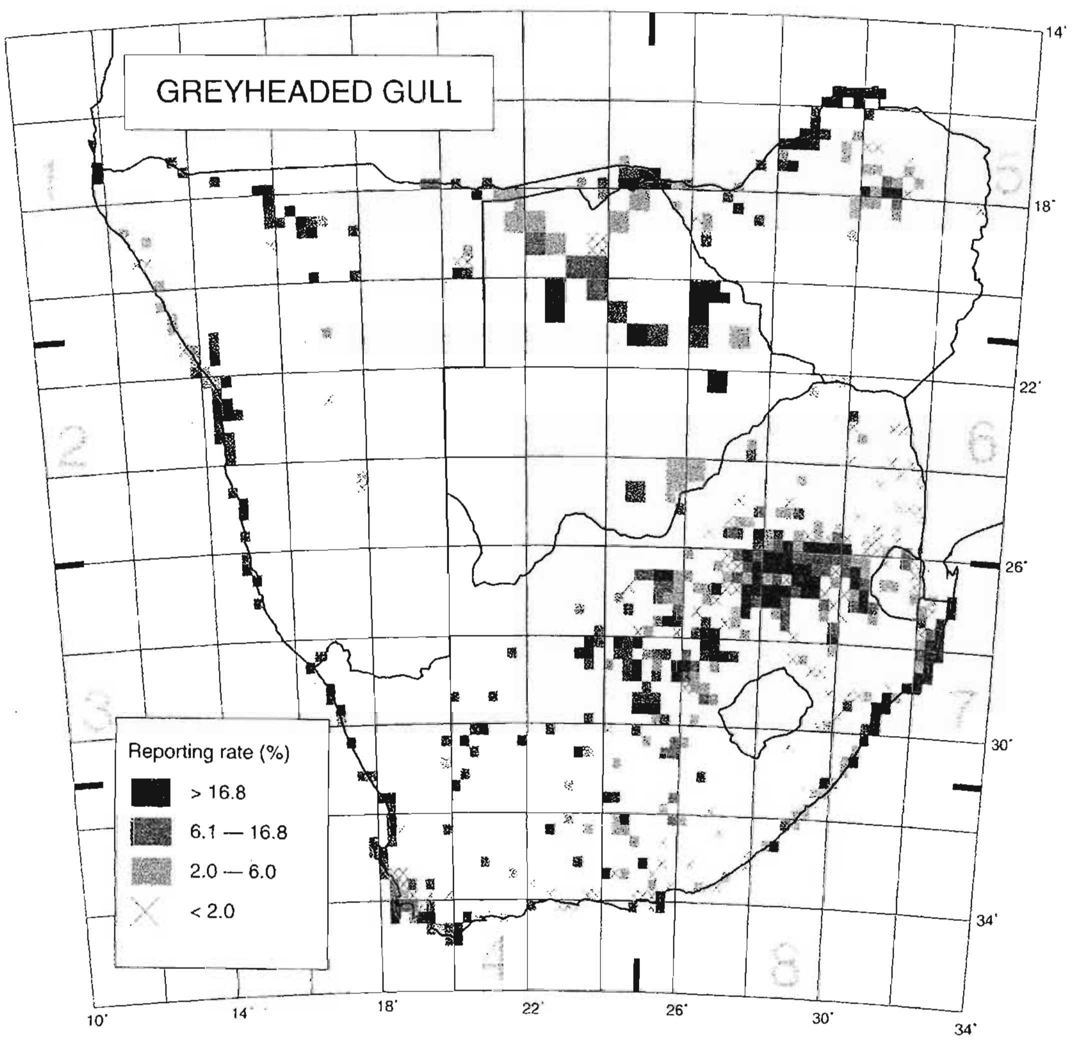


Figure 2.2. Distribution and relative abundance of the Grey-headed Gull in southern Africa (Brooke 1997).

more scattered. Grey-headed Gulls are absent from the higher-lying areas of the escarpment and Lesotho and are scarce in the northern and central regions of Mpumulanga.

Along the coastline they are regularly encountered in the northeast from Durban to Kosi Bay, especially around Durban and from Richards Bay to Sodwana Bay. South of Durban they become less common and are virtually absent between East London and just north of Port Elizabeth and between Cape St Francis and Cape Agulhus. They are found all along the west coast in South Africa but are less commonly reported there when compared with the northeast coast.

Breeding localities

The distribution of past and present breeding localities of Grey-headed Gulls in South Africa is illustrated in Figure 2.3 and the maximum recorded count at each of these sites is listed in Appendix 2.1. The highest concentration of breeding sites is in Gauteng. In the interior, breeding localities are otherwise widespread but thinly distributed. Along the east coast, there are two nodes of breeding locations: in Maputuland, mostly around Lake St Lucia; and four sites around Port Elizabeth. Sixteen breeding localities have been recorded for this species in the Western Cape, between Soetendalsvlei in the south and Bird Island, Lamberts Bay in the north.

Abundance

This study

Counts during the breeding season

a) Gauteng

The total number of breeding pairs estimated for all sites counted in Gauteng during 2004 and 2005 is given in Table 2.1. A total of 2409 breeding pairs was estimated from six sites during 2004 and a total of 2185 breeding pairs was estimated from nine sites during 2005.

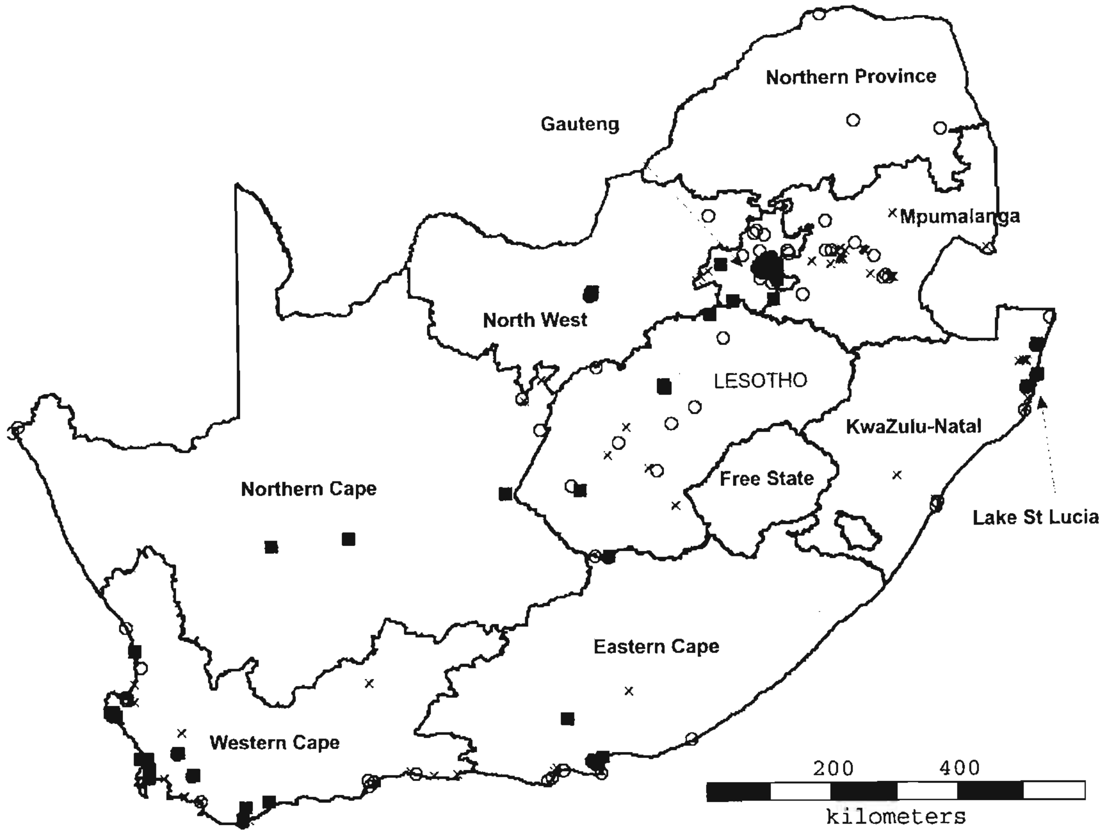


Figure 2.3. Confirmed breeding localities (solid squares) for the Grey-headed Gull in South Africa, and CWAC count localities showing sites where Grey-headed Gulls were recorded (open circles) and sites where Grey-headed Gulls were not recorded (crosses) in South Africa.

The highest number of breeding pairs at any site was at Bonaero Park during 2005, viz. 1153 breeding pairs, followed by 1054 breeding pairs estimated at Steward's Pan during 2004. Site selection by breeding Grey-headed Gulls varied between 2004 and 2005. Bonaero Park and Stewards Pan were the only sites to have substantial numbers of breeding pairs during both years. Varkfontein Pan was only occupied during 2004 and Parkhaven South was only occupied during 2005. Korsman's Bird Sanctuary had supported 350 breeding pairs during 2004 compared to 29 breeding pairs during 2005.

b) Lake St Lucia

At Lake St Lucia's Lane Island a total of 132 breeding pairs was estimated from the total number of active nests counted (i.e. nests with eggs) during 2004. The maximum

Table 2.1. Estimates of numbers of Grey-headed Gull breeding pairs at different sites in Gauteng and totals for all sites for the 2004 and 2005 breeding seasons. To estimate the total number of breeding pairs for sites that were visited more than once, the total number of new nests attended in subsequent visits was added to the original maximum counts if the period between these visits was shorter than 27 days (i.e. the estimated incubation period, see Chapter 3). The total number of breeding pairs for all sites was calculated from counts marked 'a' for 2004 and for counts marked 'b' for 2005.

Location	Co-ordinates	Map reference (Fig. 2.1)	Date d	Date m	Date y	Breeding pairs	Nests with eggs	% at egg stage
Bonaero Park	26°07'S, 28°16'E	6	13	5	2004	1[a]	1	100
			23	6	2004	103	89	86
			5	7	2004	314[a]	276	88
			25	8	2004	248	229[a]	92
			12	5	2005	438[b]	396	90
			23	5	2005	341	221	65
			22	6	2005	761	715[b]	94
Varkfontein Pan	26°03'S, 28°22'E	7	13	5	2004	25[a]	24	96
			23	6	2004	52	42	81
			5	7	2004	215[a]	181	84
			1	9	2004	276	210[a]	76
Korsman's B. S.	26°11'S, 28°18'E	2	13	5	2004	108[a]	97	90
			23	6	2004	269	237[a]	88
			28	8	2004	5	5[a]	100
			12	5	2005	8[b]	8	100
			21	6	2005	37	21[b]	57
Stewards Pan	26°12'S, 28°17'E	1	13	5	2004	396	146	37
			20	5	2004	497[a]	221	44
			23	6	2004	478	195	41
			5	7	2004	370	227[a]	61
			25	8	2004	530	330[a]	62
			12	5	2005	339[b]	174	51
			21	6	2005	222	58[b]	26
Parkhaven North	26°08'S, 28°16'E	5	23	6	2004	4[a]	3	75
			21	6	2005	8b	4	50
Parkhaven South	26°09'S, 28°16'E	4	11	5	2005	49[b]	39	80
			21	6	2005	70	38[b]	54
Lakefield Pan	26°11'S, 28°17'E	3	4	7	2004	6[a]	6	100
			21	6	2005	404[b]	258	64
Modderfontein Pan	26°09'S, 28°31'E	10	15	6	2005	60[b]	18	30
Etwatwa Pan	26°07'S, 28°29'E	9	20	5	2005	7[b]	7	100
Loch Ness Pan	26°02S, 28°25E	8	20	5	2005	40[b]	20	50
	Total 2004[a]					**2409**		
	Total 2005[b]					**2185**		

Table 2.2. Estimates of Grey-headed Gull numbers from various counts coming from this study, between 2004 and 2005 in South Africa during the breeding and non-breeding seasons.

Site	Date	Season	Ad	Non- adult	Total
Durban Bay	January 2005	non-breeding	431	115	546
Durban beachfront	January 2005	non-breeding	81	72	153
Durban, Umgeni River	January 2005	non-breeding	47	27	74
Durban total	January 2005	non-breeding	559	214	773
Gauteng breeding	May - September 2004	breeding	4818	?	4818
Kimberley	March 2005	non-breeding	120	114	234
Lane Island	July 2004	breeding	220	0	220
Lane Island	March 2005	pre-breeding	129	1	130

number of breeding adults observed during all five visits during the breeding season was 220 on 26 July 2004 (Table 2.2). A total of 129 Grey-headed Gulls was counted during March 2005 (pre-breeding season) of which one bird was a non-adult (Table 2.2).

Counts during the non-breeding season

a) Kimberley landfill

Grey-headed Gulls were counted at Kimberley landfill on three days in March 2005. An average of 234 Grey-headed Gulls visited this site on all days counted and these included 120 adults and 114 non-adult birds (Table 2.2).

b) Durban

The results of six years of monthly Durban Bay counts of Grey-headed Gulls are illustrated in Figure 2.4. A maximum of 920 Grey-headed Gulls were counted during January 2001 and for all months counted numbers were consistently high during the summer months. Marked seasonality was evident during all years with very few birds being observed during the winter months. There was a decline in overall Grey-headed Gull numbers between 2003 and 2004 but numbers appeared to have recovered somewhat during 2006. A total of 153 (81 adults) Grey-headed Gulls was counted on Durban's beachfront during January 2005 and a total of 74 (47 adults) was counted at Umgeni River Estuary during the same month at low tide. Together with the low-tide count for Grey-headed Gulls counted in Durban Bay during this month, the total number of Grey-headed Gulls estimated for Durban during this period was 773 birds, of which 559 (72%) were adults Table 2.2.

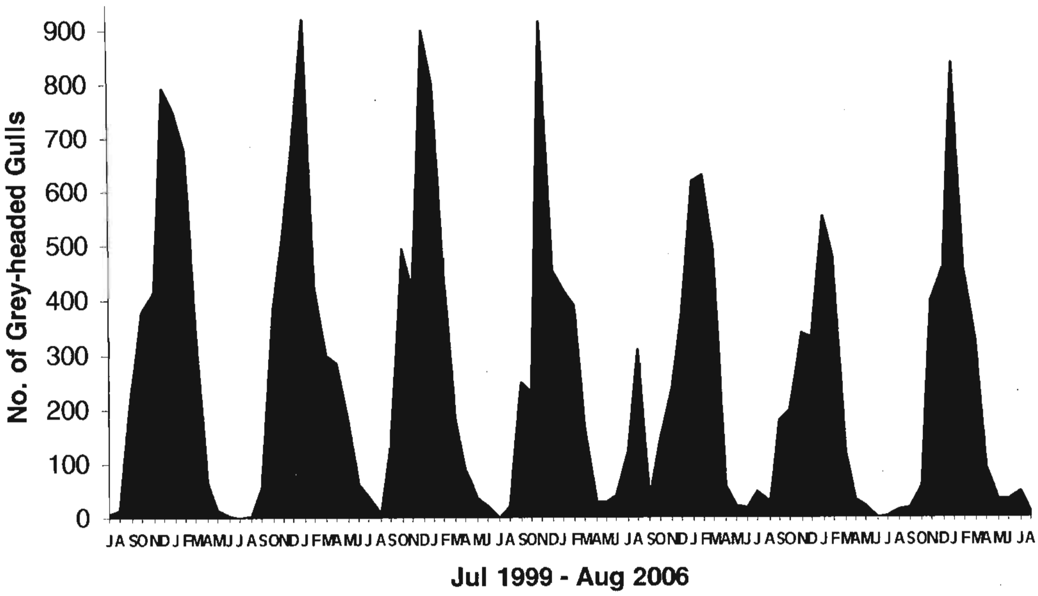


Figure 2.4. Monthly total counts of Grey-headed Gulls in Durban Bay, KwaZulu-Natal from July 1999 to August 2006 (source: D.G. Allan & A.M. McInnes unpubl.).

CWAC counts

Waterbirds were counted at 146 localities during both winter and summer of 2004 in South Africa. Five sites had count data for only one season and included four localities in the Western Cape, none of which had Grey-headed Gulls present, and Umvoti River Estuary at which three Grey-headed Gulls were counted during winter. These sites were discarded from this analysis. The distribution of sites counted is illustrated in Figure 2.3 and details of count data for Grey-headed Gulls during both seasons are shown in Appendix 2.2. Grey-headed Gulls were found at 84 (58%) of these localities and these included: 11 (73%) of the 15 localities counted in the Eastern Cape, nine (69%) of 13 in the Free State; 26 (84%)of 31 in Gauteng; seven of 15 (47%) in KwaZulu-Natal; ten (37%) of 27 in Mpumalanga, both localities in North West province; four (67%) of six in the Northern Cape; all three in the Northern Province; and 12 (36%) of 33 in the Western Cape.

A total of 4273 Grey-headed Gulls was counted at all sites during 2004 in summer and a total of 6851 was counted during the same year in winter. The estimate of Grey-headed Gull numbers in Gauteng amounted to 37% and 79% of the total number of

Grey-headed Gulls counted in South Africa for summer and winter, respectively (Appendix 2.2, Figure 2.5). The number of Grey-headed Gulls counted during summer in the Free State (1325 birds) approached that of Gauteng (1592 birds) and together with KwaZulu-Natal, these three provinces were the only areas to have over 700 birds recorded in any one season (Appendix 2.2, Figure 2.5). Despite the large number of wetlands counted in Mpumalanga and the Western Cape, both of these provinces had fewer than 100 birds during both seasons (Appendix 2.2).

The most marked seasonal differences in Grey-headed Gull numbers were in Gauteng and the Free State, and to a lesser extent in KwaZulu-Natal (Figure 2.5).

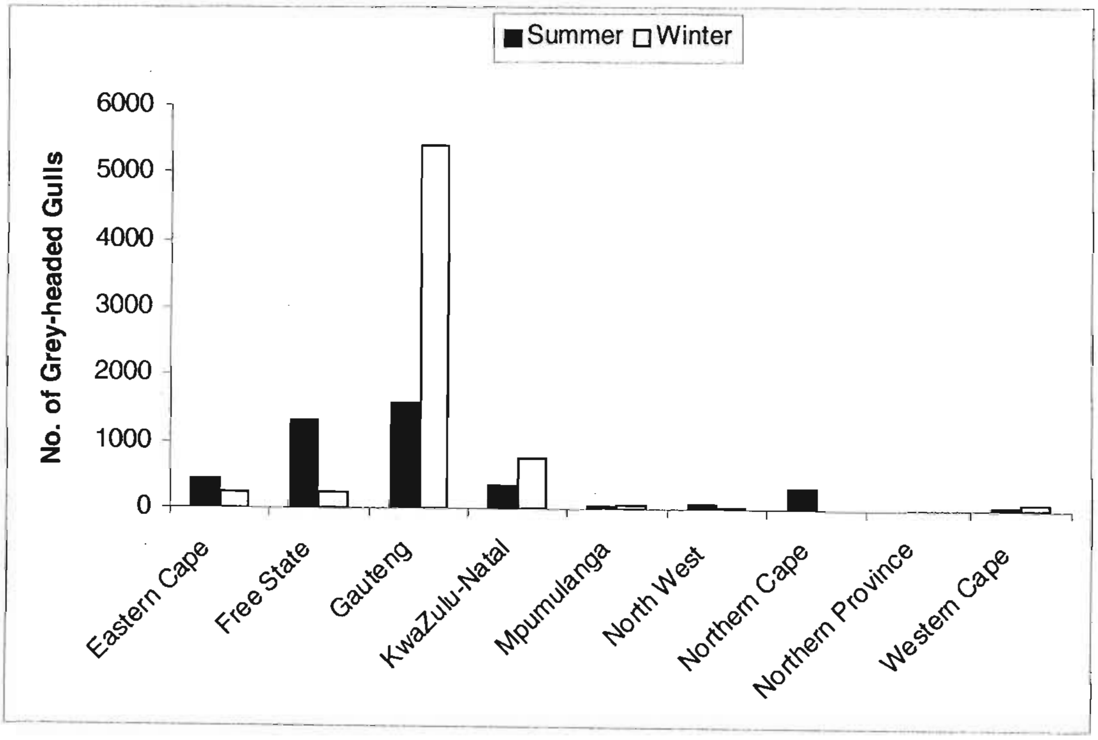


Figure 2.5. Seasonal abundance of Grey-headed Gulls in nine provinces in South Africa during 2004 (source: CWAC data).

Relative sizes of breeding colonies

All known Grey-headed Gull breeding localities, together with the number of birds present at each, are listed in Appendix 2.1. Six sites in Gauteng and one site in KwaZulu-Natal, Lake St Lucia, were the only breeding localities to hold over 1000 birds. The largest colony was Parkhaven Pan – North during 2001 where 3800 Grey-headed Gulls were counted. Other large colonies with over 1500 birds included Bonaero Park Pan, Korsman's Bird Sanctuary, Rolfe's Pan, Stewards Pan and Varkfontein Pans; all of these sites are situated in the East Rand, Gauteng. Intermediate-sized colonies of between 300 and 360 Grey-headed Gulls were recorded in the Eastern Cape and the Free State. Although Grey-headed Gulls were recorded at many breeding localities in the Western Cape, most of these sites had fewer than 50 birds present.

Movements

This study

A total of 358 adult Grey-headed Gulls was trapped in South Africa during 2004 and 2005. These comprised 343 birds from Gauteng's landfill sites and 15 birds from Durban's Blue Lagoon beach (Table 2.3). Four adults ringed in Gauteng during the breeding season were re-sighted in other provinces during the non-breeding breeding season (Table 2.4). Two of these birds and another adult, originally ringed as an immature bird, were re-sighted at the Kimberley landfill during March 2005. These birds comprised 3.3 % of all adults at this site. There were two re-sightings of adult

Table 2.3. Details of numbers and proportions of adult Grey-headed Gulls ringed in Gauteng and Durban during 2004 and 2005 and re-sighted distant from their ringing locality.

				No. adults re-sighted & % of total ringed					
Locality	Adult population estimate	No. adults ringed	% of adult pop. ringed	Durban	% of total	Kimberley Landfill	% of total	Lane Island	% of total
Gauteng	4818	343	7	2	0.6	3	0.9	-	-
Durban	559	15	3	-	-	-	-	4	27

Table 2.4. Details of ring recoveries of adult Grey-headed Gulls ringed during this study in Gauteng and Durban in 2004/2005, and by Digby Cyrus at Lake St Lucia in 1987/1988. Age: A – adult, I – immature, C – chick.

	Ringed							Re-sighted						
Ring	**Age**	**Day**	**Month**	**Year**	**Locality**	**Lat.**	**Long.**	**Age**	**Day**	**Month**	**Year**	**Locality**	**Lat.**	**Long.**
This study														
redAC	A	17	5	2004	Gauteng, Weltevreden Landfill	2612	2821	A	25	1	2006	Durban Bay	2953	3101
redGR	A	29	6	2004	Gauteng, Weltevreden Landfill	2612	2821	A	1	2	2005	Durban Bay	2953	3101
redHG	A	3	7	2004	Gauteng, Rooikraal Landfill	2618	2815	A	7	3	2005	Kimberley Landfill	2844	2442
redRQ	A	31	8	2004	Gauteng, Rooikraal Landfill	2618	2815	A	7	3	2005	Kimberley Landfill	2844	2442
redHA	I	3	7	2004	Gauteng, Rooikraal Landfill	2618	2815	A	7	3	2005	Kimberley Landfill	2844	2442
blueAN	A	19	11	2004	Durban Beachfront	2949	3103	A	20	3	2005	St Lucia, Lane Island	2800	3227
blue?	A	?	?	04/05	Durban Beachfront	2949	3103	A	20	3	2005	St Lucia, Lane Island	2800	3227
blue?	A	?	?	04/05	Durban Beachfront	2949	3103	A	20	3	2005	St Lucia, Lane Island	2800	3227
blue?	A	?	?	04/05	Durban Beachfront	2949	3103	A	20	3	2005	St Lucia, Lane Island	2800	3227
blueAN	A	19	11	2004	Durban Beachfront	2949	3103	A	30	9	2005	Durban Beachfront	2952	3103
D. Cyrus														
white right	C	?	6-8	87/88	St Lucia, Lane Island	2800	3227	A	3	8	2003	St Lucia	2800	3227
yellow left	C	?	6-8	87/88	St Lucia, Lane Island	2800	3227	A	10	6	2004	St Lucia	2800	3227
yellow left	C	?	6-8	87/88	St Lucia, Lane Island	2800	3227	A	30	7	2004	St Lucia	2800	3227
white right	C	?	6-8	87/88	St Lucia, Lane Island	2800	3227	A	12	11	2004	Durban Bay	2953	3101
white right	C	?	6-8	87/88	St Lucia, Lane Island	2800	3227	A	15	12	2004	Durban Bay	2953	3101
yellow left	C	?	6-8	87/88	St Lucia, Lane Island	2800	3227	A	15	12	2004	Durban Bay	2953	3101
white right	C	?	6-8	87/88	St Lucia, Lane Island	2800	3227	A	28	12	2004	Durban Bay	2953	3101
yellow left	C	?	6-8	87/88	St Lucia, Lane Island	2800	3227	A	28	12	2004	Durban Bay	2953	3101
yellow left	C	?	6-8	87/88	St Lucia, Lane Island	2800	3227	A	12	1	2005	Durban Bay	2953	3101
white right	C	?	6-8	87/88	St Lucia, Lane Island	2800	3227	A	21	1	2005	Durban Beachfront	2952	3103
white right	C	?	6-8	87/88	St Lucia, Lane Island	2800	3227	A	31	1	2005	Umgeni River Estuary	2949	3102
yellow left	C	?	6-8	87/88	St Lucia, Lane Island	2800	3227	A	20	3	2005	St Lucia, Lane Island	2800	3227
white right	C	?	6-8	87/88	St Lucia, Lane Island	2800	3227	A	1	11	2005	Umgeni River Estuary	2949	3102

birds in Durban that were both originally ringed in Gauteng during the breeding season. Assuming that most Grey-headed Gulls were scanned for rings in Durban, this amounted to 0.3 % of all Grey-headed Gulls at this site during summer. Of the 15 adults ringed in Durban during summer, four were subsequently re-sighted at Lake St Lucia's Lane Island on 20 March 2005 (Table 2.4). One of these birds (blueAN) was re-sighted again on Durban's beachfront on 30 September 2005.

The total number of birds ringed at each site and the proportion of these birds to the estimated total adult population at each site, as well the number re-sighted in other provinces are shown in Table 2.3. Only small proportions of adults ringed in Gauteng were re-sighted in other provinces during the non-breeding season: 0.6% in Durban and 0.9% at the Kimberley landfill. Conversely a relatively large proportion (27%) of adult Grey-headed Gulls ringed in Durban were re-sighted at Lake St Lucia.

There were a number of Grey-headed Gulls, originally ringed as chicks at Lane Island by Digby Cyrus, that were re-sighted as adults in Durban during the 2003, 2004 and 2005 non-breeding seasons, and at Lake St Lucia throughout the year (Table 2.4). Although we can identify the origin of these birds, it was not possible for us to establish the number of birds present due to the duplication of ring colour-types used and the concomitant possibility that the same birds were re-sighted on subsequent visits.

SAFRING data

A summary of all SAFRING ring recoveries of Grey-headed Gulls in South Africa is shown in Table 2.5. A total of 1154 birds was ringed between 1957 and 2004. Most of these birds were ringed as chicks and only three birds were ringed as adults. Of the 581 chicks ringed in Gauteng, 83 (14%) were recovered. A large proportion (67%) of these recoveries was from their natal province when the birds were on average two years old. Gauteng birds recovered in the Free State and KwaZulu-Natal constituted 14% and 11% of all birds recovered from this province, respectively. The average age of these birds when recovered was between one and two years old. A large proportion (73%) of birds ringed in North West Province were recovered, most of these being

Table 2.5. Summary of SAFRING ring recoveries of Grey-headed Gulls in South Africa. Unless stipulated all birds were ringed as chicks at their breeding colonies.

Province ringed/ recovered	No. recovered	% recovery	No. adults	Distance (km)				Elapsed time (days)			
				mean	sd	min	max	mean	sd	min	max
Gauteng											
Total ringed: 582	**83**	**14**	**1**								
Eastern Cape	1	1	0	903	-	-	-	446	-	-	-
Free State	12	14	0	252	81	80	255	435	349	18	1037
Gauteng	56	67	0	16	25	0	80	705	854	0	2905
KwaZulu-Natal	9	11	0	486	8	473	496	509	543	91	1678
Mpumalanga	1	1	1	131	-	-	-	452	-	-	-
Northern Cape	1	1	0	786	-	-	-	808	-	-	-
Northern Province	1	1	0	420	-	-	-	206	-	-	-
North West	1	1	0	270	-	-	-	461	-	-	-
Western Cape	1	1	0	1270	-	-	-	596	-	-	-
North West											
Total ringed: 33	**24**	**73**	**1**								
Free State	1	4	0	124	-	-	-	72	-	-	-
Gauteng	2	8	0	232	35	207	257	259	155	149	368
Northern Cape	1	4	0	511	-	-	-	737	-	-	-
North West	20	83	1	0	-	-	-	116	254	0	1079
KwaZulu-Natal											
Total ringed: 264	**14**	**5**	**1**								
KwaZulu-Natal	13	93	1	103	91	10	254	1866	1533	341	5855
Mpumalanga	1	7	0	399	-	-	-	2563	-	-	-
Eastern Cape											
Total ringed: 275	**7**	**0.03**	**0**								
Eastern Cape	6	86	0	3	6	0	15	248	282	22	732
KwaZulu-Natal	1	14	0	683	-	-	-	124	-	-	-

within their natal province within their first year of life. A small proportion (5%) of chicks ringed in KwaZulu-Natal were recovered. Most (93%) of these birds were recovered in their natal province with the average age of recovery being approximately five years. In the Eastern Cape, seven of the 275 chicks ringed were recovered, six of these being within their natal province within their first two years of life.

Review of historical distribution and abundance

The earliest records of Grey-headed Gulls in South Africa are from the latter half of the 19^{th} century where they appeared to have been widespread but patchily distributed throughout South Africa (Layard 1869; Stark & Sclater 1906; Winterbottom 1962). The most comprehensive account of Grey-headed Gull distribution at this time was that of Stark & Sclater (1906): coastal areas occupied by this species were limited to Durban northwards, including Durban Harbour and the Umfolosi River Mouth (Lake St Lucia area); and inland they were recorded at Bredasdorp in the Western Cape, Colesberg near the Free State/ Northern Cape border, and Lake Chrissie in Mpumulanga. The earliest known breeding locality was that of a colony at Broedenhurst Pan, Northern Cape during 1884 (Winterbottom 1962).

In KwaZulu-Natal, breeding colonies of Grey-headed Gulls have been regularly encountered since 1925 at Lake St Lucia, especially at Lane and Bird islands (Brooke et al. 1999). Numbers of breeding pairs at these sites have fluctuated between approximately 100 and 700 breeding pairs between 1932 and 1977 (Berruti 1980) and there numbers have fluctuated in similar proportions between 1992 and 2004 (CWAC data, Figure 2.6). Numbers have decreased quite dramatically in recent times from 1356 birds observed in 2000 to 472 birds in 2004 (Figure 2.6). They have been present in Durban at least since 1930, both at Durban Bay and the Umgeni Estuary where they were noted as being the common gull species in the area, and where, at Umgeni River Estuary during 1932, approximately 300 birds were counted (Godfrey 1931, 1932). Since 1974, Grey-headed Gulls have been counted relatively frequently in Durban Bay (Figure 2.7). In all years counted during this period, numbers have fluctuated dramatically between the winter and summer months. The highest counts have been during summer, with up to 800 birds being counted during 1977, a similar number to that recorded in more recent times during this season.

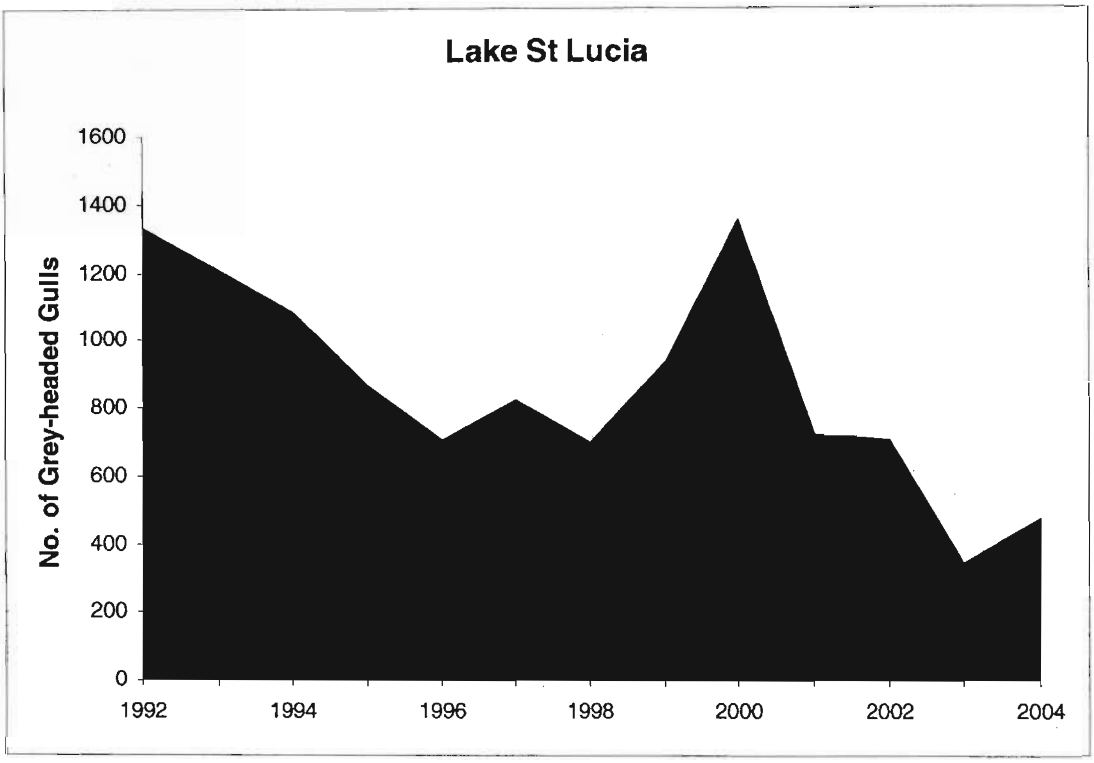


Figure 2.6. CWAC count data of Grey-headed Gull numbers at Lake St Lucia during the winters of 1992-2004.

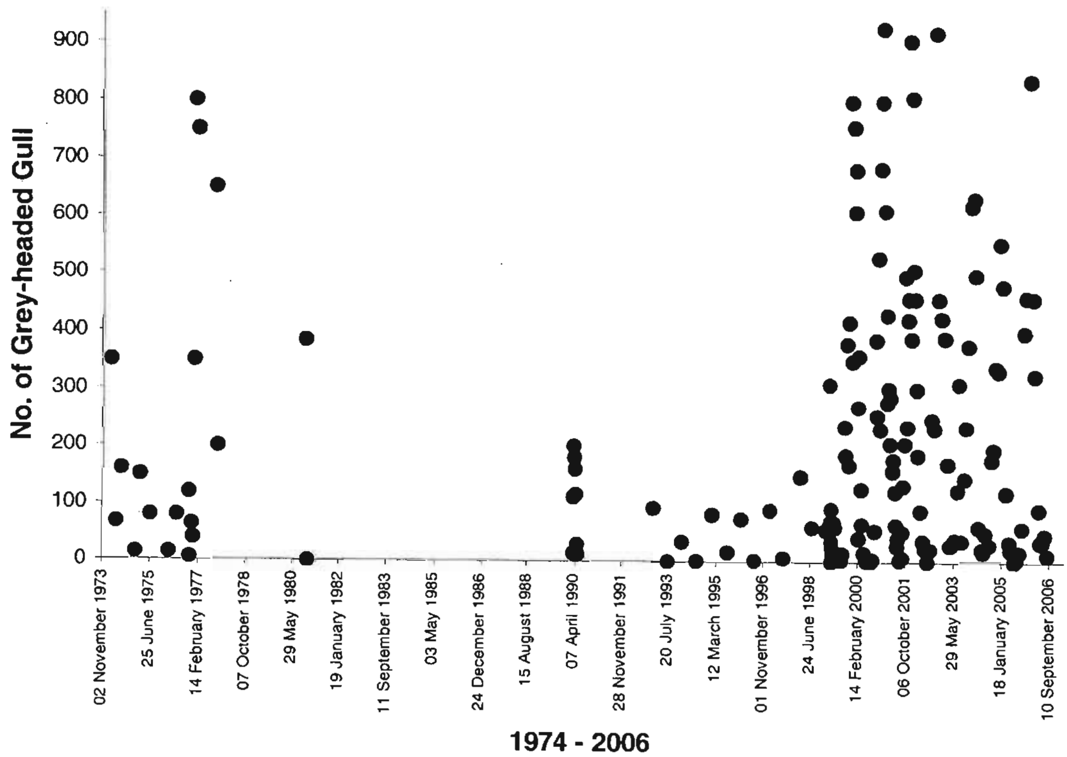


Figure 2.7. Grey-headed Gull numbers in Durban Bay 1974-2006 (D.G. Allan & A.M. McInnes unpubl.).

Ryan *et al.* (1986) in a summer survey of waterbird numbers along the entire KwaZulu-Natal coastline and at associated coastal wetlands, estimated the entire coastal KwaZulu-Natal Grey-headed Gull population to be 2166 birds. A large proportion (88%) of these birds were found at wetlands, such as estuaries and coastal lakes, while only 253 birds were found along the open coastline. South of Durban Bay, 154 Grey-headed Gulls were recorded; this amounted to seven percent of the KwaZulu-Natal population. More than half (55%) of the number Grey-headed Gulls counted in KZN were counted in Durban's wetlands, especially Durban Bay and Umgeni River Estuary. The second and third highest counts were recorded at the wetlands of Lake St Lucia and Richards Bay, where 451 and 115 Grey-headed Gulls were counted, respectively. These three sites accounted for 81 % of all Grey-headed Gulls in the province.

In the Eastern Cape, Grey-headed Gulls have increased since the middle of the 20^{th} century. A small population (approximately 50 birds) were more or less resident at Graaf Reinet from the mid 1960s (Skead 1967) and numbers in Port Elizabeth appear to have increased between 1955 and 1960 (Taylor 1964), especially during the summer months. The first breeding record of the Grey-headed Gull in this province was that of a colony of 28 pairs at Swartkops River Estuary during the winter of 1982 (Randall & Hosten 1983). In a survey of water birds in the coastal region of this province during the summer of 1978/79, Underhill *et al.* (1980) recorded very few Grey-headed Gulls along the entire stretch of this coastline and associated wetlands, with the exception of Port Elizabeth where an isolated population of 48 birds was found. Thirty (62.5%) of these birds were found at seasonal vleis at the Power Station Pans. Three sites in the vicinity of Port Elizabeth, Chatty Saltpans, Redhouse Saltpans and Zwartkops River Estuary have been counted during the winter months of all years between 1995 and 2004 (CWAC data) and there has been a steady increase from 33 birds at the onset of these counts to 163 birds in 2004 (Figure 2.8).

In the Western Cape, Grey-headed Gulls have been present in small numbers at least since 1865 (Layard, 1869). A small colony of four pairs occupied De Hoop Vlei near Bredasdorp, after it had been inundated, during September 1959 (Uys & Macleod

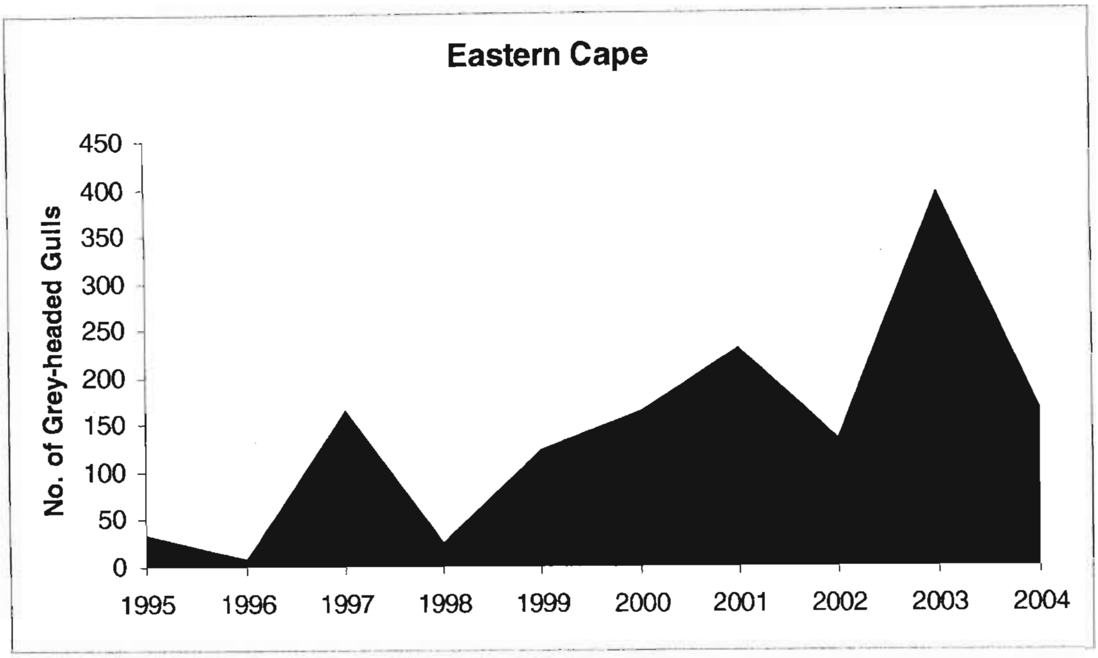


Figure 2.8. CWAC count data of Grey-headed Gull numbers at three sites in the Eastern Cape (Chatty Salt Pans, Redhouse Saltpan and Swartkops River Estuary) during the winters of 1995-2004.

1967). This colony increased to 30 pairs during the 1963 and 1964 breeding seasons. Small numbers of Grey-headed Gulls hybridized with Hartlaub's Gulls *Larus hartlaubii* in the latter species' breeding colonies at Robben Island in September 1953 (Zoutendyk & Feely 1953) and at Malgas and Jutten islands during 1977 (Sinclair 1977). Three pairs bred at Strandfontein Sewage Works in November 1980 (Brooke *et al.* 1999). In a census of waterbirds along the coastline and associated wetlands of the southwestern Cape, between Mossel Bay and the Olifants River estuary during the summer of 1980/81, Ryan *et al.* (1988) recorded a total of 47 Grey-headed Gulls (37 along the coastline and ten birds at coastal wetlands). Ryan & Cooper (1985), in a similar census in the northwestern Cape, between the Olifants River and Orange River estuaries during the summers of 1979/80 and 1981/82, counted a total of 46 Grey-headed Gulls along the coast (14 birds) and associated wetlands (32 birds). Since 1990 there has been an increase in breeding localities of Grey-headed Gulls in the Western Cape, although numbers of breeding pairs have remained low (Brooke *et al.* 1999). Since 1992, numbers have remained relatively stable with the exception of an influx of birds at Paarl Bird Sanctuary during the winter of 1993 where 272 birds were counted (CWAC data, Figure 2.9).

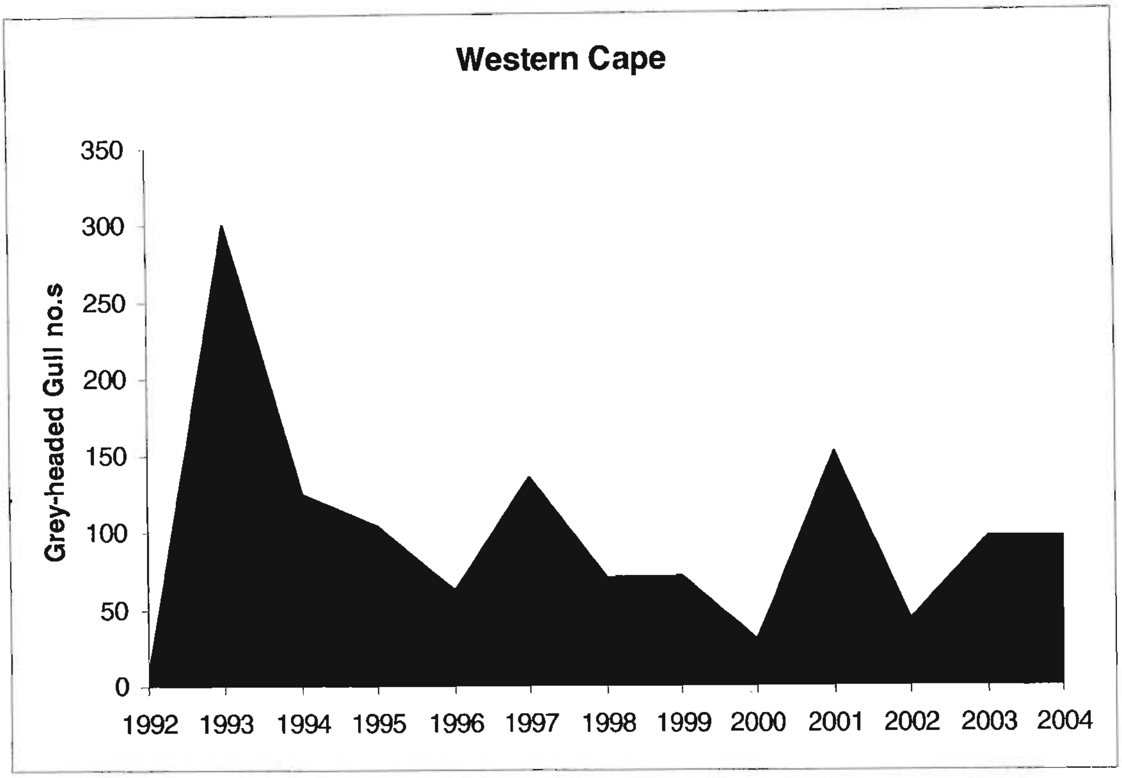


Figure 2.9. CWAC count data for Grey-headed Gulls in the Western Cape 1992-2004 for summer and winter.

Grey-headed Gulls have been recorded at various localities in the interior of South Africa, at least since the latter half of the 19th century (see above). In the North West Province at Barberspan, between 1955 and 1960, numbers fluctuated between one and 150 birds, the majority of birds being present during the winter and early spring months (Shewell 1959; Farkas 1962). Information on Grey-headed Gull numbers for the period 1968 to 1970 reveal an apparent increase in numbers at this site with between 80 and 337 birds having been recorded in most months during this period (Milstein 1975). There are no known records of Grey-headed Gulls in Gauteng prior to 1940 and the earliest known breeding record of this species there was in November 1947 when a single pair was noted breeding at Benoni (Brooke *et al.* 1999). Numbers have increased fairly rapidly since this time with 396 pairs found breeding at Blesbokspruit in September 1956, 793 pairs breeding at Korsman's Bird Sanctuary during 1963 and 1101 pairs recorded at the same site during 1970 (Brooke *et al.* 1999). In a survey of waterbird numbers at pans in the East Rand during the winters of 1985 and 1986, Allan (1988) estimated there to be 700 breeding pairs of Grey-headed Gulls at three sites, Korsman's Bird Sanctuary, Stewards Pan and Rolfe's Pan. In more recent times, between 2000 and 2004, numbers of Grey-headed Gulls at confirmed breeding localities have fluctuated between 1770 and 5093 birds (CWAC data, Appendix 2.3). The largest colonies have been recorded at (in order of abundance): Parkhaven Pan – North, Varkfontein Pans, Stewards Pan, Korsman's Bird Sanctuary and Bonaero Park.

Discussion

Distribution and abundance

The distribution of the Grey-headed Gull in South Africa, like that of many waterbird species, is widespread but patchy. Grey-headed Gulls become scarcer as one moves west into the drier areas of South Africa where wetlands become increasingly ephemeral. They are more abundant in the wetter sub-tropical regions and are especially prolific in Gauteng, their largest South African population.

Their ability to breed at both inland and at coastal localities is commonly found in other masked gull species, e.g. Slender-billed *Larus genei*, Bonaparte's *Larus philadelphia*, Black-headed *Larus ridibundus*, Brown-headed *Larus brunnicephalus*, Silver *Larus novaehollandiae* and Black-billed *Larus bulleri* gulls (Higgins & Davies 1996; Olsen & Larsson 2003). These species breed in or close to open, shallow water systems, usually placing their nests on open or vegetated islands, sandspits or within marshy vegetation; an exception is the Black-billed Gull which breeds on riverbanks (Higgins & Davies 1996).

Coastal populations

At the coast, the majority of Grey-headed Gulls inhabit the northeastern regions, from Durban northwards. The most popular sites within this area, viz. Durban, Richards Bay and Lake St Lucia, all share a common feature in that they have extensive wetland systems in close proximity to the coast. The only long-term, frequently used breeding site of this species in South Africa is Lake St Lucia. This system is unique in the context of the east coast in that it is a large shallow lake in close proximity to the coast that is characterised by fluctuating water levels (Whitfield & Cyrus 1978; Berruti 1983). It is the most important juvenile fish nursery on the east coast of South

Africa (Blaber 1980) and is a protected wilderness area. The receding water levels during winter are advantageous to scavenging birds, such as the Grey-headed Gull that take advantage of exposed invertebrates in the backwaters of this system (Whitfield & Cyrus 1978). They have also been observed kleptoparasitising fish-eating species such as White-breasted Cormorants *Phalacrocorax lucidus* and Pink-backed Pelicans *Pelecanus rufescens* that exist in large numbers in this system (pers. obs, CWAC data). During winter, refuges in the form of islands, e.g. Lane and Bird islands, become more exposed and are less frequently inundated (Berruti 1983). Lake St Lucia appears to be less favourable to this species in drought years, as was the case during this study, when increased predation leads to poorer reproductive output (see Chapter 3). This would explain the decline in numbers of breeding pairs in more recent times.

Richards Bay and Durban Bay are similar sites in that they both have natural embayments as well estuarine systems associated with major rivers. Both of these sites have large areas of intertidal sand and mudflats associated with rich supplies of benthic animal communities (Cyrus & Forbes 1996; Forbes *et al.* 1996). They are both highly populated areas, especially when compared to Lake St Lucia, and have large numbers of recreational fisherman and associated activities, such as bait harvesting. Durban is the most popular non-breeding destination of the Grey-headed Gull and a large proportion of their population has been observed foraging on invertebrates in the intertidal areas of Durban Bay (McInnes *et al.* 2005a). The abundance of macro-benthic fauna at this site is said to be two to three times higher than at Richards Bay (Forbes *et al.* 1996). A popular food item for Grey-headed Gulls here is the sand prawn *Callianassa kraussi* which becomes available through the activities of bait harvesters, especially at Fish Wharf, the most selected for of all sites within this area by Grey-headed Gulls (McInnes *et al.* 2005a). Grey-headed Gulls are also commonly associated with the beachfront of Durban, where they scavenge for fish bait and other human discards, as well as Umgeni River Estuary, which is a popular feeding and roosting locality for this species (pers. obs., CWAC data).

The scarcity of Grey-headed Gulls as one moves south of Durban is probably related to the scarcity of large coastal wetlands and embayments (Figure 2.10). A small isolated population at Port Elizabeth is typically associated with various salt pans in the area, especially when breeding, and the relatively recent colonisation of this site may be related to the establishment of these artificial environments. In the Western Cape, Grey-headed Gulls are most commonly associated with inland wetlands, where they have bred in small numbers since historical times. The presence of these birds on the west coast may be related to the abundance of the parapatric Hartlaub's Gull and the attraction that feeding flocks of this species provide to wandering Grey-headed Gulls. These two species are known to exist in mixed flocks and there are isolated incidences of hybridisation between them.

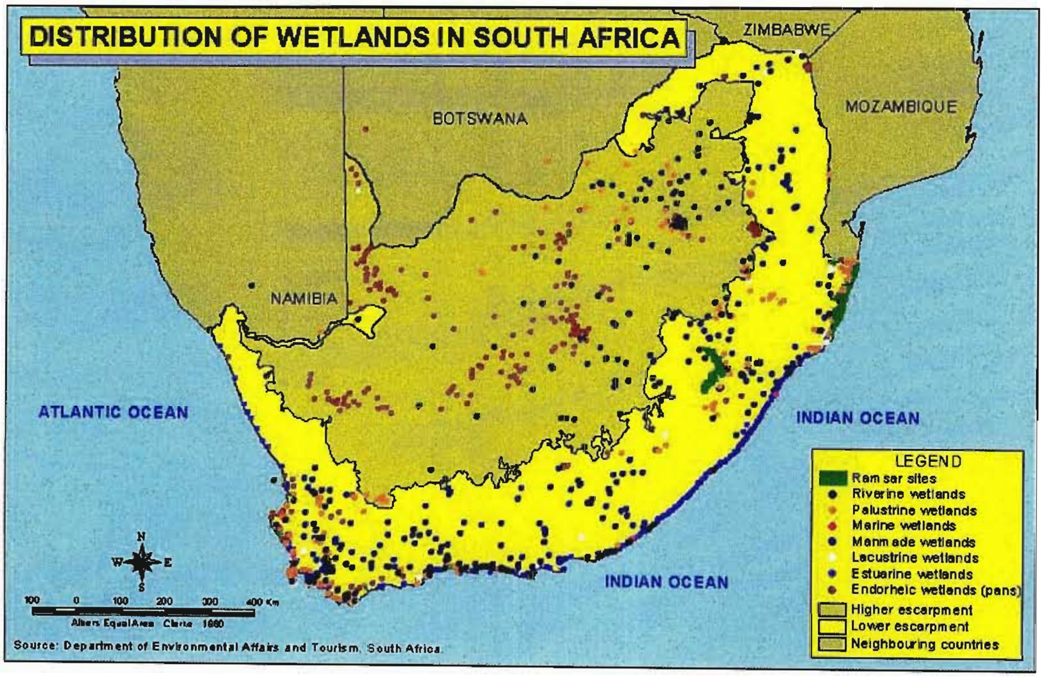


Figure 2.10. Distribution of wetlands in South Africa (source: Department of Environmental Affairs and Tourism, www.deat.gov.za).

Inland populations

The largest population of Grey-headed Gulls in South Africa is in Gauteng and this area has only been occupied by this species since the first half of the 20^{th} century. Before this time, the closest recorded locality was at Mpumulanga's Lake Chrissie and although scarcer than today, Grey-headed Gulls were widespread throughout the South African interior during the 19^{th} century. Due to the large numbers of natural ephemeral pans in the eastern regions of Gauteng, it is likely that Grey-headed Gulls would have visited, albeit in fewer numbers, this area before recorded times, especially in exceptionally wet years. The rapid increase in population of this species here can only be related to various factors associated with the accelerated anthropogenic transformation of this area. Gauteng is the most urbanised province in South Africa with the highest concentration of humans (Figure 2.11). The many landfill sites in this area have no doubt played a major role in influencing numbers here. Landfill sites are popular feeding grounds for other gull species, e.g. Herring Gulls *Larus argentatus* (Hunt 1972; Pons 1992; Belant *et al.* 1993), Laughing Gulls

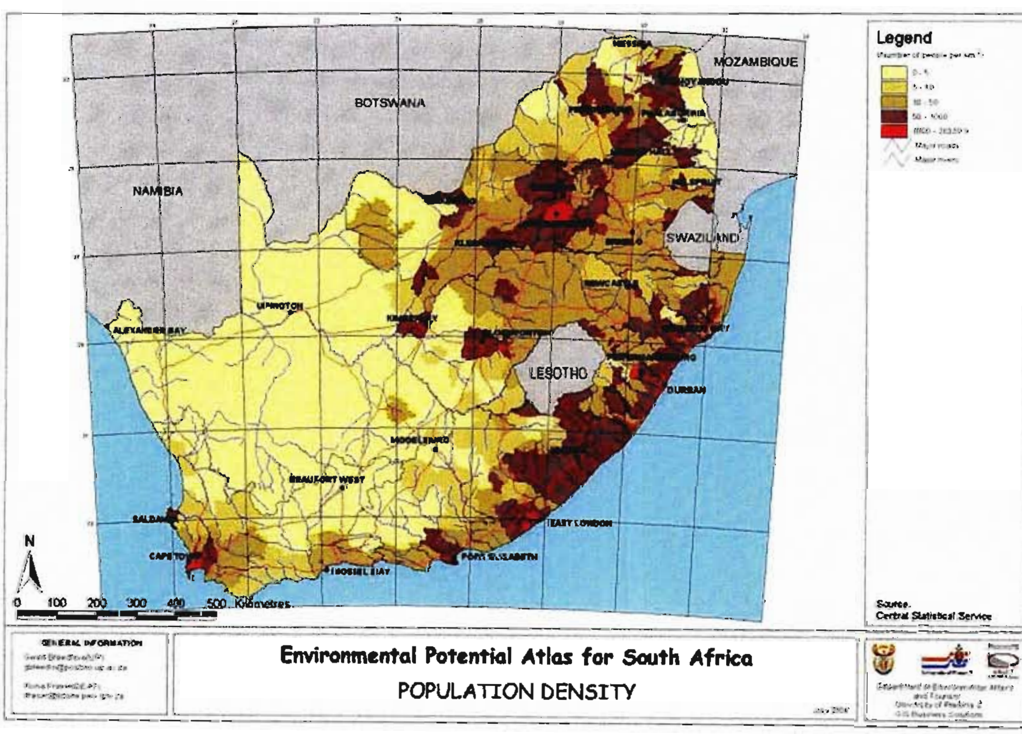


Figure 2.11. Human population density in South Africa (source: Department of Environmental Affairs and Tourism, www.deat.gov.za).

Larus atricilla (Burger & Gochfeld 1983), and Silver Gulls *Larus novaehollandiae* (Higgins & Davies 1996), and this artificial food source has been known to influence the population dynamics of some of these species (Hunt 1972; Burger & Gochfeld 1983; Pons 1992; Belant *et al.* 1993). However, the abundance of landfill sites in the area cannot exclusively explain the proliferation of this species in Gauteng. Grey-headed Gulls need wetlands to roost and breed and this requirement has been abundantly met in the eastern parts of Gauteng where many ephemeral wetlands have been transformed into permanent and semi-permanently inundated systems (see Chapter 3 for a more detailed discussion). Certain agricultural land-uses in the eastern regions of Gauteng, e.g. maize and poultry, provide attractive feeding opportunities for Grey-headed Gulls and have also benefited their existence here (Chapter 4).

The scattered distribution of Grey-headed Gull records in the western interior (Figure 2.2) reflects the opportunistic and dispersive nature of this species. This distribution pattern, especially in the Northern Cape, correlates with the distribution of certain endorheic pans in the region (Figure 2.10). These wetlands can remain dry for many years before becoming inundated (Allan *et al.* 1995). Substantial rains in these ephemeral environments promote the proliferation of invertebrates and amphibians that provide rewarding feeding opportunities to many waterbird species (Allan *et al.* 1995; Simmons *et al.* 1998) including the Grey-headed Gull (Simmons *et al.* 1998; Heermann *et al.* 2004). Simmons *et al.* (1998) suggested that the ability of waterbirds to follow massive thunderstorms contributed to the efficacy with which they located these pans. This ability of Grey-headed Gulls to exploit isolated and sporadic ecological episodes is testament to their opportunistic nature in colonising favourable feeding and breeding sites as they become available. The historical breeding record of this species at Broedenhurst Pan in 1884, as well as other breeding records in the Northern Cape in more recent times, exemplifies this point.

Seasonality and movements

Grey-headed Gulls are well known for their movements within and outside of South Africa (Underhill 1999) but little evidence exists for regular migrations of adult birds between breeding and non-breeding localities. Movements in other gull species range from the mostly sedentary Hartlaub's Gull (Hockey & Crawford 2005), to species that have regular short distance migrations, e.g. Western Gulls *Larus occidentalis* (Spear 1988), Laughing Gulls (Belant & Dolbeer 1993), and Silver Gulls (Higgins & Davies 1996), to long distance migrants, e.g. Franklin's Gull *Larus pipixcan* and Sabine's Gull *Larus sabini* (Olsen & Larsson 2003).

The paucity of re-sightings in Durban of adult birds marked in Gauteng during this study provides little evidence for regular coastal movements of significant numbers of post-breeding Gauteng birds to the KwaZulu-Natal coast. A meaningful proportion (27%) of adult birds ringed in Durban, however, were subsequently re-sighted in Lake

St Lucia in the pre-breeding season. Together with the Durban re-sightings of adults originally ringed by Digby Cyrus at Lake St Lucia's Lane and Bird islands, and the decline in numbers of Grey-headed Gulls at both sites during recent times, there is convincing evidence to suggest regular movements between St Lucia and Durban. The proportion of birds that migrate between these two areas is unclear and the count data between these two sites suggests that Durban numbers are augmented by Grey-headed Gulls originating from other localities.

Results of CWAC counts in Gauteng show strong seasonality suggesting movements to other provinces during the non-breeding season (Figure 2.5). The SAFRING data, although mostly representing birds ringed as chicks, do show movements to all provinces within South Africa and the resightings of adult birds in Kimberley and Durban do confirm the ability of Grey-headed Gulls to disperse widely from this site. However, the available information can not negate the possibility of a large number of Gauteng birds remaining within this province during the non-breeding season; this because Grey-headed Gulls are known to frequent non-wetland areas while feeding (see Chapter 4) that may not have been covered by the CWAC counts. This would explain the large seasonal difference in abundance of this species in Gauteng, the magnitude of which cannot be accounted for by the numbers recorded in other provinces (Figure 2.5). It is possible that the majority of Grey-headed Gulls that breed in Gauteng disperse over the highveld during the non-breeding season (explaining the augmentation of birds in the Free State), with a significant portion remaining within or near to Gauteng, while only a small number reach the coast. Clearly, more resighting information is needed to validate this hypothesis.

Conclusion

Grey-headed Gulls have become increasingly abundant in South Africa in recent times, especially in Gauteng. The rate of population growth in this province, however, is fairly poorly documented, largely due to a lack of consistency in count coverage. The number of sites counted in Gauteng during this study is the most comprehensive coverage to date but provides only a ‘snapshot’ of current numbers. Future counts covering the same areas in Gauteng should allow resource managers to track future population trends. An important discovery is the evidence for regular and large-scale movements of Grey-headed Gulls between Durban and Lake St Lucia. This information is significant as it demonstrates the apparent importance of both sites to the continued existence of these birds at current levels of abundance. The future existence of intertidal feeding habitat in Durban Bay remains precarious, due to an accelerated demand for increased container terminals in Durban harbour. These habitats are significant feeding grounds for Grey-headed Gulls and their displacement may ultimately have an effect on the breeding population at Lake St Lucia. The seasonal movements of adult Grey-headed Gulls that breed in Gauteng still remain somewhat of an enigma and a large concerted effort is needed to accumulate enough ring-resighting information to solve this mystery. There currently is a significant number of birds with individually recognisable colour rings to facilitate this process.

Appendix 2.1. Confirmed breeding localities of Grey-headed Gulls in all provinces of South Africa, with maximum number of breeding birds recorded at each site. Highlighted rows indicate localities for which there is data from more than one reference.

Locality	Co-ords Lat.	Co-ords Long.	Max count	Year	Reference
Eastern Cape					
Bar None Saltpan	3350	2533	228	2000	CWAC
Chatty Saltpans	3351	2535	190	1990	Brooke et al. 1999
Chatty Saltpans	3351	2535	345	2003	CWAC
Coega Salt Pans	3347	2541	62	1996	Brooke et al. 1999
Lake Mentz	3310	2508	2	1992	Brooke et al. 1999
PE Power Station Pans	3352	2536	360	2001	CWAC
Redhouse Salt Pans	3350	2535	56	1982	Brooke et al. 1999
Free State					
Fauresmith	2937	2522	?	1991	Brooke et al. 1999
Gariep Dam (East)	3038	2550	154	2004	CWAC
Klippan			8	1966	Brooke et al. 1999
St Helena Mine Dam	2802	2644	6	1968	Brooke et al. 1999
Toronto Pan, Welkom	2759	2642	2	1966	Brooke et al. 1999
Vaal Dam, Parys	2654	2727	2	1962	Brooke et al. 1999
Welkom	2759	2642	18	1960	Brooke et al. 1999
Witpan, President Brand Mine	2801	2642	300	1966	Brooke et al. 1999
Gauteng					
Benoni	2611	2819	2	1947	Brooke et al. 1999
Blesbokspruit	2622	2831	792	1956	Brooke et al. 1999
Bonaero Park	2607	2816	1649	2000	CWAC
Bonaero Park	2607	2816	1522	2005	This study
Bullfrog Pan	2608	2819	42	2002	CWAC
Etwatwa Pan	2607	2829	14	2005	This study
Gebuld	2613	2825	200	1953	Brooke et al. 1999
Jack Ellis Park			398	1975	Brooke et al. 1999
Kleinfontein	2611	2819	8	1967	Brooke et al. 1999
Korsman's Bird Sanctuary	2611	2818	2202	1970	Brooke et al. 1999
Korsman's Bird Sanctuary	2611	2818	1835	2003	CWAC
Korsman's Bird Sanctuary	2611	2818	538	2004	This study
Lakefield Pan	2611	2817	264	2002	CWAC
Lakefield Pan	2611	2817	808	2005	This study
Loch Ness Pan	2602	2825	80	2005	This study
Modderfontein Pan	2609	2831	120	2005	This study
Parkhaven Pan - North	2608	2816	3800	2001	CWAC
Parkhaven Pan - North	2608	2816	16	2004	This study
Parkhaven Pan - South	2609	2816	20	2001	CWAC
Parkhaven Pan - South	2609	2816	140	2005	This study
Randfontein	2607	2737	?	-	Brooke et al. 1999
Rolfe's Pan	2610	2813	>2000	1987	Brooke et al. 1999
Springs	2615	2828	4	1952	Brooke et al. 1999

Appendix 2.1 (continued).

Locality	Co-ords Lat.	Co-ords Long.	Max count	Year	Reference
Gauteng					
Stewards Pan	2612	2817	980	1985	Brooke et al. 1999
Stewards Pan	2612	2817	2800	2004	CWAC
Stewards Pan	2612	2817	1060	2004	This study
Sub-Nigel Mine dam	2640	2828	72	1969	Brooke et al. 1999
Union Settlements			8	1972	Brooke et al. 1999
Vaal Dam			40	1974	Brooke et al. 1999
Vanderbijl Park	2642	2749	500	1968	Brooke et al. 1999
Varkfontein Pans	2603	2822	3000	2001	CWAC
Varkfontein Pans	2603	2822	552	2004	This study
KwaZulu-Natal					
Cape Vidal to Sodwana Bay	2752	3236	78	2003	CWAC
Lake St Lucia	2804	3227	1500	1972	Brooke et al. 1999
Lake St Lucia	2804	3227	1356	2000	CWAC
Lake St Lucia	2804	3227	264	2004	This study
Muzi Pan	2724	3237	2	2004	CWAC
Northern Cape					
Brandvlei	3027	2029	8	1954	Brooke et al. 1999
Broadenhurst Pan	2940	2412	?	1884	Brooke et al. 1999
Vanwyksvlei	3020	2142	?	1907	Brooke et al. 1999
North West					
Barberspan	2635	2535	99	2001	CWAC
Leeupan	2632	2536	9	2001	CWAC
Western Cape					
Athlone Sewage Works	3357	1831	6	1992	Brooke et al. 1999
Bird Island, Lambert's Bay	3205	1818	2	1996	Brooke et al. 1999
Caltex Oil Refinery	3346	1830	4	1997	Brooke et al. 1999
De Hoop Vlei	3427	2024	46	1961	Brooke et al. 1999
Dyer Island			8	1991	Brooke et al. 1999
Jutten Island	3305	1757	4	1977	Brooke et al. 1999
Malgas Island	3303	1755	2	1977	Brooke et al. 1999
Marcus Island	3302	1758	4	1977	Brooke et al. 1999
near Bredasdorp	3432	2002	4	1959	Brooke et al. 1999
Paarl Bird Sanctuary	3341	1858	50	1993	Brooke et al. 1999
Paarl Bird Sanctuary	3341	1858	7	2004	CWAC
Rietvlei	3350	1829	22	1995	Brooke et al. 1999
Robben Island	3347	1822	6	1994	Brooke et al. 1999
Schaapen Island	3306	1801	2	1990	Brooke et al. 1999
Soetendalsvlei	3443	1959	2	1865	Brooke et al. 1999
Strandfontein Sewage Works	3405	1831	6	1980	Brooke et al. 1999
Theewaterskloof Dam	3402	1913	80	2004	CWAC

Appendix 2.2. CWAC (Co-ordinated Waterbird Count) data of Grey-headed Gull numbers at sites in all provinces of South Africa during 2004 for winter and summer.

	Co-ords		Count	
Locality	**Lat.**	**Long.**	**Summer**	**Winter**
Eastern Cape				
Bar None Saltpan	3350	2533	0	65
Cape Recife Reclamation Works	3401	2541	50	0
Chatty Saltpans	3351	2535	173	128
Gamtoos River (False Mouth)	3358	2505	1	2
Gamtoos River: Mouth - 6km upstream	3358	2502	0	0
Great Fish River Estuary	3329	2707	4	0
Kabeljous River Estuary	3400	2456	0	0
Krom River Mouth	3408	2450	0	1
Malangskraal Dam	3244	2607	0	0
Mondplaas Ponds	3357	2458	0	0
PE Power Station Pans	3352	2536	53	2
Perseverance Vleis	3350	2532	0	3
Redhouse Saltpan	3350	2535	3	6
Seekoei River Estuary	3405	2454	0	3
Zwartkops River Estuary	3352	2538	177	29
Total			**461**	**239**
Free State				
Allemanskraal Dam	2818	2712	32	0
Bloemhof Dam	2741	2540	775	45
Donkerpoort Farm Dam 1	2917	2629	0	0
Erfenis Dam	2834	2650	54	13
Gariep Dam (East)	3038	2550	33	154
Gariep Dam (West)	3037	2537	11	4
Kalkfontein Dam	2932	2515	223	7
Koppies Dam	2715	2741	30	18
Krugersdrift Dam	2852	2600	149	6
Rusfontein Dam	2918	2637	18	2
Sunnyside Pan	2839	2608	0	0
Vaalbank Farm Dam	2905	2549	0	0
Welbedacht Dam	2952	2653	0	0
Total			**1325**	**249**
Gauteng				
Anglo Reserve	2618	2830	0	13
Apex Pan	2613	2820	0	35
Blaauwpan	2607	2815	3	82
Bon Accord Dam	2537	2811	0	187
Bonaero Park Pan	2607	2816	0	736
Bronkhorstspruit Dam	2554	2842	38	47
Cowles Dam	2613	2828	31	2
De Pan	2613	2726	0	0

Appendix 2.2 (continued).

Locality	Co-ords		Count	
	Lat.	Long	Summer	Winter
Diepsloot Nature Reserve	2557	2800	0	4
Elandsvlei	2559	2827	0	71
Groenfontein Pan	2556	2844	0	394
Grootvaly on Blesbok	2616	2830	0	9
Grootvaly Wetland Reserve	2614	2829	0	1
Korsman's Bird Sanctuary	2611	2818	206	393
Lakefield Pan	2611	2817	0	247
Leeupan	2614	2819	61	15
Marievale Bird Sanctuary - Area A	2621	2830	0	0
Marievale Bird Sanctuary - Area B	2621	2831	1	3
Mooirivier Loop 1 (Abe Bailey NR)	2619	2720	0	0
Mooirivier Loop 2 (Abe Bailey NR)	2621	2716	0	0
Mooirivier Loop 3 (Abe Bailey NR)	2621	2715	0	0
Parkhaven Pan - North	2608	2816	0	133
Parkhaven Pan - South	2609	2816	0	15
Rietspruit (Rooikraal)	2620	2817	51	1
Rietvlei & Marais Dams	2553	2817	0	6
Rolfe's Pan	2610	2813	22	165
Roodeplaat Dam	2538	2821	7	1
Rooiwal Sewage Works	2534	2814	57	15
Sand Pan	2607	2819	122	16
Stan Madden Bird Sanctuary	2624	2828	42	9
Stewards Pan	2612	2817	951	2800
Total			**1592**	**5400**
KwaZulu-Natal				
Albert Falls Dam	2926	3024	0	0
Cape Vidal to Sodwana Bay	2752	3236	0	225
Durban Bayhead NHS	2953	3101	71	2
Kosi Bay Lake System	2658	3250	7	1
Lake St Lucia	2804	3227	145	472
Mfazana Pan	2815	3228	0	0
Mfolozi Estuary	2824	3225	9	17
Muzi Pan	2724	3237	0	2
Neshe Pan	2739	3224	0	0
Northern Treatment Works	2948	3100	0	0
Nsumo Pan	2740	3219	0	0
nTshanetshe Pan	2740	3226	0	0
St Lucia Sewage Works	2823	3225	0	0
Umgeni River Estuary	2949	3102	127	37
Yengweni Pan	2739	3226	0	0
Total			**359**	**756**
Mpumalanga				
Arnot Pan	2546	2946	0	2
Blaauwwater Pan	2617	3016	1	0
Blinkpan (Arnot)	2554	2953	0	0
Blinkpan (Lothair)	2620	3020	0	0

Appendix 2.2 (continued).

Locality	Co-ords		Count	
	Lat.	Long	Summer	Winter
Blinkpan Oranje	2603	2931	0	0
Breyten Pan	2618	3000	0	0
Coetzerspruit (source of)	2603	2934	0	0
Coetzerspruit Dam	2555	2936	0	0
Daybreak Farm: Modderfontein	2609	2832	5	10
Goedehoop Pans 1&2	2620	3018	1	0
Goedenhoop Pan	2555	2928	0	0
Grootpan	2555	2954	0	0
Kanhym Pan 3	2552	2932	0	0
Kwena Dam	2521	3022	0	0
Lake Banagher (East)	2620	3022	0	0
Lake Banagher (West)	2620	3021	0	0
Lake Chrissie	2619	3013	4	5
Leeuwpan	2635	2857	14	1
Loskop Dam	2526	2919	0	2
Masibekela Wetlands	2553	3150	0	0
Mavella Pan	2554	2924	0	39
Nooitgedacht Dam	2559	3004	13	6
Ogies Pans	2605	2904	0	0
Oranje Pan	2601	2932	0	0
Otter Pan	2555	2956	0	0
TNC Proposed Bird Sanctuary	2608	2922	0	0
Witbank Dam	2553	2918	21	10
Total			**59**	**75**
North West				
Barberspan	2635	2535	93	20
Vaalkop Dam	2520	2728	2	0
Total			**95**	**20**
Northern Cape				
Dampoort Dam	2811	2429	3	0
Ganspan B	2754	2447	0	0
Kamfers Dam	2840	2446	325	12
Orange River: Bridge - Hohenfels	2833	1633	2	0
Orange River: Mouth	2838	1628	0	1
So Ver Myn Dam	2813	2431	0	0
Total			**330**	**13**
Northern Province				
Den Staat Irrigation Dams	2213	2916	0	3
PMC Wetlands	2401	3110	1	0
Turfloop Dam	2353	2946	0	1
Total			**1**	**4**
Western Cape				
Berg 1: Mouth & Estuary	3247	1809	0	0
Berg 10: Kersefontein Floodplain	3253	1819	0	0
Berg 3: Hotel Mudflats & Estuary	3247	1811	0	1
Berg 4: Hotel Saltpans	3248	1811	0	0

Appendix 2.2 (continued).

Locality	Co-ords		Count	
	Lat.	Long	Summer	Winter
Berg 5: De Plaat	3248	1812	0	0
Berg 6: Kliphoek Saltpans	3250	1812	1	0
Berg 8: Kruispad Floodplain	3252	1815	0	0
Botriviervlei: Combined (A1,A2,B,C & D)	3421	1906	0	0
De Mond Estuary	3443	2007	0	0
Eerste River Estuary	3405	1846	0	0
Hartebeeskuil Dam	3406	2200	0	3
Jakkalsvlei	3205	1819	0	0
Keurbooms River Estuary	3402	2324	0	0
Kleinmond River Estuary (section E)	3421	1905	0	0
Kleinriviersvlei (Klein River Estuary)	3425	1921	0	1
Knysna Lagoon	3403	2302	0	0
Leeu Gamka Dam	3236	2201	0	0
Mossel Bay Sewage Works	3407	2206	4	1
Mossgas Dams	3411	2201	6	3
Noord Agter Paarl Irrigation Dam	3340	1858	4	0
Olifants River Mouth (South Bank)	3142	1812	1	0
Paarl Bird Sanctuary	3341	1858	10	2
Rocher Pan	3236	1818	0	0
Rondevlei Nature Reserve	3404	1830	0	0
Strandfontein Sewage Works-Combined	3405	1831	0	0
Theewaterskloof Dam	3402	1913	25	80
Verlorenvlei	3220	1825	0	2
Voelvlei Dam	3322	1903	0	0
Wadrif Saltpan	3213	1821	0	0
Wilderness Lakes - Swartvlei System	3400	2245	0	2
Wilderness Lakes - Touw System	3359	2240	0	0
Wildevoelvlei	3408	1821	0	0
Zandvlei - Lower Estuary	3407	1828	0	0
Zandvlei - Upper Estuary	3406	1828	0	0
Total			**51**	**95**

Appendix 2.3. Co-ordinated Waterbird Count (CWAC) data for wetlands counted in Gauteng during the winters of 2000 to 2004. Ticks indicate that the site was counted in that particular year but there were no actively breeding Grey-headed Gulls recorded, crosses indicate that the site was not counted in that year, and values are the total number of Grey-headed Gulls counted (all ages) only at sites where breeding was confirmed.

Site	Co-ords	2000	2001	2002	2003	2004
Abe Bailey NR	26°19'S, 27°20'E	✔	✔	✔	✔	✔
Anglo Reserve	26°18'S, 28°30'E	✔	✔	✔	✔	✔
Apex Pan	26°13'S, 28°20'E	✕	✕	✔	✔	✔
Blaauwpan	26°07'S, 28°15'E	✕	✕	✔	✔	✔
Bon Accord Dam	25°37'S, 28°11'E	✕	✕	✕	✔	✔
Bonaero Park Pan	26°07'S, 28°16'E	1649	90	632	✔	736
Bronkhorstspruit Dam	25°54'S, 28°42'E	✔	✔	✔	✔	✔
Bullfrog Pan	26°08'S, 28°19'E	✕	✕	✔	✕	✕
Con Joubert Bird Sanctuary	26°11'S, 27°41'E	✔	✔	✔	✔	✔
Cowles Dam	26°13'S, 28°28'E	✔	✔	✔	✔	✔
De Pan	26°13'S, 27°26'E	✔	✔	✔	✔	✔
Diepsloot Nature Reserve	25°57'S, 28°00'E	✔	✔	✔	✔	✔
Elandsvlei	25°59'S, 28°27'E	✔	✔	✔	✔	✔
Groenfontein Pan	25°56'S, 28°44'E	✕	✕	✔	✔	✔
Grootvaly on Blesbok	26°16'S, 28°30'E	✔	✔	✔	✔	✔
Grootvaly Wetland Reserve	26°14'S, 28°29'E	✔	✔	✔	✔	✔
Korsman's Bird Sanctuary	26°11'S, 28°18'E	121	✔	284	1835	393
Lakefield Pan	26°11'S, 28°17'E	✕	150	264	✔	247
Leeupan	26°14'S, 28°19'E	✔	✕	✔	✔	✔
Marievale Bird Sanctuary	26°21'S, 28°30'E	✔	✔	✔	✔	✔
Parkhaven Pan - North	26°08'S, 28°16'E	✕	3800	850	✔	133
Parkhaven Pan - South	26°09'S, 28°16'E	✕	20	✔	✔	✔
Rietspruit (Rooikraal)	26°20'S, 28°17'E	✔	✔	✔	✔	✔
Rietvlei & Marais Dams	25°53'S, 28°17'E	✔	✕	✕	✔	✔
Rolfe's Pan	26°10'S, 28°13E	✔	✔	✔	✔	✔
Rondebult Bird Sanctuary	26°18'S, 28°12'E	✕	✕	✔	✔	✔

Appendix 2.3 (continued).

Site	Co-ords	2000	2001	2002	2003	2004
Roodeplaat Dam	25°38'S, 28°21'E	✔	✔	✔	✔	✔
Rooiwal Sewage Works	25°34'S, 28°14'E	✔	✔	✔	✔	✔
Rynfield Dam	26°09'S, 28°21'E	✔	✕	✕	✕	✕
Sand Pan	26°07'S, 28°19'E	✕	✕	✔	✔	✔
Stan Madden Bird Sanctuary	26°24'S, 28°28'E	✔	✔	✔	✔	✔
Stewards Pan	26°12'S, 28°17'E	✕	✔	1063	2400	2800
Varkfontein Pans	26°03'S, 28°22'E	✕	3000	2000	✕	✕
Totals		3770	9061	7095	6238	6313

Chapter 3

Breeding biology of the Grey-headed Gull *Larus cirrocephalus* in Gauteng Province and Lake St Lucia, South Africa – the nest and egg stage

Summary

The nest and egg stages of the Grey-headed Gull's breeding biology were studied at four sites in Gauteng: Bonaero Park, Korsman's Bird Sanctuary, Lakefield Pan and Modderfontein Pan during the 2004 and 2005 breeding seasons, and at Lake St Lucia's Lane Island during the winter of 2004. Nests were situated on exposed and vegetated shorelines, as well as on hygrophylous vegetation in the water. Nearest-neighbour distances were greatest for nests at Modderfontein Pan, a small colony situated in agricultural land on the periphery of their core breeding range, and smallest for nests at Lakefield Pan, a larger colony situated in suburbia within their core breeding range. Grey-headed Gulls were highly synchronous in their egg laying at Lane Island when compared with Gauteng colonies and this is likely influenced by the high level of African Fish Eagle predation at this site (which ultimately led to complete breeding failure during 2004). There was a significant difference between the laying dates of different sub-colonies at Bonaero Park during 2004, the largest colony studied. The mean clutch size for 332 nests at all sites was 2.42 eggs; similar to that previously recorded for the species. The smallest clutch sizes were at Lane Island, likely associated with the extreme drought conditions prevalent during the study period. There were significant intra- and inter-clutch differences in egg dimensions. The largest eggs were at Modderfontein Pan and the smallest eggs were from Lakefield Pan. These differences are tenuously attributed to density dependent factors, proximity to nutritional food sources and parental quality. The mean incubation period for 35 eggs from 22 nests was 24.9 days. Males and females contributed approximately equally to incubation duties while males spent more time in attendance at the nest and participated in more aggressive encounters. Overall daily egg survival was high for all sites in Gauteng and low for Lane Island. The variables most strongly associated with daily egg survival were the time elapsed between

successive observer visits (longer periods resulted in more eggs failing), differences between sub-colonies (daily egg survival at Lane Island was significantly lower that at the other sites), hatching synchrony (eggs laid before the mean starting date had a higher chance of hatching than eggs laid after the mean starting date) and the number of days since incubation started (mostly negatively influenced towards the end of the incubation period).

Introduction

The majority of gulls breed in colonies, with most species nesting at or near to ground level (del Hoyo *et al.* 1996). Gulls are ideal candidates for research on breeding biology as most nest sites are easily accessible and their gregarious habits ensure large sample sizes in a relatively short space of time. Gulls have interesting and complex social systems during the breeding season (e.g. Kirkman 1937; Tinbergen & Moynihan 1952; Moynihan 1955; Pierotti 1980; van Rhijn 1981). Certain gull species present management problems, e.g. for conservationists and airports officials (e.g. Blokpoel 1976; Skorka *et al.* 2005), motivating studies of factors regulating their breeding success (Coulson *et al.* 1982). These are some of the reasons why the literature on many aspects of the breeding biology of different gull species throughout the world is extensive (e.g. Patterson 1965; Coulson 1968; Mills 1969; Schreiber 1970; Hunt 1972; Smith 1972; Burger 1974; Davis 1975; Hunt & Hunt 1975; Parsons 1976; Mills 1979; Butler & Trivelpiece 1981; Butler & Janes-Butler 1982; Coulson *et al.* 1982; Fetterolf 1983; Mousseau 1984; Pierotti & Bellrose 1986; Verbeek 1986; Meathrel & Ryder 1987; Ottaway *et al.* 1988; Williams 1990; Williams *et al.* 1990; Sydeman *et al.* 1991; Pons 1992; Sydeman & Emslie 1992; Watanuki 1992; Belant *et al.* 1993; Bukacinska *et al.* 1996; Kilpi *et al.* 1996; Oro *et al.* 1999; Velarde 1999; Gill *et al.* 2002; Oro 2002; Crawford & Underhill 2003; Prieto *et al.* 2003; Bull *et al.* 2004; Garcia-Borboroglu & Yorio 2004; Skorka *et al.* 2005).

Research on gulls has included the study of various breeding parameters that give an indication of a species breeding success and the associated strategies involved in different cost-benefit trade-offs. Certain breeding parameters can be calculated from the nest and egg stage during a bird's breeding cycle and include: the timing of laying; nest spacing; clutch size; egg dimensions; and the incubation period. Of these parameters, those involving eggs can be compared between eggs in the same clutch, between eggs in different clutches, between eggs from different sites, and between eggs from different time periods. Furthermore, the daily survival rates of eggs can be used to estimate which of these parameters are likely to have an influence on breeding success. Daily survival rates are ultimately determined by egg mortality that may occur due to a number of reasons. These have been summarised by O'Connor (1984) and include: hatching failure due to infertility or death of the embryo; predation; competitive egg destruction; and nest desertion. The rate at which any of these factors operate on egg survival is likely to be influenced by the quality of the parental birds (e.g. Sydeman *et al.* 1991, Sydeman & Emslie 1992 and references therein), which is reflected in the variability of breeding parameters.

While many northern hemisphere gull species have been extensively studied, information on the breeding biology of the Grey-headed Gull *Larus cirrocephalus* has mostly been anecdotal (Crawford & Hockey 2005; Fitzpatrick reference database). In this chapter I look at the nest and egg stage of the Grey-headed Gull's breeding biology studied at various breeding localities in South Africa during 2004 and 2005. Breeding parameters studied include nest characteristics (i.e. general nest descriptions and nest spacing), laying synchrony, clutch sizes, egg dimensions, and incubation. The clutch size and oometric data, viz. laying synchrony and egg dimensions, are then used to compare differences in breeding parameters between different populations of Grey-headed Gulls in Gauteng and Lake St Lucia. Daily egg survival rates are then compared between all colonies and sub-colonies taking into consideration the influences of both intrinsic factors (i.e. laying synchrony, days elapsed since the start of incubation and clutch size) and the extrinsic influence of the time elapsed between successive nest visits.

Methods and Study Area

Study period

Grey-headed Gull breeding colonies in Gauteng Province were studied between 13 May and 1 September 2004 and between 13 May and 15 July 2005, and a colony at

Lane Island, Lake St Lucia, KwaZulu-Natal Province was studied between 26 July and 10 September 2004.

Location of breeding colonies

Grey-headed Gull colonies in Gauteng were searched for during 2004 in areas where the species had previously been recorded breeding (Co-ordinated Waterbird Count (CWAC) data; Whittington-Jones pers. comm.). During 2005, in addition to the ground covered during 2004, an aerial census was conducted over the extensive network of pans in the agricultural areas east of their known breeding range (flight route illustrated in Figure 2.1). All sites observed with Grey-headed Gulls were noted and their co-ordinates were recorded with a Geographic Positioning System (GPS); these sites were re-visited by vehicle between two and five days later to establish if the birds were breeding there. All breeding localities found in both years are illustrated in Figure 2.1.

Lane Island at Lake St Lucia was visited five times during the 2004 breeding season. An inflatable boat with a 5 hp motor was used to access the island from Hell's Gate. Between two and seven observers were used to search the areas where Grey-headed Gulls were observed breeding.

Selection of breeding colonies in Gauteng

Between 24 June and 9 July 2004, the nest and egg stages of the Grey-headed Gull's breeding biology were investigated at two sites in Gauteng: Bonaero Park and Korsman's Bird Sanctuary. The selection of these sites was based on: a comparison of the total number of breeding pairs present at each site within Gauteng (see Chapter 2); nesting substrate (i.e. on the dry shoreline or on floating vegetation in the wetland); and security reasons, i.e. Steward's Pan which local officials (Gauteng Nature Conservation) warned us against using as a study site. Between 13 May and 15 July 2005, research into the Grey-headed Gull's breeding biology continued at three sites in Gauteng: Bonaero Park, Lakefield Pan, and Modderfontein Pan. In addition to the selection criteria used in the 2004 study, Modderfontein Pan was selected due its relative isolation when compared to the other, more suburban sites.

Description of study colonies

Gauteng - Bonaero Park

(26°07'S 28 °16'E) (Figure 3.1)

This site is situated north of Johannesburg International Airport in suburban Benoni. Bonaero Park was originally an ephemeral pan (Whittington-Jones pers. comm.) but has since become permanently inundated as various storm-water outlets from the surrounding suburbs supply it with water year-round. The site has open water at its centre, two vegetated islands situated within its core and marshy vegetation covering a large portion of its periphery. The vegetated islands are dominated by *Phragmites australis* and *Typha capensis.* The marshy peripheral areas are dominated by the hygrophilous grass *Leersia hexandra* and the exotic *Persicaria lapathifolia*, and, to a lesser degree, by sedges (Cyperacea spp.). The western and northern areas of this site are dominated by dense *Leersia hexandra* marsh, while habitat in the eastern and southern parts has sparser hygrophilous vegetation with more extensive open water. The outer shoreline is mostly grassed with some trees and there is regular movement of humans through these areas; the site is not fenced. The locations of Grey-headed Gull sub-colonies at the pan during both years of the study period are illustrated in Figure 3.1.

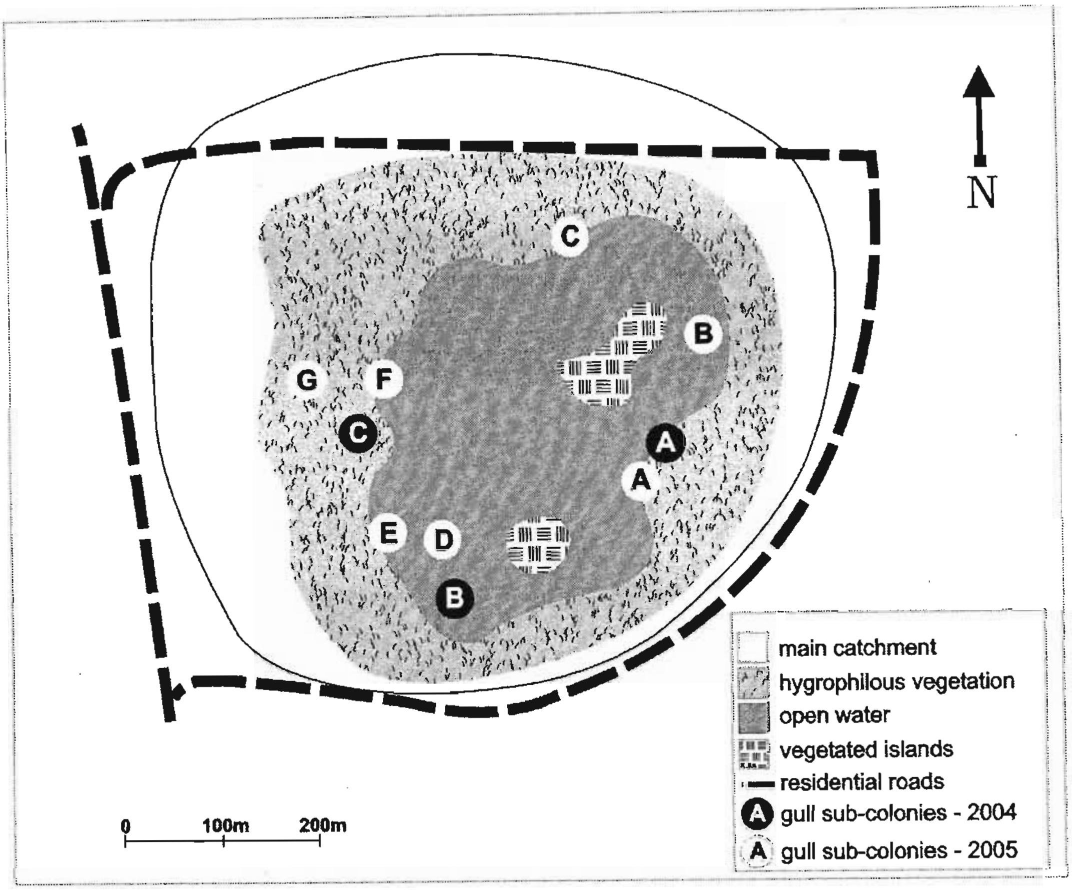


Figure 3.1. Bonaero Park showing habitat features and localities of Grey-headed Gull sub-colonies: 2004 A - East, B South, C West, 2005 A - EastA, B - EastB, C - North, D - South WestA, E - South WestB, F - WestA, and G - WestB.

Gauteng – Korsman's Bird Sanctuary

(26°11'S 28 °18'E) (Figure 3.2)

This site is a protected nature reserve and is situated in suburban Benoni. Water levels at Korsman's fluctuate annually and seasonally but there is usually some water year-round, supplemented by surrounding suburban drainage. It has a large open-water component, a vegetated island that is connected to the mainland by a narrow concrete causeway, and a shoreline that alternates between tall littoral vegetation (mostly *Phragmites australis* and *Typha capensis*) and open rocky shores. There is a bird-hide opposite the northeastern entrance gate and a well-maintained fence encloses the entire wetland. The location of three different Grey-headed Gull sub-colonies at this site are illustrated in Figure 3.2. Most gulls bred at sub-colony A.

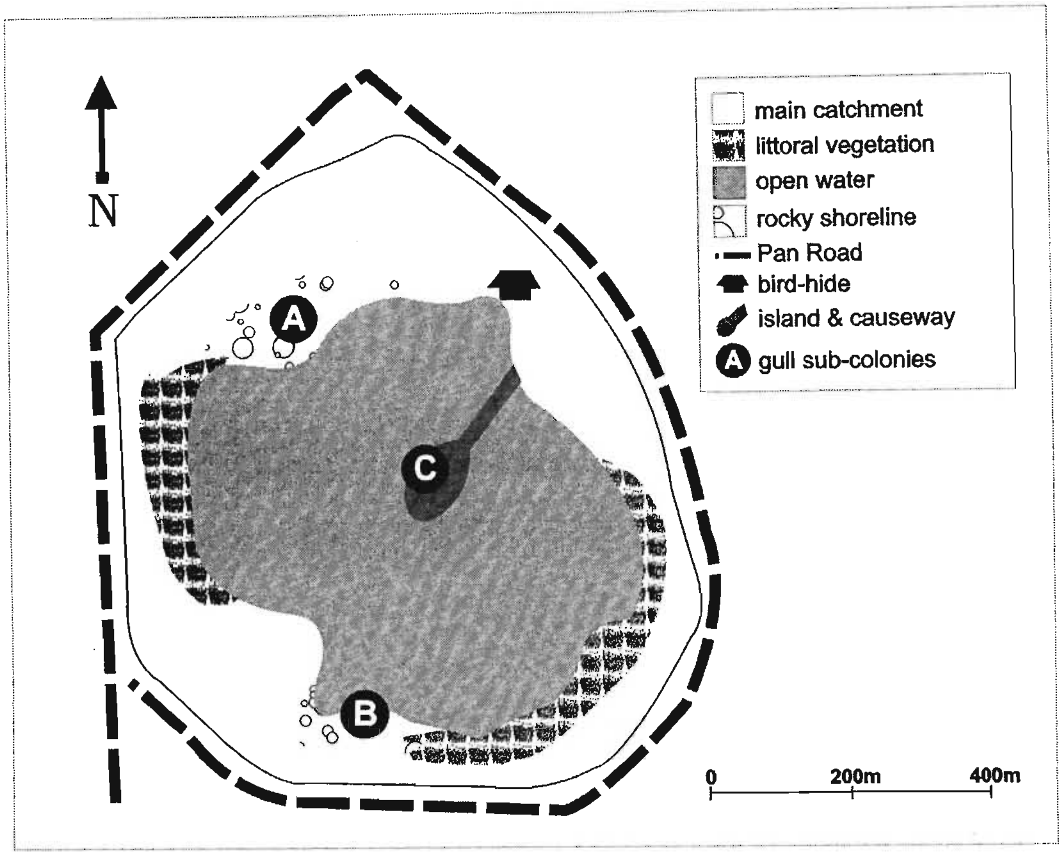


Figure 3.2. Korsman's Bird Sanctuary showing habitat features and localities of Grey-headed Gull sub-colonies.

Gauteng - Lakefield Pan

(26°11'S 28 °17'E) (Figure 3.3)

This site is situated in suburban Benoni and abuts Atlas Rd on its western border. Water levels fluctuate annually and seasonally and are supplemented by surrounding suburban storm-water drainage. The pan is a mosaic of open water, vegetated islands and hygrophilous vegetation (*Leersia hexandra*, *Persicaria lapathifolia* and Cyperacae *spp.*). *Phragmites australis* and *Typha capensis* are prominent both in the wetland and along its shoreline; the latter being discontinuous and interrupted by open grassy areas interspersed with trees. The area forms part of a secure residential complex that was under construction during 2005 and the pan is to be incorporated as a water feature in this development. There were two distinctive sub-colonies at this site during the study period, A and B (Figure 3.3).

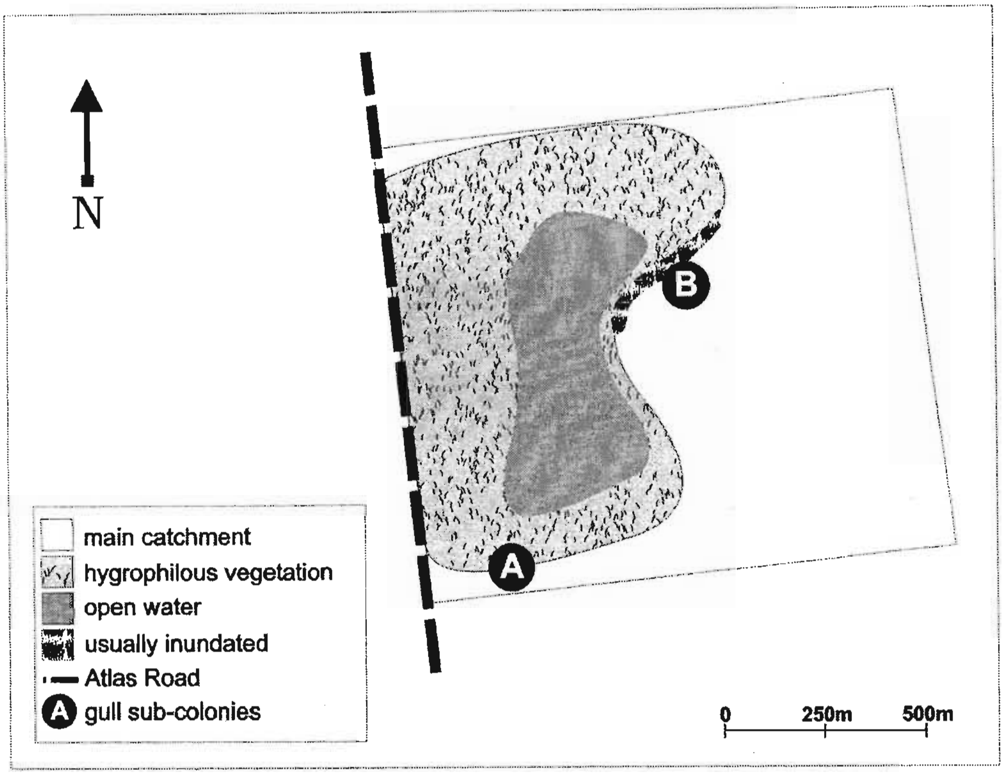


Figure 3.3. Lakefield Pan showing habitat features and localities of Grey-headed Gull sub-colonies.

Gauteng - Modderfontein Pan

(26°09'S 28 °31'E) (Figure 3.4)

This pan is situated on the farm Modderfontein approximately 5 km southeast of Etwatwa. The surrounding area largely comprises crop farms, mostly maize, and there are numerous chicken hatcheries in the area, as well as a chicken abattoir approximately 1.5 km northeast of the site where the gulls regularly scavenge. Until recently, the pan was mostly ephemeral, retaining water during winter only in wetter years. The pan is now permanently inundated by water that is pumped from the adjacent dam to the north, opposite the abattoir. The pan is typically marshy and is dominated by the hygrophilous grass *Leersia hexandra*. The only open water occurs in a small area towards the western end of the pan. The site is mostly secluded and receives little human disturbance. Grey-headed Gulls breeding at the pan were divided into two sub-colonies, A and B, (Figure 3.4).

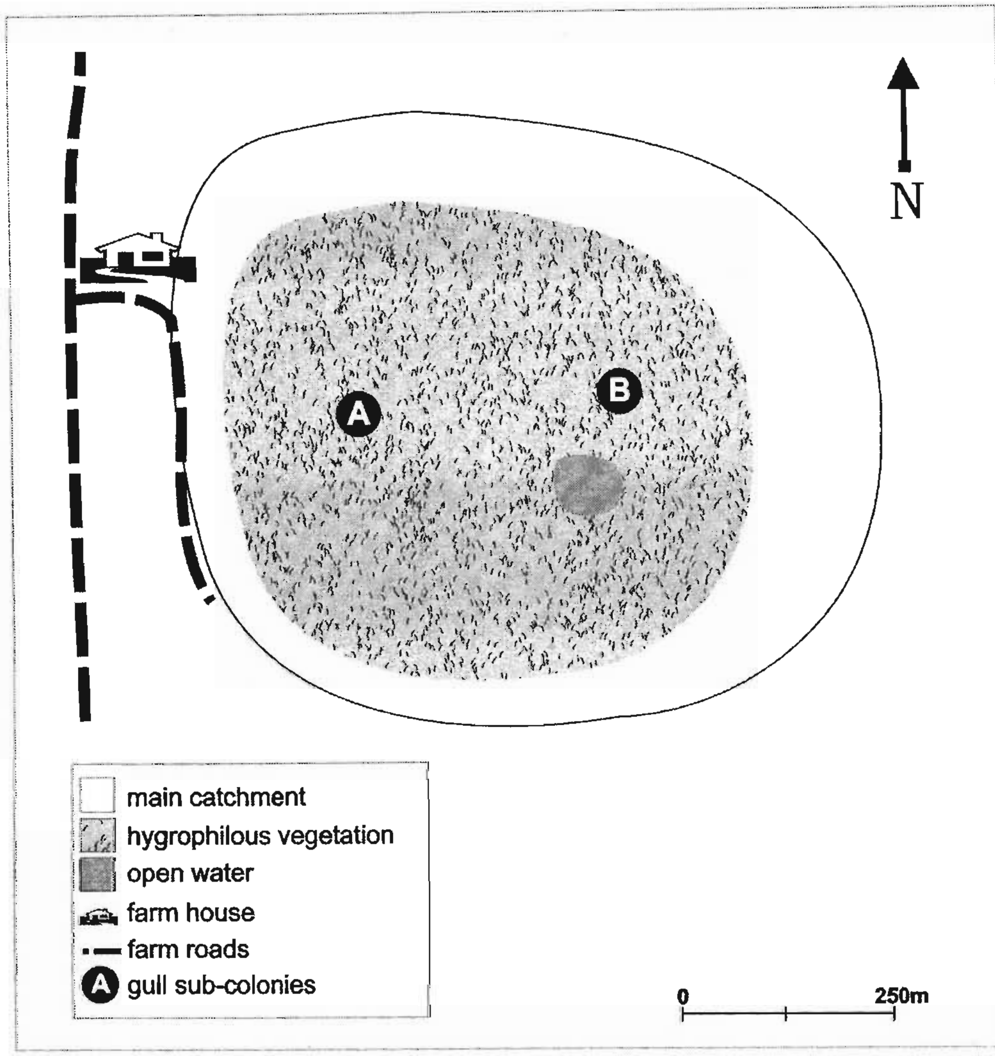


Figure 3.4. Modderfontein Pan showing habitat features and localities of Grey-headed Gull sub-colonies.

KwaZulu-Natal - Lake St Lucia, Lane Island

(28°04'S 32°27'E) (Figure 3.5)

Lane Island is a large island in the extensive St Lucia Lake system. It is situated approximately 2 km east of Hell's Gate, the entrance to False Bay. During drought (low-water) years, as was the case during this study, it ceases to be an island and is connected to the mainland by a shallow sandbar. The island is dominated by grasses, mostly *Paspalum vaginatum*. It is surrounded by a sandy shoreline.

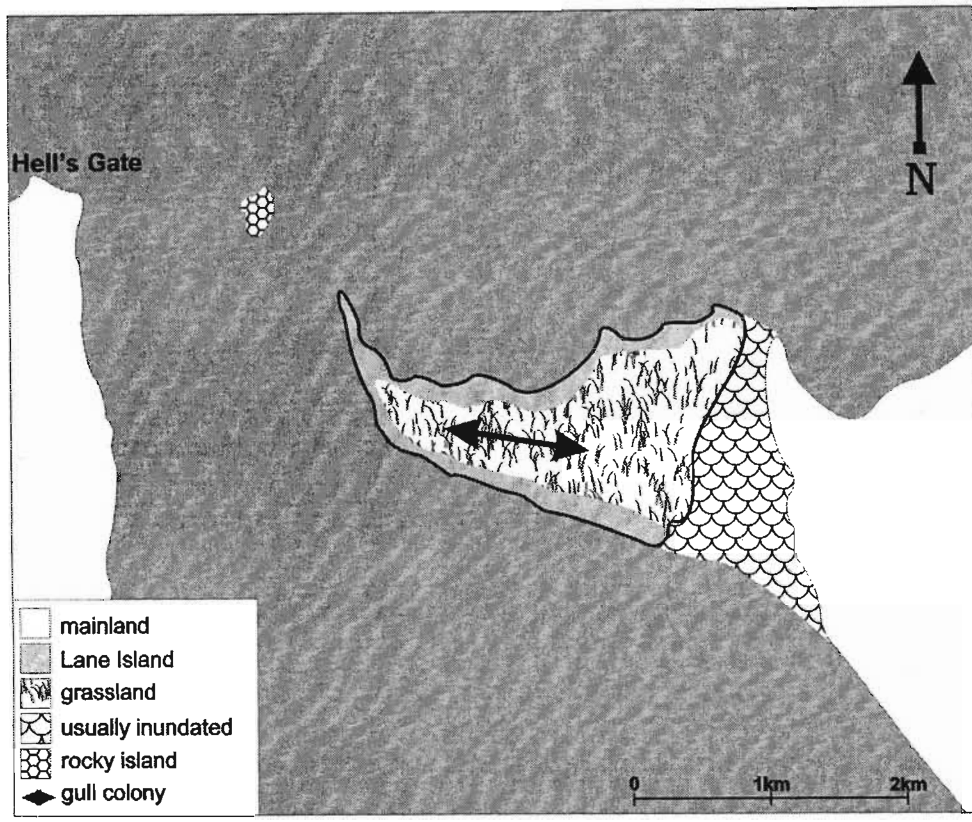


Figure 3.5. Lane Island, Lake St Lucia showing habitat features and Grey-headed Gull breeding colony.

Breeding biology

At Bonaero Park, Korsman's Bird Sanctuary and Lakefield Pan, samples of nests were chosen randomly by walking straight lines through the centres of all apparent sub-colonies and selecting each nest and their nearest neighbours along this line. At Lane Island and Modderfontein Pan all nests located were used in the analysis. Each nest was numbered with either a wooden peg (nests located on the ground) or a plastic tag, secured with a cable-tie (nests on floating vegetation in the water). During all visits, the contents of each nest were recorded. All eggs were numbered with a waterproof pen on both ends and were measured with dial callipers to the nearest 0.1mm (two breadth measurements at right angles to each other and one length measurement). All eggs were weighed with a digital scale to the nearest 0.1 grams and a number of eggs were re-weighed on subsequent visits to determine the proportion of egg mass lost over time. For all nests in Gauteng, nearest neighbour distances were recorded with a measuring tape to the nearest cm.

Nests at Lakefield Pan (site B, Figure 2.3) were observed from a hide during 7 June - 12 July 2005. Observations commenced between 06h30 and 07h00, usually just after first light, and lasted between four and seven hours. The small hide (dimensions: 1m length X 1m breath X 1.5m height) was placed approximately five metres from the most distant nest under observation and approximately one metre from the nearest nest. In order to mask the effect of entering the hide, I was accompanied by another person who subsequently left soon after. This proved to be effective as the birds immediately settled once my accomplice had left. Between one and five nests were observed at any given time and the owners of these nests were scrutinized for any apparent differences in sex. These factors were based on previous studies of other gull species (e.g. see review by Rodriguez & Pugesek 1996, Chapter 5) and included the overall size of the bird (i.e. larger/bulkier or slighter) when compared to its mate, the more or less aggressive role taken on by the individual in territorial confrontations, and the sex-related role in pre-copulation (e.g. courtship feeding) and copulation activities. All obvious activities at each nest were continuously recorded and these included incubation changeovers, attendance, aggressive encounters, courtship feeding and various displays.

Data analysis

Oometrics

Laying dates were estimated using the method by Underhill & Calf (2005). This method uses the three linear measurements and mass of an egg to calculate the percentage egg mass lost, taking into account the approximately 15-16 % decrease in mass over the incubation period (Ar & Rahn 1980). The method uses the following formula to determine the estimated number of days that the egg has been incubated:

$$t = (k\, L\, B_1\, B_2 - M_1)/(r\, k\, L\, B_1\, B_2),$$

where k is a parameter calculated from the mean of a sample of fresh eggs (i.e. just laid and before being incubated) using the formula:

$$k = M_0/L\, B_1\, B_2,$$

where M_0 is the mass of the fresh egg, L is the length measurement and B_1 and B_2 are the breadth measurements. M_1 represents the mass of the egg when weighed and r is the daily rate of mass loss per day calculated from regressing the rate of mass loss from a sample of eggs that were weighed more than once. Eggs were considered fresh only if additional eggs were added to the clutch on subsequent visits.

All three-egg clutches observed were included in the clutch size analysis. Due to the potential for two females to lay their eggs in one nest (del Hoyo *et. al* 1996; Higgins & Davies 1996), all four-egg clutches were discarded from this analysis. Only confirmed clutch sizes, i.e. from nests examined on more than one occasion, were used in this analysis.
In order to determine intra-clutch oometric differences (i.e. differences between the measurements of a- (first-laid), b- (second-laid) and c- (third-laid) eggs within the same clutch) the length and breadth values of each b-egg, within two and three-egg clutches, were subtracted from the corresponding a-egg measurements. Similarly, c-egg dimensions were subtracted from their corresponding b-egg dimensions to see if there were any differences.

Egg volume was calculated from the formula:

$$V(cm^3) = 0.000485.\ length.\ breadth^2,$$

Oro (2002). Breadth was taken as the average of the two measurements.

Model for estimating egg survival

Modelling principles

At the start of an observation period the number of eggs in a nest is counted and then at the end of the period the number surviving is counted again. If the number in the nest is n at the start then the possible number in the nest at the end will be r = 0, 1, … n. An egg can either survive or be lost and if the survival probability of all n eggs in the nest is the same, p, then an appropriate model is the binomial model:

$$Prob(r/n,p) = {}_nC_r p^r (1-p)^{n-r},$$

where ${}_nC_r$ = n!/(r!(n-r)!) and is called the binomial co-efficient, n! = n(n-1)(n-2) ... 3.2.1 and is called n-factorial while Prob(r/n,p) = the probability that r eggs will survive from an initial n eggs, given that each egg has the same survival probability p. There is an exact way to model this process using generalised linear models (GLM) (McCullagh & Nelder 1989) in which a model of the following form is erected:

$$\mathrm{Logit}(p) = \mathrm{Ln}(p/(1-p)) = f(.),$$

where Logit(p) is the logit function and is defined in terms of the odds ratio, as shown above, where ln(x) is the natural logarithm (i.e. to the base 2=2.718282...) of any non-negative number, x and where f(.) is some function of the explanatory variables which is hopefully linear. The reverse transformation is:

$$p = e^{f(.)}/(1+e^{f(.)}).$$

As described above, the survival of eggs from one observation period to another is likely to be a function of the following intrinsic variables: clutch size, number of days of incubation, laying synchrony as well as site or site-section. The extrinsic variable is the number of days that have elapsed between successive observations.

Based upon an understanding of the biology of incubation and nest loss, a set of 11 candidate models were constructed. These models were fitted using GLM Model and Fit functions of Genstat 8th Edition, version 8.1.0.152 (see also GENSTAT Committee etc.). For each model the following statistics were computed: R2, deviance of the residuals and associated degrees of freedom, goodness-of-fit between the observed number of eggs surviving each observational period and the predicted number (measured by the chi-squared statistic) and the Akaike's information criterion (AIC). In addition, the number of outliers and points with high leverage were counted.
The model with the lowest AIC was used as the final model.

Empirical models

A set of 11 simple empirical models were built which do not take into account the exact nature of the survival process but which try to approximate it:

E_0: Assume that f(p) is a constant, i.e.

$$\text{Logit}(p) = a_0.$$

E_1: Assume that f(p) varies linearly with the number of days elapsed between successive observation, i.e.

$$\text{Logit}(p) = a_0 + a_1*\text{Elapsed}.$$

E_2: Assume that f(p) varies linearly with the number of days elapsed between successive observation and with clutch size, i.e.

$$\text{Logit}(p) = a_0 + a_1*\text{Elapsed} + [\text{Clutch size factors}],$$

where [Clutch size factors] will be a set of parameters, one for each clutch size.

E_3: Assume that f(p) varies linearly with the number of days elapsed between successive observation and with study site, i.e.

$$\text{Logit}(p) = a_0 + a_1*\text{Elapsed} + [\text{Study site factors}],$$

where [Study site factors] will be a set of parameters, one for each study site.

E_4: As for Model E_3 but with Sub-colony replacing Study site, i.e.

$$\text{Logit}(p) = a_0 + a_1*\text{Elapsed} + [\text{Sub-colony factors}],$$

where [Sub-colony factors] will be a set of parameters, one for each sub-colony.

E_5: Assume that f(p) varies linearly with the number of days elapsed between successive observation, with study site and with clutch size, i.e.

$$\text{Logit}(p) = a_0 + a_1*\text{Elapsed} + [\text{Study site factors}] + [\text{Clutch size factors}],$$

where the factors are as defined above.

E_6: As for model E5 but with Sub-colony replacing Study site, i.e.

$$\text{Logit}(p) = a_0 + a_1*\text{Elapsed} + [\text{Sub-colony factors}] + [\text{Clutch size factors}],$$

where the factors are as defined above.

E_7: As for Model E_5 but also assuming that f(p) varies linearly with the number of days the clutch has been incubated, i.e.

$$\text{Logit}(p) = a_0 + a_1\text{*Elapsed} + [\text{Study site factors}] + [\text{Clutch size factors}] + a_2\text{*Incubation},$$

where the factors are as defined above.

E_8: As for Model E_7 but also assuming that f(.) varies linearly with the laying synchrony, i.e.

$$\text{Logit}(p) = a_0 + a_1\text{*Elapsed} + [\text{Study site factors}] + [\text{Clutch size factors}] + a_2\text{*Incubation} + a_3\text{*Synchrony},$$

where the factors are as defined above.

E_9: As for Model E_7 but with Study site being replaced by Sub-colony, i.e.

$$\text{Logit}(p) = a_0 + a_1\text{*Elapsed} + [\text{Sub-colony factors}] + [\text{Clutch size factors}] + a_2\text{*Incubation},$$

where the factors are as defined above.

E_{10}: As for Model E_8 but with Study site being replaced by Sub-colony, i.e.

$$\text{Logit}(p) = a_0 + a_1\text{*Elapsed} + [\text{Sub-colony factors}] + [\text{Clutch size factors}] + a_2\text{*Incubation} + a_3\text{*Synchrony},$$

where the factors are as defined above.

E_{11}: As for Model E_{10} but assuming that f(.) varies quadratically with Incubation, i.e.

$$\text{Logit}(p) = a_0 + a_1\text{*Elapsed} + [\text{Sub-colony factors}] + [\text{Clutch size factors}] + a_2\text{*Incubation} + a_3\text{*Synchrony} + a_4\text{*Incubation}^2,$$

where the factors are as defined above.

Results

Nests

Nest site characteristics were recorded at Bonaero Park and Korsman's Bird Sanctuary during 2004. The mean diameter of all nests measured at both sites was 285 mm (sd=7.2, n=108 nests). All nests at Korsman's Bird Sanctuary were built on the rocky shoreline, usually adjacent to small outcrops of rocks and were mostly built of grass and reed stems and occasionally grass rootlets. Grey-headed Gull nests at

Bonaero Park were built on floating mats of vegetation. These mats were invariably *Persicaria lapathifolia* stems, *Leersia hexandra* stems, Cyperacea spp. stems or *Typha capensis* leaves; nests were built on top of the mat structure and were usually lined with grass stems. A small number of Red-knobbed Coot *Fulica cristata* nests were occupied by breeding Grey-headed Gulls at Bonaero Park during the 2004 and 2005 breeding seasons; no other bird species' nests were observed as being occupied by Grey-headed Gulls.

Nest spacing

Results of nearest-neighbour distances for nests at different sites in Gauteng are given in Table 3.1 and illustrated in Figure 3.6. There was a highly significant difference in nest spacing between these sites (ANOVA $F_3=18.84$, $P<0.0001$). Most of this variation was from Modderfontein Pan ($t=5.894$, $P<0.0001$); nests here were on average 7.4 m further apart than nests at Bonaero Park. At the other extreme, nests at Lakefield Pan were on average 2.3 m closer together than Bonaero Park nests ($t=-2.017$, $P=0.045$).

Table 3.1. Grey-headed Gull nearest-neighbour distances for all Gauteng sites during 2004 and 2005. Values for Bonaero Park in 2004 and 2005 are pooled.

		Nearest-neighbour distance (cm)			
Site	**n**	**mean**	**s.d.**	**min**	**max**
Bonaero Park	118	315.6	739.1	30	7500
Korsman's B.S.	51	128.9	124.6	40	750
Lakefield Pan	56	84.2	42.7	30	230
Modderfontein Pan	44	1051.6	1254.3	90	6600

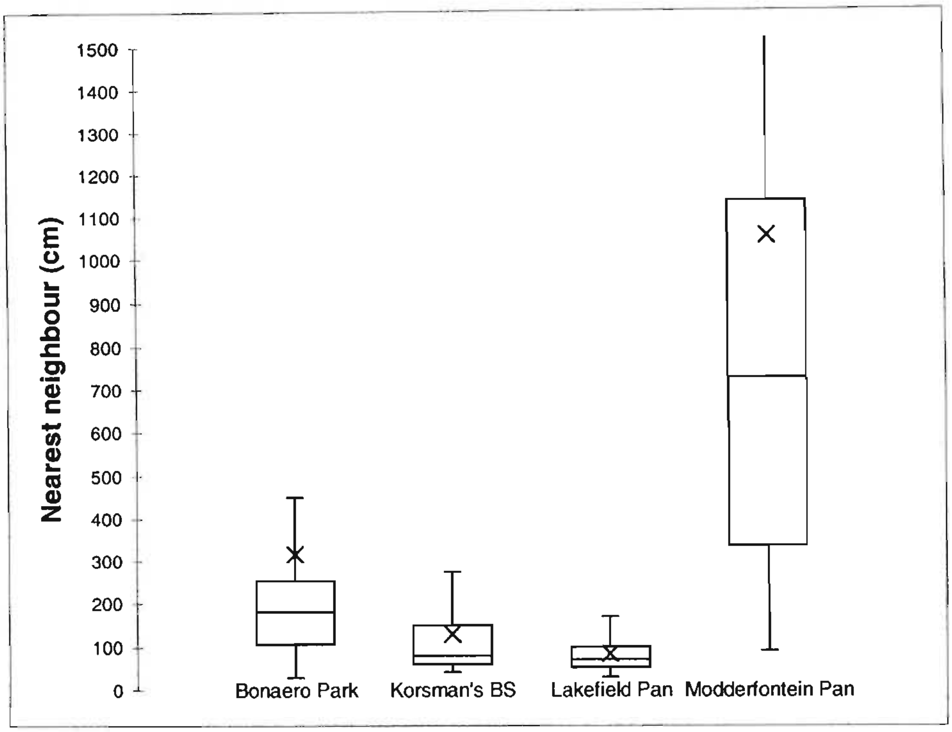


Figure 3.6. Box and whisker plots of Grey-headed Gull nearest neighbour distances for four Gauteng breeding sites during 2004 and 2005. Bonaero Park data for 2004 and 2005 are pooled. Crosses denote means.

Laying period

The numbers of breeding pairs and the proportions of nests containing eggs for three sites in Gauteng (Bonaero Park, Varkfontein Pan and Stewards Pan), counted during all months between May and August 2004, are illustrated in Figure 3.7. Breeding numbers were relatively low during May and June but increased during July and August. A large proportion of these nests contained eggs in all months, especially between June and August.

Oometric data

Laying synchrony

The value 'k' used in estimating fresh-egg mass was determined for a sample of 32 fresh-egg measurements coming from 21 nests from all sites during 2004 and 2005. This value was 0.000530424 with a standard deviation of 0.00000903. The rate of egg

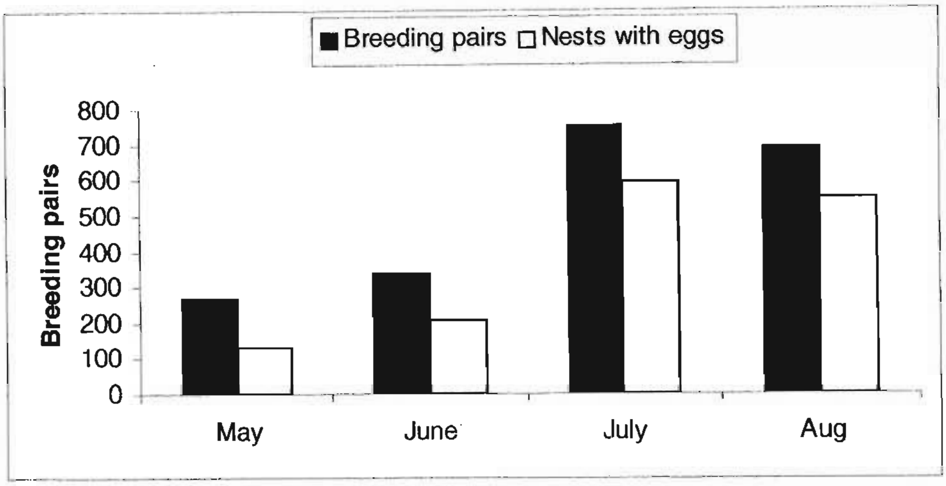


Figure 3.7. Number of breeding pairs and proportion of breeding pairs incubating at three sites (Bonaero Park, Stewards Pan and Varkfontein Pan) in Gauteng, between May and August 2004.

mass loss per day 'r' was determined for 253 eggs from 118 nests at the three sites examined during 2004; all of these eggs were weighed between two and four times each. This value was 0.00547 grams per gram fresh egg mass loss per day.

The frequency distributions of laying dates for all sites are shown in Figure 3.8 and the ranges, means, standard deviations and total number of laying days for each colony and sub-colony are described in Table 3.2. Laying dates for Grey-headed Gulls at Lane Island were highly synchronised when compared to all other sites, with all laying taking place within nine days between 24 July and 9 August 2004. Laying dates for Gauteng sites were more variable, spanning 27-34 laying days. In Gauteng, site visits were conducted earlier in the breeding season during 2005 than during 2004. For all sites in Gauteng during 2005, there was a peak in egg-laying activity during the first half of May, this being prolonged at Modderfontein Pan. There were a few early nesters in the latter half of April at Bonaero Park and Lakefield Pan.

Comparing the mean laying dates for Grey-headed Gulls at each sub-colony in each colony, there was little difference for all sites except Bonaero Park during 2005. There was a highly significant difference between the mean laying dates for all sub-colonies at this site (ANOVA F_6=4.896, P<001) with most birds in sub-colony West A laying earlier than in other sub-colonies (ANOVA t=2.78, P<0.05, Figure 3.9).

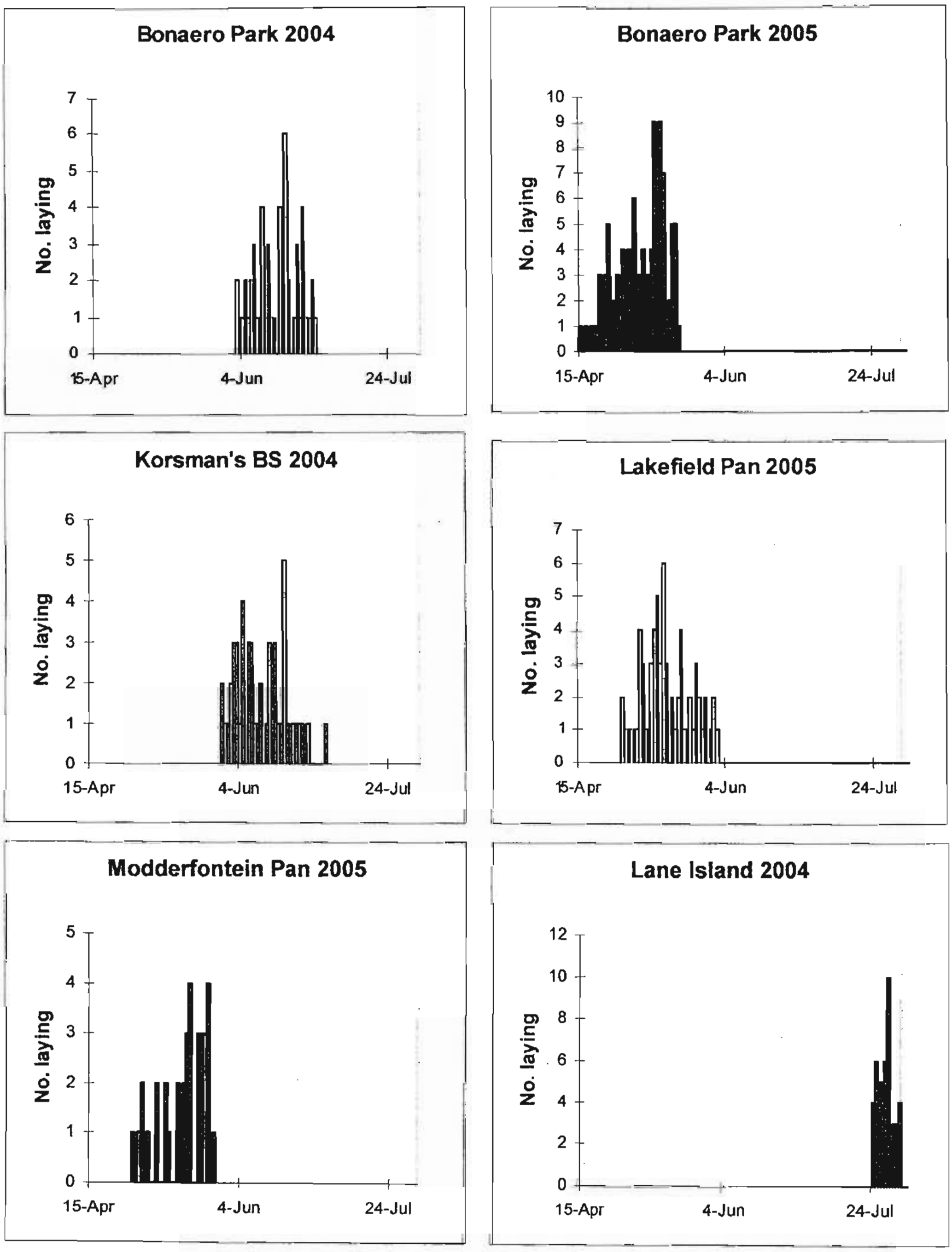


Figure 3.8. Frequency distribution of laying dates for Grey-headed Gulls in five Gauteng sites and Lane Island, Lake St Lucia.

Table 3.2. Laying dates for Grey-headed Gulls, as calculated from oometric data, for Grey-headed Gulls for all sites and all sections during 2004 and 2005.

Site (Section)	Year	No. nests	Laying dates first	last	mean	sd (days)	Laying days
Bonaero Park	2004	53	02-June	29-June	16-June	7.62	27
(East)		7	03-June	25-June	13-June	8.01	22
(South)		11	02-June	28-June	14-June	8.12	26
(West)		35	02-June	29-June	17-June	7.36	27
Bonaero Park	2005	103	15-April	19-May	06-May	8.47	34
(East A)		13	22-April	18-May	05-May	8.41	26
(East B)		10	22-April	19-May	07-May	8.44	27
(North)		14	23-April	16-May	07-May	6.79	23
(South West A)		16	15-April	13-May	09-May	6.67	28
(South West B)		19	25-April	18-May	11-May	7.04	23
(West A)		18	17-April	10-May	28-April	6.92	23
(West B)		13	20-April	18-May	06-May	9.76	28
Korsman's BS	2004	50	29-May	03-July	11-June	8.47	34
Lane Island	2004	45	24-July	03-August	29-July	2.67	9
Lakefield Pan	2005	65	30-April	01-June	15-May	8.32	31
(A)		27	30-April	28-May	14-May	7.11	28
(B)		38	30-April	01-June	16-May	9.04	31
Modderfontein Pan	2005	36	29-April	26-May	16-May	7.86	27
(A)		26	29-April	24-May	14-May	8.13	25
(B)		10	04-May	26-May	19-May	6	22

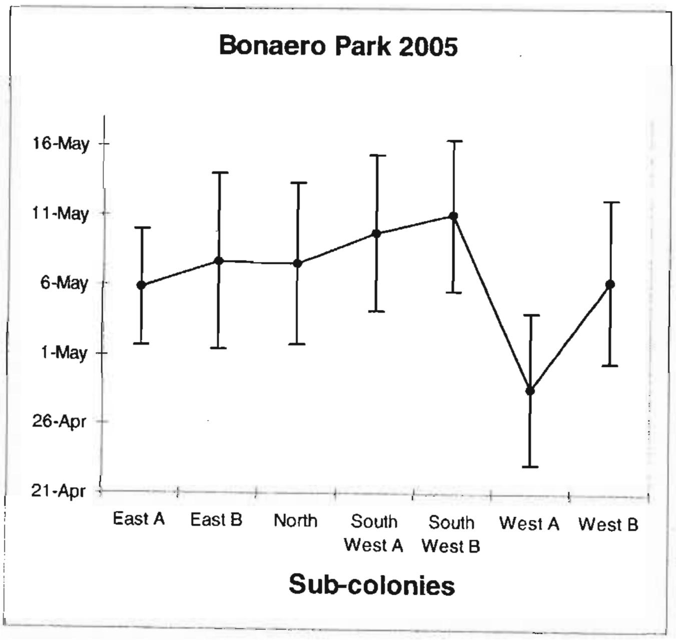


Figure 3.9. Mean laying dates for Grey-headed Gulls within different sub-colonies at Bonaero Park during 2005. Error bars denote 95% confidence limits.

Clutch size

The mean clutch size for all sites in Gauteng and Lake St Lucia was 2.42 eggs (s.d.= 0.65, n=339). Clutch size details for all sites are given in Table 3.3. The highest average clutch size was recorded at Korsman's Bird Sanctuary (mean=2.52, s.d.=0.63, n=58) and the lowest mean clutch size was recorded at Lane Island (mean=2.36, s.d.=0.59, n=36). A median clutch size of three eggs was recorded for Grey-headed Gulls at both Korsman's Bird Sanctuary and Modderfontein Pan, and Lane Island was the only site to have a median clutch size of two eggs. Despite these apparent differences, there were no significant differences between the clutch sizes of all sites (χ^2=5.572, df=8), between the clutch sizes of Gauteng sites (χ^2=2.994, df=6), and between the clutch sizes of Gauteng sites and Lane Island (χ^2=2.518, df=2).

Table 3.3. Grey-headed Gull clutch-size values (Clutch 1, Clutch 2 etc.) for all sites during 2004 and 2005. Values for Bonaero Park in 2004 and 2005 are pooled.

	Locality		n	Clutch 1	Clutch 2	Clutch 3	Clutch 4	mean	sd	median
Gauteng	Bonaero Park	no.	144	16	55	71	2	2.39	0.68	2.5
		%		11.1	38.2	49.3	1.4			
	Korsman's BS	no.	58	4	20	34	0	2.52	0.63	3
		%		6.9	34.5	58.6	0			
	Lakefield Pan	no.	58	4	24	28	2	2.43	0.63	2.5
		%		6.9	41.4	48.3	3.4			
	Modderfontein Pan	no.	47	3	20	24	0	2.45	0.62	3
		%		6.4	42.6	51.1	0			
	All sites	no.	303	27	119	157	4	2.43	0.65	3
		%		8.9	39.3	51.8	1.3			
Lane Island		no.	36	2	19	15	0	2.36	0.59	2
		%		5.6	52.8	41.7	0.0			

Egg dimensions

Intra-clutch variation

Differences between the dimensions of eggs of known laying order coming from different clutch sizes are shown in Table 3.4 and Figures 3.10 – 3.12. All eggs in three-egg clutches were the largest of all eggs in all clutches. There was a statistically significant difference between the breadth (ANOVA F_5=3.373, P<0.05) and volume (ANOVA F_5=3.340, P<0.05) of all eggs in all clutches. In three-egg clutches, first- and second-laid eggs were on average 1.17 mm and 1.39 mm broader (t=2.49, P=0.015 and t=2.96, P=0.004, respectively) than eggs in one-egg clutches, for volume, these eggs were on average 3.3 cm^3 and 3.46 cm^3 larger (t=2.69, P=0.009 and t=2.83, P=0.006, respectively) than eggs in one-egg clutches. For each two-egg clutch, first-laid eggs were on average larger than second-laid eggs, especially in length (Figure 3.11). There were few differences between the dimensions, i.e. length and breadth, of first- and second-laid eggs for each three-egg clutch but third-laid eggs were on average smaller than second-laid eggs.

Table 3.4. Grey-headed Gull oometric data for eggs of known laying order (a-,b-,c-eggs) from different clutch sizes. Data from all sites are pooled.

Clutch size	n	Egg-a,b,c	Length(mm) mean	Length(mm) sd	Breadth(mm) mean	Breadth(mm) sd	Volume(cm^3) mean	Volume(cm^3) sd
1	29	a-egg	51.81	2.64	36.42	1.15	33.40	3.19
2	11	a-egg	52.28	1.79	36.50	1.31	33.85	3.01
		b-egg	51.40	2.13	36.14	1.52	32.67	3.74
3	8	a-egg	53.58	2.36	37.59*	0.99	36.69*	1.71
		b-egg	53.11	2.56	37.81*	0.86	36.86*	2.77
		c-egg	52.46	2.57	37.06	0.87	35.00	2.90

*ANOVA, P<0.05

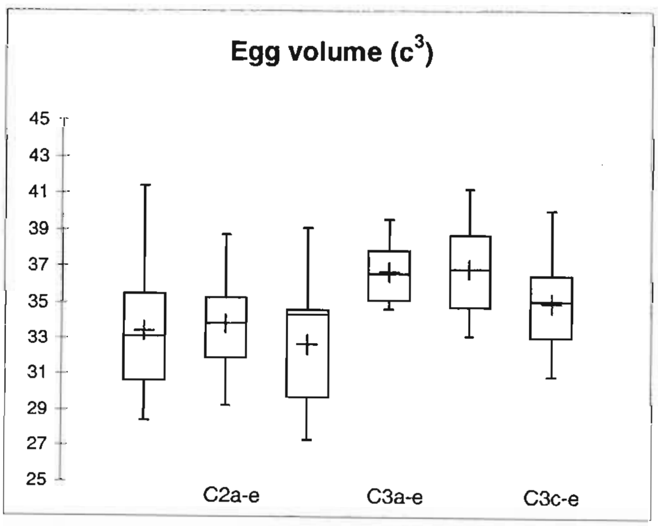


Figure 3.10. Box and whisker plots of the differences in Grey-headed Gull egg volumes of known laying order (a-,b-,c-eggs(e)) for eggs from different clutch sizes (C1,C2,C3). + denote means.

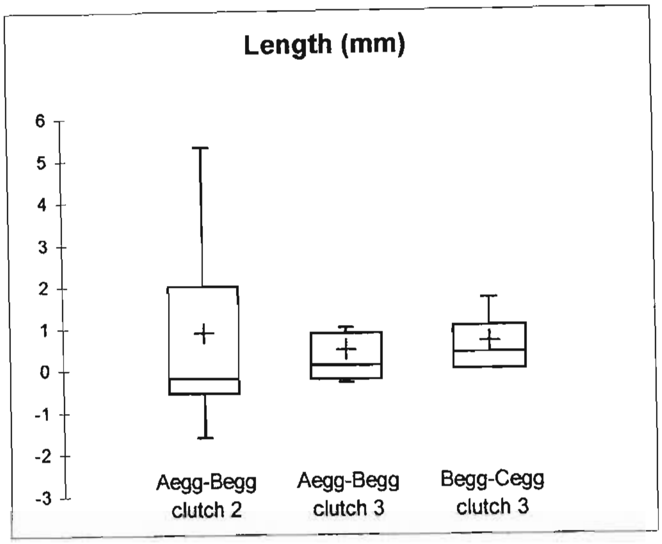


Figure 3.11. Box and whisker plots of the differences in length measurements between Grey-headed Gull eggs of known laying order in different clutch sizes. Length values are for the differences between eggs in the same clutches only. + denote means.

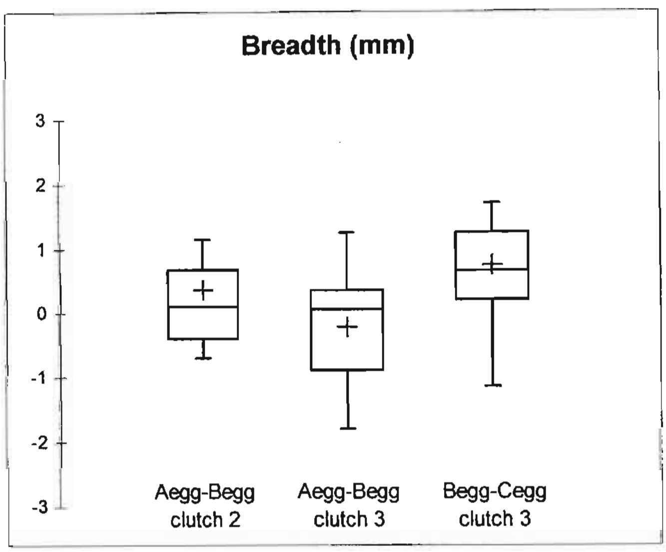


Figure 3.12. Box and whisker plots of the differences in breadth measurements between Grey-headed Gull eggs of known laying order in different clutch sizes. Breadth values are for the differences between eggs in the same clutches only. + denote means.

Inter-clutch variation

A total of 793 eggs from 303 clutches was measured. The mean egg length for all eggs was 51.4 mm (s.d.=2.41 mm, range=41.9-58.5 mm) and the mean breadth was 36.7 mm (s.d.=1.31 mm, range=29.9-40 mm). The mean volume for all eggs was 33.9 cm^3 (s.d.=3.33 cm^3, range=19.2-43.4 cm^3). Egg dimensions differed between colonies (Table 3.5) in length (ANOVA F_4=3.782, P<0.05), breadth (ANOVA F_4=5.871, P<0.001) and, not surprisingly, especially in volume (ANOVA F_4=6.460, P<0.0001). Eggs from Modderfontein Pan were on average 0.8 mm longer (t=2.899, P=0.004), 0.45 mm broader (t=3.119, P=0.002) and 1.44 cm^3 larger (t=3.715, P<0.0001) than eggs from Bonaero Park, and eggs from Lakefield Pan were on average 0.34 mm narrower (t=-2.56, P=0.011) and 0.75 cm^3 smaller (t=-2.079, P=0.038) than eggs from Bonaero Park (Figures 3.13 – 3.15).

Table 3.5. Grey-headed Gull oometrics data for all eggs from confirmed clutch sizes for all sites during 2004 and 2005. Values for Bonaero Park in 2004 and 2005 are pooled.

				Length(mm)		Breadth(mm)		Egg volume (cm^3)	
Province	**Site**	**Clutch**	**N**	**mean**	**sd**	**mean**	**sd**	**mean**	**sd**
Gauteng	**Bonaero Park**	1	16	51.52	2.39	36.68	1.10	33.69	3.22
		2	52	51.29	2.79	36.61	1.47	33.46	3.85
		3	51	51.18	2.52	36.74	1.29	33.59	3.30
		all	119	51.24	2.61	36.69	1.35	33.55	3.51
	Korsman's B.S.	1	4	53.33	3.30	35.44	0.81	32.50	2.74
		2	20	52.25	2.21	36.94	1.43	34.59	2.57
		3	29	51.17	2.11	36.66	1.22	33.42	1.22
		all	53	51.56	2.24	36.70	1.30	33.75	2.93
	Lakefield Pan	1	4	51.30	3.64	35.83	1.20	31.99	3.70
		2	24	51.37	2.33	36.30	1.14	32.86	2.68
		3	28	50.65	2.14	36.39	1.43	32.62	3.27
		all	56	50.93	2.26	36.34*	1.33	32.69*	3.06
	Modderfontein Pan	1	3	51.70	3.48	37.10	1.10	34.64	4.55
		2	19	52.13	1.92	36.91	1.13	34.51	2.81
		3	23	52.00	2.64	37.26	1.09	35.09	3.12
		all		52.04*	2.41	37.14*	1.11	34.88**	3.03
	All sites	1	27	51.77	2.73	36.41	1.18	33.37	3.27
		2	115	51.61	2.50	36.65	1.36	33.70	3.31
		3	131	51.21	2.41	36.74	1.30	33.61	3.29
		all	273	51.37	2.46	36.69	1.32	33.63	3.29
KZN	**Lane Island**	1	2	52.25	1.20	36.48	0.84	33.75	2.67
		2	16	51.41	2.08	36.50	1.30	33.30	3.18
		3	12	51.80	2.74	36.85	1.22	34.22	3.66
		all	30	51.63	2.41	36.68	1.25	33.79	3.41

*ANOVA, P<0.05
**ANOVA, P<0.001

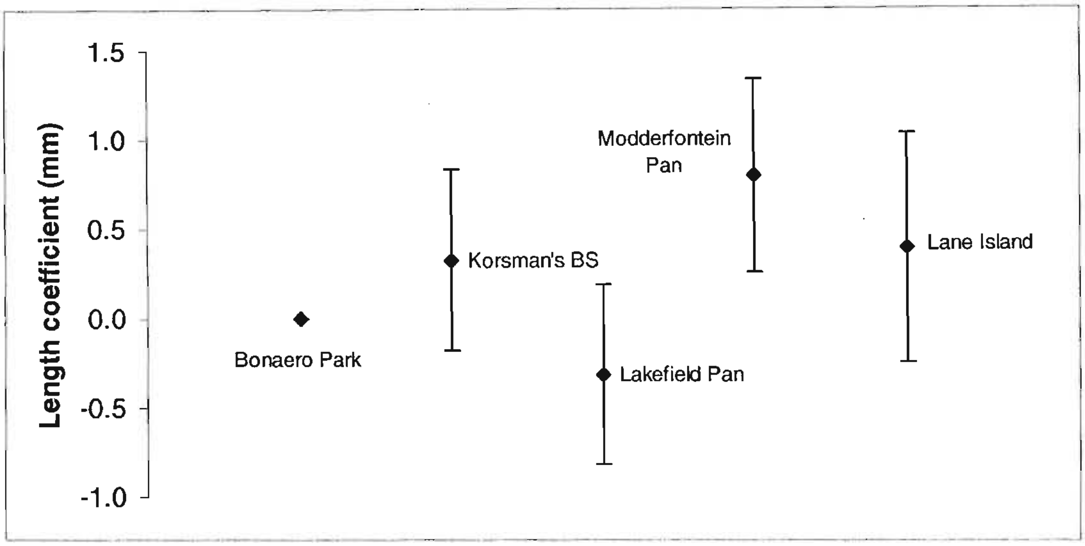


Figure 3.13. Differential coefficients (means +- 95% confidence levels) for length measurements (Bonaero Park sample as base-point) of Grey-headed Gull eggs from all clutch sizes for all sites during 2004 and 2005.

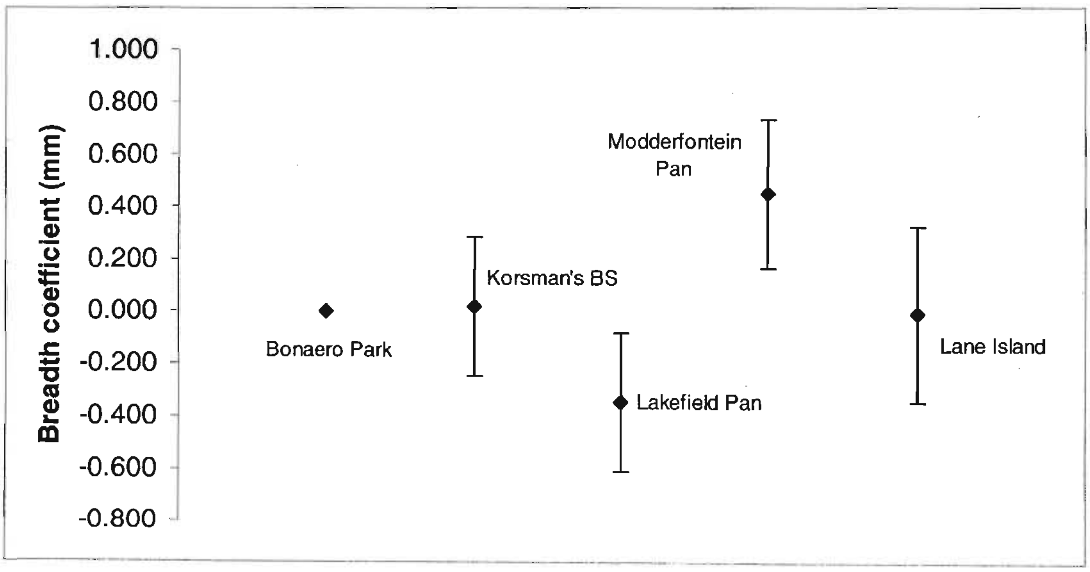


Figure 3.14. Differential coefficients (means +- 95% confidence levels) for breadth measurements (Bonaero Park sample as base-point) of Grey-headed Gull eggs from all clutch sizes for all sites during 2004 and 2005.

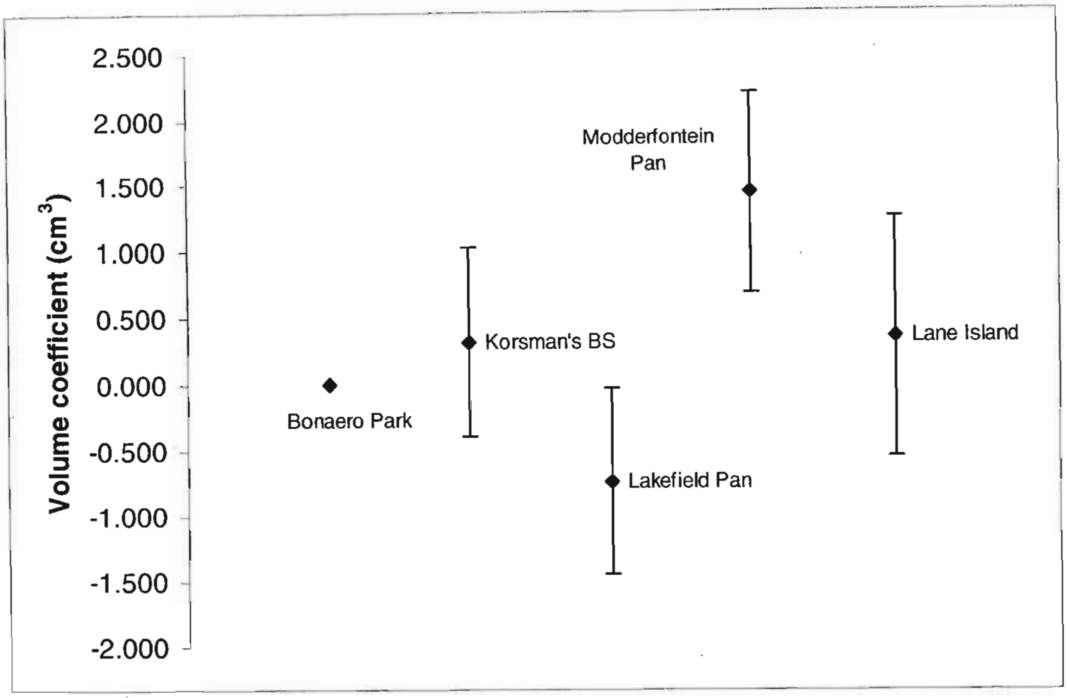


Figure 3.15. Differential coefficients (means +- 95% confidence levels) for volumes (Bonaero Park sample as base-point) of Grey-headed Gull eggs from all clutch sizes for all sites during 2004 and 2005.

Although there were no significant differences when comparing egg dimensions with clutch sizes in Gauteng (length: ANOVA F_2=2.339, N.S.; breadth: ANOVA F_2=0.987, N.S.; volume: ANOVA F_2=0.152, N.S.; Figures 3.16 - 3.18), it is interesting to note that there was a trend for eggs in three-egg clutches to be shorter but broader than those in two-egg clutches, which in turn were shorter but broader than eggs in one-egg clutches. Associated with this finding, eggs in two-egg clutches had greater volumes than eggs in both one- and three-egg clutches. There was no statistical difference in dimensions between eggs from Gauteng sites and those from Lane Island (length: ANOVA F_1=0.699, N.S.; breadth: ANOVA F_1=0.011, N.S.; volume: ANOVA F_1=0.206, N.S.).

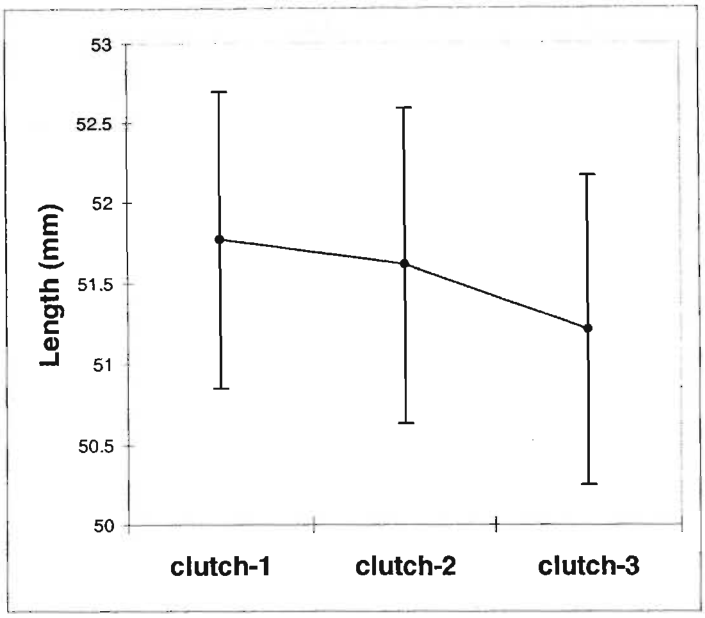


Figure 3.16. Length measurements (means +- 95% confidence limits) for Grey-headed Gull eggs from different clutch sizes for all sites during 2004 and 2005.

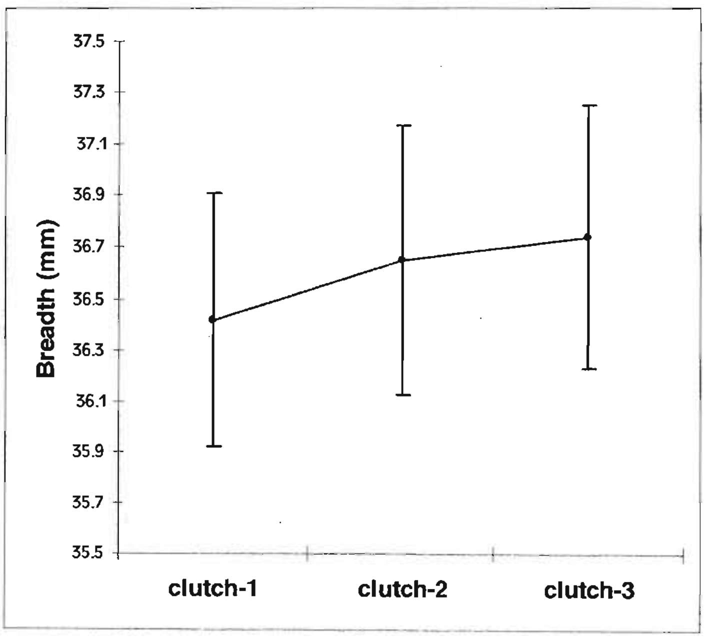


Figure 3.17. Breadth measurements (means +- 95% confidence limits) for Grey-headed Gull eggs from different clutch sizes for all sites during 2004 and 2005.

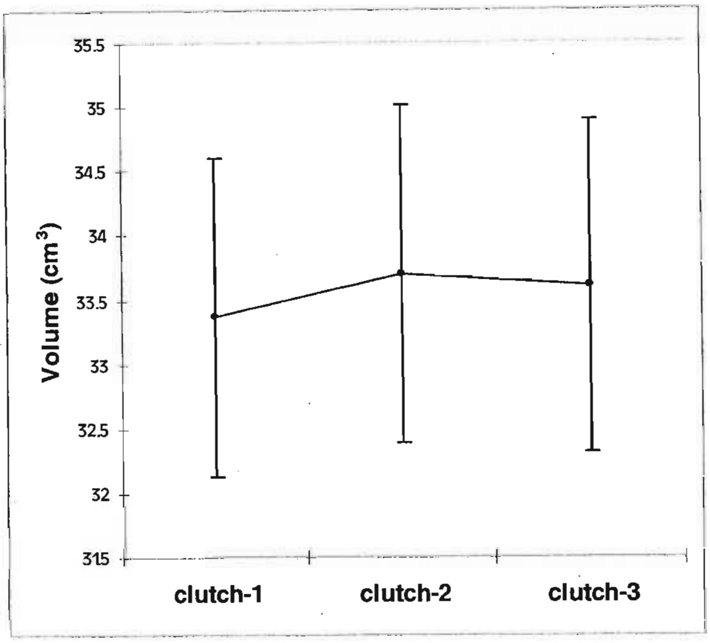


Figure 3.18. Grey-headed Gull egg volumes (means +- 95% confidence limits) from different clutch sizes for all sites during 2004 and 2005.

Incubation

The mean incubation period for Grey-headed Gulls in Gauteng was 24.9 days (min=23 days, max=27 days, n=22 nests, 35 eggs). A total of 193 nest hours was spent observing 12 nests with incubating adults and details of these observations are given in Table 3.6. Incubation was split almost equally between the sexes with males incubating slightly longer than females. Male incubation shifts were on average longer but there was greater variation in their duration when compared to females. Males spent more time at the nest, when not incubating, compared to females and participated in more aggressive encounters than females. Incubation shifts at first light (i.e. first shifts) were mostly by females (n=17) and to a lesser extent by males (n=12) The duration of first shifts for males was more variable than the duration of first-shifts for females (Figure 3.19). When females were incubating, the mean time of first-shift relief by males was 7h50, and when males were incubating, the mean time of first-shift relief by females was 8h03. The duration of second shifts was more variable for females. The temporal spread of the proportion of time that each sex invested in incubation is illustrated in Figure 3.20. The longest incubation shifts were in the morning, the midpoint of these shifts being between 7h30 and 8h30, and were mostly by males. Females incubated more frequently during mid-morning and were replaced by males towards mid-day. Shifts were generally shorter towards mid-day, between 11h30 and 13h30, compared to morning shifts.

Table 3.6. Duration and proportions (%) of male and female Grey-headed Gull incubation shifts, nest attendance (while opposite sex was incubating), and numbers of aggressive encounters. Data coming from 193 hours of observations at Lakefield Pan, Gauteng during 2005.

	Incubation total		Incubation shifts			Attendance		
Sex	minutes	%	n	mean	sd	total minutes	%	Aggressive encounters
male	6062	52.3	81	74.8	57.8	1616	60.1	297
female	5522	47.7	83	66.5	42.9	1075	39.9	102

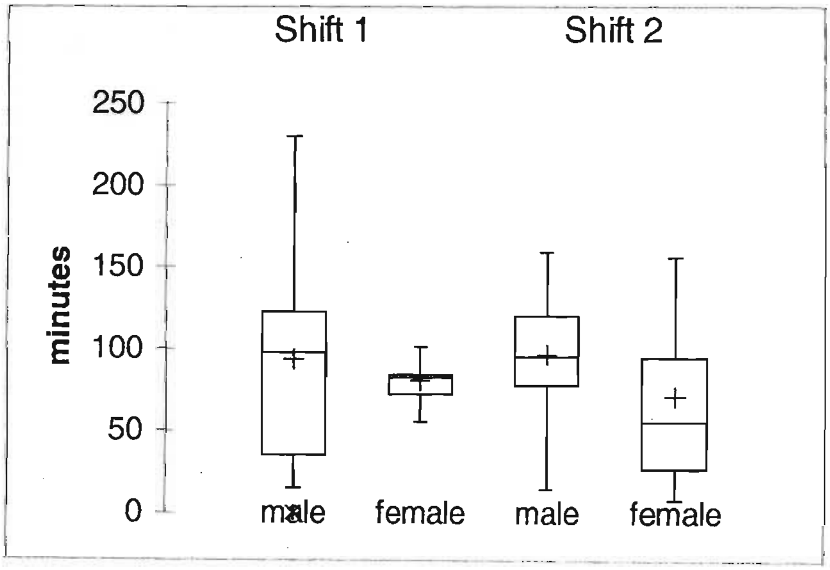


Figure 3.19. Box and whisker plots of durations of first and second incubation shifts (since sunrise) for male and female Grey-headed Gulls at Lakefield Pan, 2005.

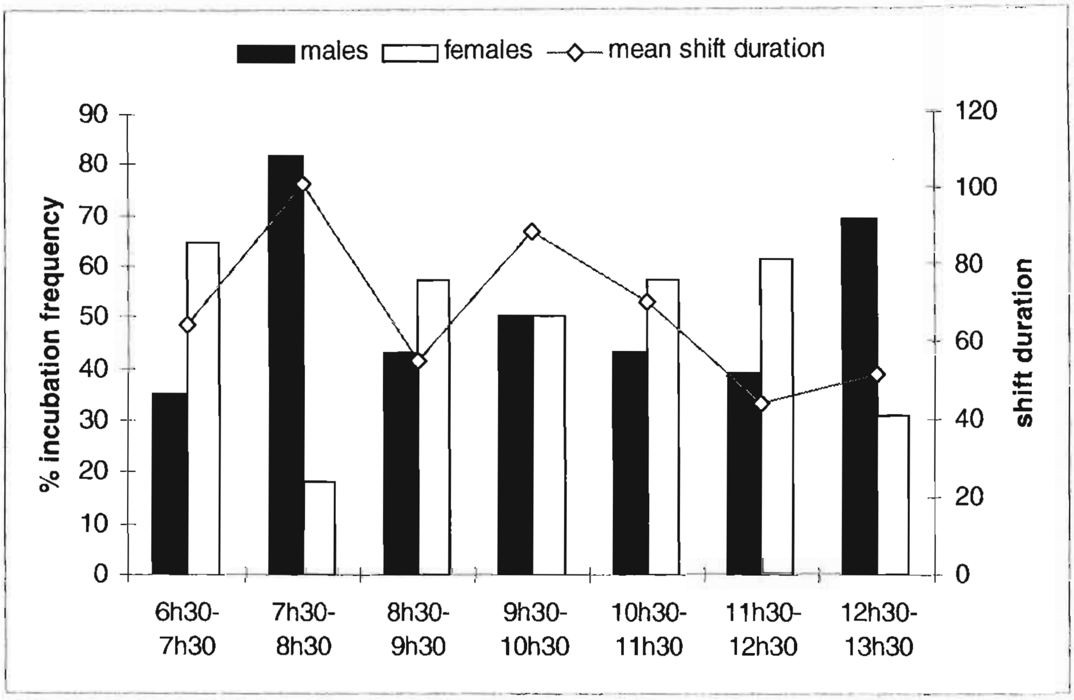


Figure 3.20. Proportionate (%) investment by male and female Grey-headed Gulls in incubation for different time categories and mean shift durations (minutes) for both sexes at Lakefield Pan, 2005.

Egg survival

General Linear Model

The original dataset of 2161 entries was reduced to 1377 entries based on the elimination of the following unfeasible entries:

1. the number of eggs at the start of the observation period was zero (i.e. all the eggs had hatched), and
2. the number of eggs at the end of the observation period was greater than at the start of the observation period (i.e. the possibility of another female laying her eggs in the same nest).

Empirical models

The results of the different empirical models are given in Table 3.7 and are listed below:

E0 – this model gave a constant daily egg survival of 0.928668 and had an AIC of 1365; this was used as the baseline with which all other models were compared.

E1 – this model estimated that the greater the time elapsed between successive visits, the greater the chance of eggs being lost. Incorporation of this model greatly reduces the AIC value compared with the previous model indicating its superiority.

E2 – this model shows that the inclusion of clutch size has little influence on the AIC value when compared to E1 (by only two units). Nevertheless, three-egg clutches had the highest probability of survival.

E3 – this model revealed that different colonies had a statistically significant influence on the determination of egg survival, with Bonaero Park 2004 having the highest egg survival rate and Lane Island having the lowest egg survival rate. The AIC value was markedly affected by the inclusion of this variable.

E4 – the inclusion of sub-colonies in colonies as a factor greatly reduced the AIC value, again indicating superiority.

E5 – results of this model indicate that by including the effects of both clutch size and colony does not improve the model.

E6 – similarly, including the combined effects of clutch size and sub-colony does not improve the model.

E7 – results of this model indicate that the greater the number of days since incubation started, the greater the chance of eggs being lost; inclusion of this factor greatly improves the model.

E8 – the inclusion of hatching synchrony as a variable has a marked improvement on the model, with eggs laid before the mean laying date having a higher chance of survival than eggs laid after the mean starting date.

E9 & E10 – these models replicate E7 and E8, except that they replace the inclusion of colony with sub-colony, and show an improvement of the model.

E11 – results of this model show that by allowing the effect of incubation to be quadratic rather than linear greatly affects the AIC value; this model has the best fit of all the models and was chosen as the final model.

The final model is (standard errors in parenthesis):

$$\text{Logit}(p) = 4.98\ (\pm 1.21) - 0.3236\ (\pm 0.0630)*\text{Elapsed} + 0.0537\ (\pm 0.0466)*\text{Incubation} - 0.0048\ (\pm 0.00113)*(\text{Incubation})^2 - 0.0854\ (\pm 0.0161)*(\text{Laying synchrony}) + (\text{Clutch size effect}) + (\text{Sub-colony effect}).$$

The parameter estimates for clutch size and sub-colony are shown with their standard errors in the last column of Table 3.7.

Model interpretation

Variation in daily egg survival as a function of laying synchrony, for the final model E11, is illustrated in Figure 3.21. Grey-headed Gulls laying earlier than the mean laying date had higher daily egg survival rates than those laying later than this date. This was especially pronounced for those birds breeding at Lane Island. The effect of clutch size had little influence on the outcome of this parameter. The probability of an egg surviving between successive visits as a function of the number of days elapsed during this time is shown in Figure 3.22. Generally, the shorter the period of time elapsed between observations, the higher the probability of an egg surviving. This factor had little effect on Bonaero Park South during 2004 but had a marked influence on Lane Island where the number of eggs surviving declined rapidly when the period between successive visits was longer than five days. The daily egg survival rate as a function of the number of days that the eggs have been incubated was mostly negatively influenced towards the end of the incubation period (Figure 3.23). For Lane Island this was especially apparent after the second week of incubation, while most sites in Gauteng experienced a drop in daily egg survival towards the end of the incubation period, i.e. 23 to 27 days. Variations in the co-efficients for each sub-colony for the final model are illustrated in Figure 3.24. Lane Island was the only site that was statistically significantly different from zero. There were no significant differences between the three different clutch sizes in the final model (Figure 3.25, Table 3.7). However, three-egg clutches had the highest probability of survival and one egg clutches had the lowest probability of survival. The accuracy of the final model is depicted in Figure 3.26. There was a slight tendency for the model to over-predict the survival of one egg, and to under-predict the survival of three and four eggs. Despite these differences the overall difference between the observed and the predicted number of eggs surviving was small.

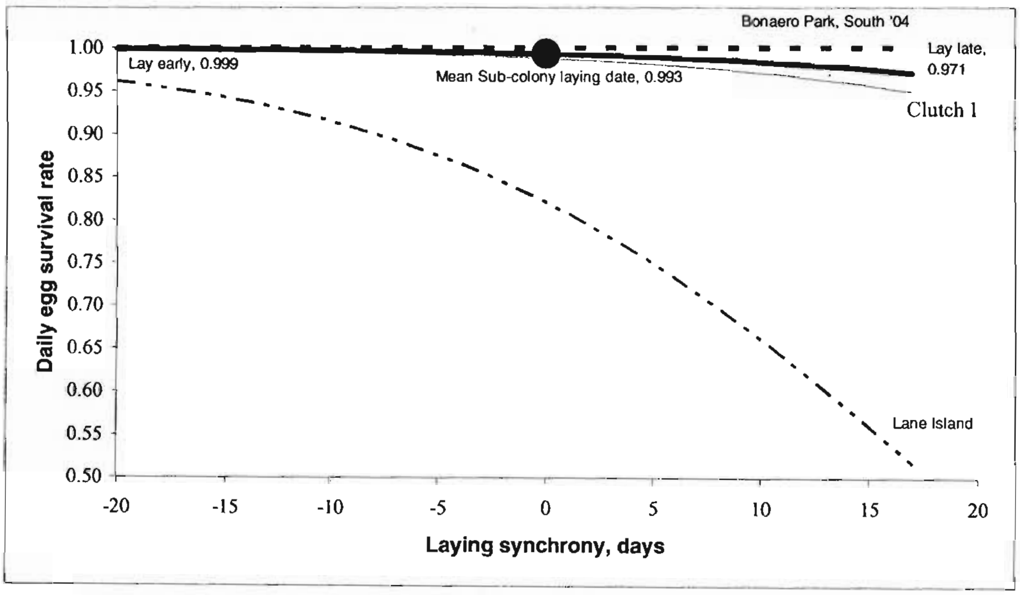


Figure 3.21. The influence of laying synchrony on daily egg survival rates for Grey-headed Gulls during 2004 and 2005. Solid line represents Bonaero Park East (2004), at 15 days after incubation had started and assuming that the eggs were checked every day, i.e. after one day had elapsed. Hatched lines represent sub-colonies with highest and lowest survival rates. Negative numbers on x-axis indicate that females laid earlier than the mean laying date and positive numbers indicate laying later. Data from best fit General Linear Model E11.

Table 3.7. Grey-headed Gull daily egg survival model parameters showing empirical model estimates. Bold values denote statistical significance.

					Empirical models						Empirical models			
Variable	**Levels**	**E_0**	**E_1**	**E_2**	**E_3**	**E_4**	**E_5**	**E_6**	**E_7**	**E_8**	**E_9**	**E_{10}**	**E_{11}**	**s.e.**
Constant		**2.5664**	**4.0530**	**3.4490**	**3.6860**	**4.1800**	**3.0510**	**3.6100**	**4.4380**	**5.3940**	**5.3800**	**6.1600**	**4.9800**	1.2100
Elapsed, days			**-0.5024**	**-0.5006**	**-0.3978**	**-0.4190**	**-0.4004**	**-0.4209**	**-0.2914**	**-0.2478**	**-0.3068**	**-0.2513**	**-0.3236**	0.0630
Incubation, days									**-0.0875**	**-0.1267**	**-0.0924**	**-0.1363**	**0.0537**	0.0466
(Incubation, days)^2													**-0.0048**	0.001
Laying synchrony										**-0.0594**		**-0.0728**	**-0.0854**	0.0161
Clutch size	C 2			0.483			0.555	0.557	0.331	0.464	0.587	0.4650	0.4050	0.357
	C 3			**0.751**			**0.75**	**0.698**	**0.895**	**0.759**	**0.842**	**0.6810**	0.5690	0.355
	C 4			-0.083			0.025	0.464	0.469	-0.069	0.704	0.3710	0.1780	0.786
Site	Bonaero Park 05				0.553		0.639		0.582	0.241				
	Bonaero Park 04				**0.654**		**0.628**		**0.77**	0.476				
	Korsman's B.S.				0.064		0.111		**0.471**	**0.602**				
	Lane Island				**-1.204**		**-1.16**		**-2.53**	**-3.353**				
	Modderfontein Pan				0.452		0.424		0.44	0.45				
Sub-colony	Bonaero South 04					**5.22**		5.23			5.29	5.21	5.37	5.42
	Bonaero West 04					-0.05		-0.01			-0.5	-0.7	-0.83	1.13
	Bonaero EastA 05					0.18		0.07			-0.05	0.4	0.28	1.15
	Bonaero EastB 05					-0.12		-0.12			-0.36	-0.08	-0.26	1.17
	Bonaero North 05					-0.7		-0.81			-1.29	-1.05	-1.24	1.13

Table 3.7 (continued).

					Empirical models						Empirical models			
Variable	**Levels**	**E_0**	**E_1**	**E_2**	**E_3**	**E_4**	**E_5**	**E_6**	**E_7**	**E_8**	**E_9**	**E_{10}**	**E_{11}**	**s.e.**
	Bonaero SWA 05					-0.04		-0.08			-0.63	-0.43	-0.65	1.13
	Bonaero SWB05					-0.54		-0.58			-0.85	-0.83	-0.96	1.12
	Bonaero WestA 05					-1.26		-1.28			-1.14	-0.78	-0.93	1.12
	Bonaero WestB 05					-0.31		-0.36			-0.85	-0.5	-0.6	1.16
	Korsmans B.S.					0.24		0.18			0.05	-0.04	-0.12	1.11
	Lakefield Pan A					-0.44		-0.49			-0.35	0.09	0.03	1.12
	Lakefield Pan B					-0.32		-0.31			-0.23	0.19	0.12	1.11
	Lane Island					-1.58		-1.6			**-3.33**	**-4.01**	**-3.43**	1.13
	Modderfontein A					0.59		0.51			0.26	0.57	0.42	1.14
	Modderfontein B					-0.96		-0.99			-1.33	-1	-1.29	1.14
R^2 (%)		69.13	74.02	74.07	74.87	75.33	74.91	75.36	75.62	76.01	75.99	76.5	76.57	
Deviance		1365	1211	1203	1171	1140	1165	1136	1109	1091	1081	1059	1042	
D.o.F.		1376	1375	1372	1370	1360	1367	1357	1366	1365	1356	1355	1354	
Outliers		15	17	17	19	18	19	18	19	14	15	14	13	
Influential points		0	19	52	93	20	52	28	63	58	29	28	39	
Delta deviance		-	154	162	194	225	200	229	256	274	284	306	323	
Delta D.o.F.		-	1	4	6	16	9	19	10	11	20	21	22	
Significance		-	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	
G.o.F.(Chi-squared)		178.6	167.2	168.5	170.4	171	171.5	171.7	170.1	171.5	171.3	172.6	169.5	
Significance		1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	
Parameters, K		0	1	4	6	16	9	19	10	11	20	21	22	
A.I.C.		1365	1213	1211	1183	1172	1183	1174	1129	1113	1121	1101	1086	
Delta A.I.C.	Min = 1086		1213	1211	1183	1172	1183	1174	1129	1113	1121	1101	1086	

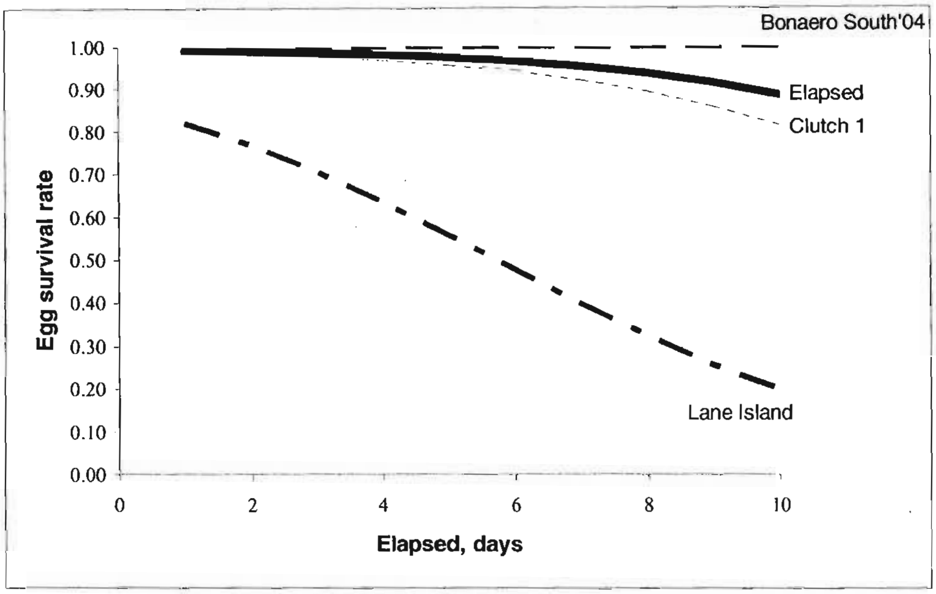


Figure 3.22. The influence of the number of days elapsed between successive nest visits on the probability of eggs surviving (egg survival rate) from their first to second inspections. Solid line represents Bonaero Park East (2004) assuming that eggs were laid at the mean laying date for its sub-colony, a clutch of three was being observed, and eggs have been incubated for 15 days. Hatched lines represent site-sections with highest and lowest survival rates. Data from best fit General Linear Model E11.

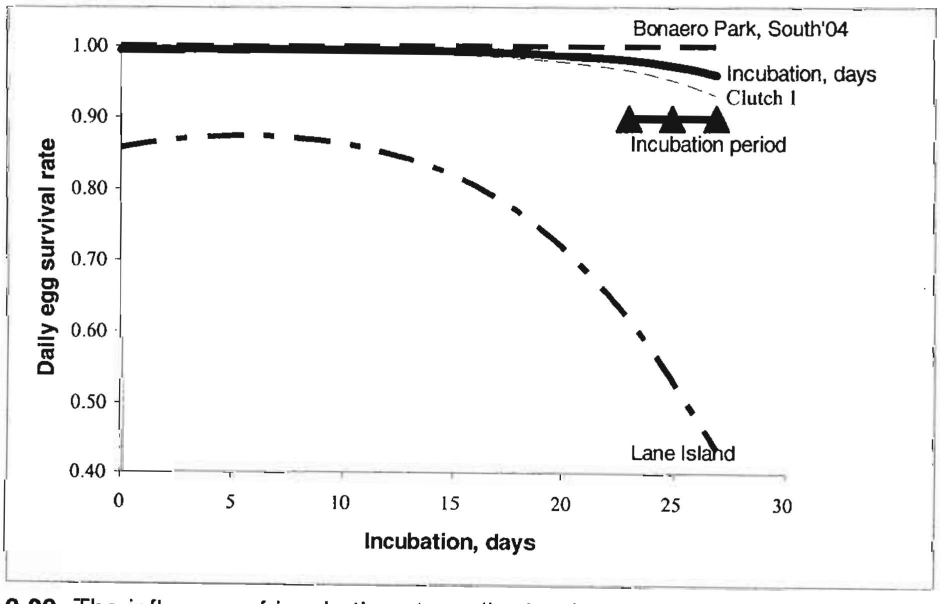


Figure 3.23. The influence of incubation stage (in days) on daily egg survival rates for Grey-headed Gulls. Solid line represents Bonaero Park East (2004) assuming that eggs were laid at the mean laying date for its sub-colony and a clutch of three was being observed. Incubation period (line with triangles) spans 23 to 27 days with a mean of 25 days. Hatched lines represent site-sections with highest and lowest survival rates. Data from best fit General Linear Model E11.

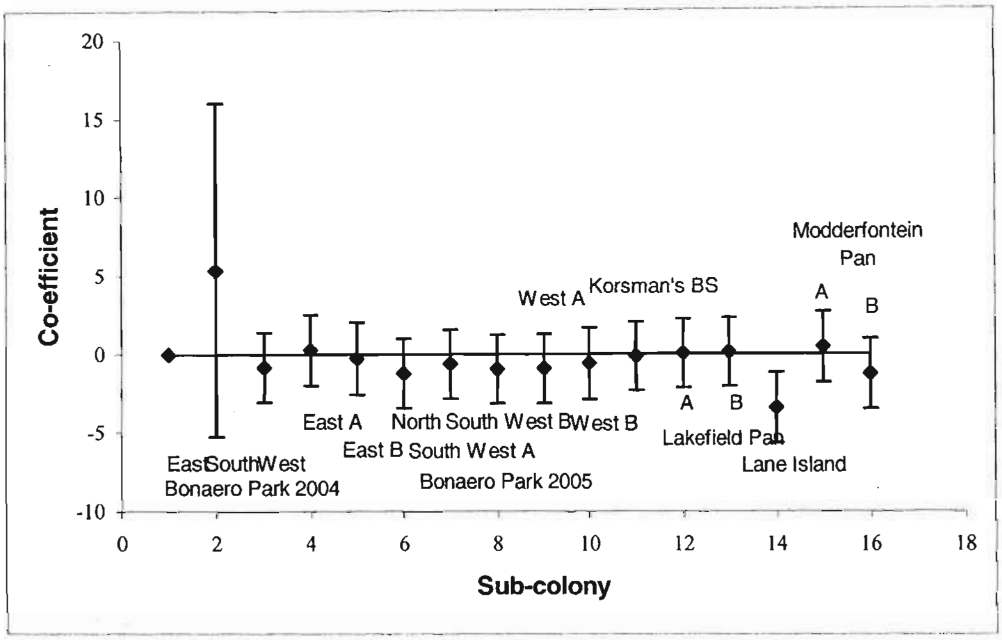


Figure 3.24. Variation in coefficients (means +- 95% confidence limits) for all sub-colonies for the final model E11.

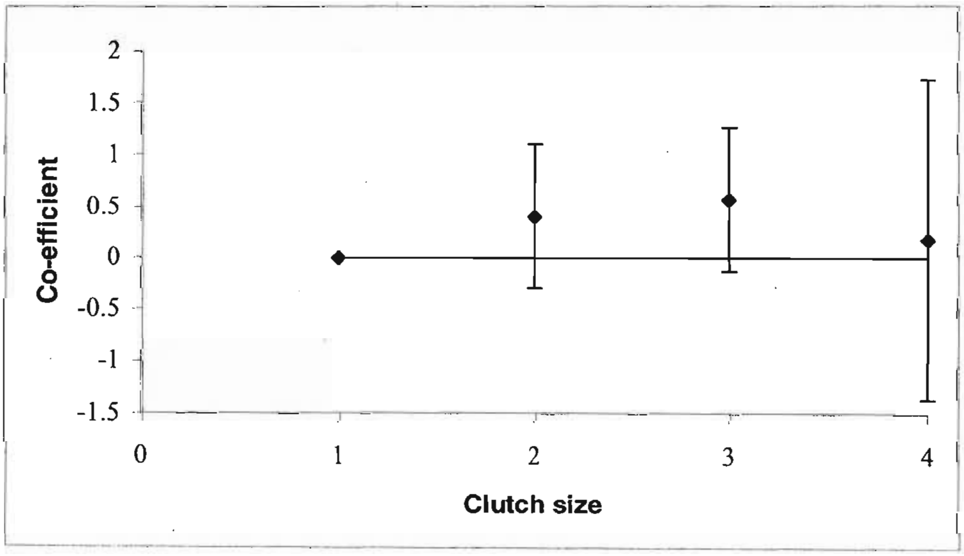


Figure 3.25. Variation in coefficients (means +- 95% confidence limits) for different clutch sizes for the final model E11.

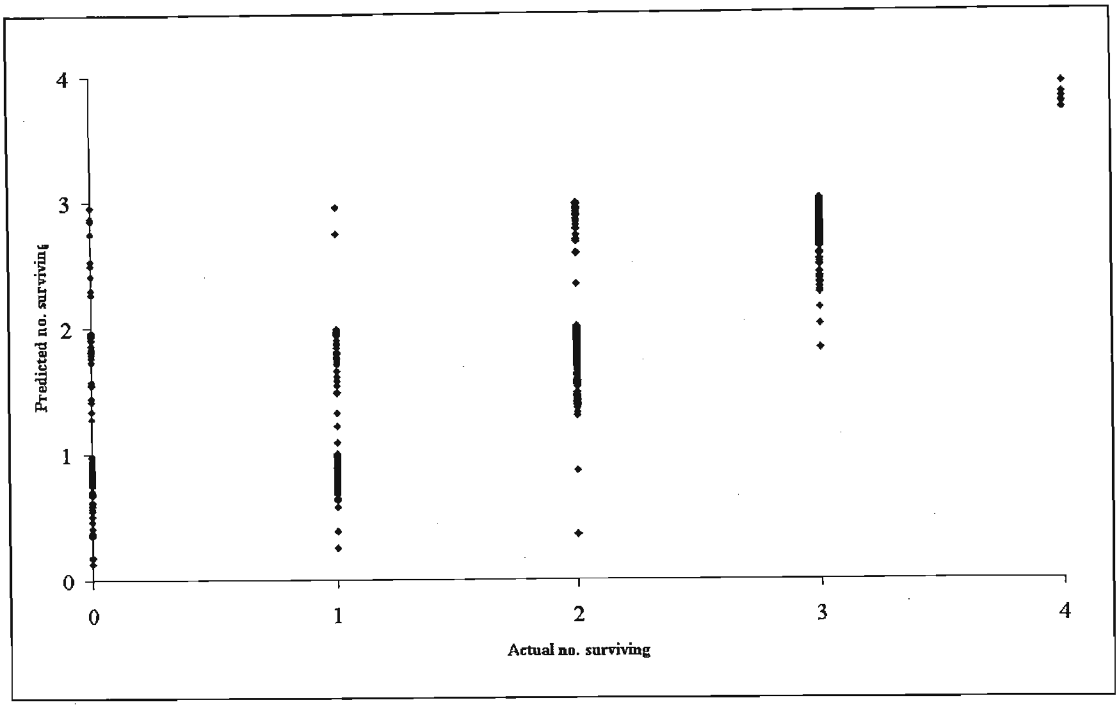


Figure 3.26. Accuracy of model E11: comparing number of eggs predicted to survive with the number of eggs that actually survived.

Discussion

Site selection

Breeding sites that were occupied more frequently, both during this study and during the CWAC counts (Table 2.1.), were located in suburban Benoni (i.e. Bonaero Park, Stewards Pan, and Korsman's Bird Sanctuary). These sites exist within an area that has been regularly occupied by Grey-headed Gulls since the earliest breeding record of this species in Gauteng during 1947 (Brooke *et. al* 1999). The abundance of suitable breeding wetlands and the close proximity to landfill sites have already been discussed as important reasons influencing their presence here (Chapter 2). The location of these three regularly used sites is within the core of their breeding range in eastern Gauteng. Outside of this core, and towards the other breeding localities eastward of this area, wetlands become typically more ephemeral in nature and are surrounded by mostly agricultural landuses. The capricious nature of this area in terms of supplying suitable breeding localities would influence the regularity at which these sites are occupied. Despite the abundance of wetlands and pans in Gauteng, results from this study indicate that only a few sites are used by Grey-headed Gulls for breeding. The excess of apparently suitable nesting localities, as was identified by the aerial and ground surveys, suggests that the availability of breeding sites in Gauteng is not a limiting factor to the Grey-headed Gull population here.

Laying period

Grey-headed Gulls have been recorded breeding in Gauteng during all months of the year (Brooke *et al.* 1999). Breeding numbers are relatively low during the summer months and the majority of birds breed during winter. This is evident, not only in the numbers of birds recorded breeding during different months (e.g. results of CWAC data and this study), but also in the high incidence of adults undergoing complete moult during summer (i.e. during the non-breeding season) and the seasonal movements of birds in and out of the breeding season (e.g. Allan *et al.* 2002, Chapter 2). Results from this study, Brooke *et al.* (1999) and CWAC data indicate that the majority of Grey-headed Gulls breed between May and September in Gauteng, with a peak in breeding activity during July and all records of Grey-headed Gulls breeding at Lake St Lucia have been during winter (Brooke *et al.* 1999). The unpredictable nature of flooding during the wetter months may be a deterrent for birds breeding during summer and rising water levels have been known to have devastating effects on Grey-headed Gull colonies, e.g. at Korsman's Bird Sanctuary (Hunter 1972). In the winter months at Lake St Lucia, Grey-headed Gulls benefit from receding water levels where they take advantage of an abundance of exposed aquatic invertebrates (Chapter 2). The laying period of the Grey-headed Gull is similar to that of the Silver Gull *Larus novaehollandiae* in Australia (Higgins & Davies 1996) and the Hartlaub's Gull *Larus hartlaubii* (Ryan 1987). Timing of breeding in these species has been invariably attributed to peak rainfall periods and the association of this period with the availability of food (Ryan 1987; Higgins and Davies 1996).

Oometrics

Laying synchrony

The evolution of coloniality in nesting seabirds appears to be highly correlated with the exposure of nests to predators (Clode 1993; Rolland *et al.* 1998; Oro *et al.* 1999) and Tinbergen (1967) suggested that the evolution of coloniality in Black-headed Gulls *Larus ridibundus* was an adaptation to predation pressure. An important measurable aspect of coloniality in seabirds is that of laying synchrony and this is said to be influenced by predation (Lack 1968; Nisbet 1975). Predation is thought to have an influence on this breeding parameter by the 'swamping' effect whereby each nest has a higher chance of survival, during periods of intermittent predation, than would occur if that nest was isolated and had more chance of selection by the would-be predator (Lack 1968). Predation on Grey-headed Gull eggs by African Fish Eagles at Lake St Lucia's Lane Island during this study ultimately led to the complete breeding failure of this colony. While these predators were the proximate factor in egg mortality, a shortage of fish in the St Lucia system at the time (Cyrus *et al.* 2004) was probably the ultimate cause of nest failure, forcing the African Fish Eagles to seek alternative food sources. The circumstances (i.e. drought conditions) surrounding this event were exceptional for this system during 2004, and it is unlikely that this level of nest predation would have been experienced regularly by Grey-headed Gulls in previous years. In comparison with the Gauteng nesting sites, breeding colonies of Grey-headed Gulls at Lane Island are more likely to experience higher levels of predation, even in wetter years. This is because the location, extent and condition of Lake St Lucia's habitats lends itself to hosting a greater abundance and diversity of prospective predators than would be expected at the Gauteng sites. Grey-headed Gulls are therefore predicted to have a higher degree of laying synchronicity during most years at Lake St Lucia that is probably exacerbated during periods of intensive predation pressure, as was the case during this study.

The differences between mean laying dates for Grey-headed Gull sub-colonies at Bonaero Park during 2005 suggested a preference for birds to breed in sub-colony West A. Nest sites in this sub-colony were typically insular, being dispersed on small islands of *Persicaria lapathifolia* stems. An advantage of selecting more insular and open sites, as opposed to sites within continuous stretches of vegetation, is the earlier detection of predators (Meathrel 1990) which in this instance was provided by a moat of open water. This section was also in close proximity to a continuous stretch of marsh grass *Leersia hexandra* that probably provided the chicks with both concealment, from aerial predators, and cover, from wind and sun (e.g. Nisbet 1975), while still affording them nearby access to the open water.

Clutch size

Crawford & Hockey (2005) give a mean clutch size of 2.5 eggs (n=73 clutches) for Grey-headed Gulls in southern Africa and Britton & Brown (1974) give means of 2.4 eggs (n=82 clutches) and 2.47 eggs (n=230 clutches) for Grey-headed Gulls at Lake Victoria and Lake Elmenteita in East Africa, respectively. The mean clutch size of 2.42 eggs recorded for Grey-headed Gulls in this study is therefore similar to these authors' results. A comparison between clutch sizes and oometric data for other masked gull species shows Grey-headed Gulls to be most similar to Black-headed, Brown-headed *Larus brunnicephalus* and Brown-hooded *Larus maculipennis* gulls (Table 3.8). These species have significantly higher average clutch sizes than the other species in this masked gull group which may be related to beneficial environmental conditions.

Table 3.8. Mean clutch sizes of eight masked gull species.

Species	Common name	Clutch size (mean)	Reference
Larus genei	Slender-billed Gull	1.5	del Hoyo et. al 1983
Larus ridibundus	Black-headed Gull	2.54	del Hoyo et. al 1983
Larus brunnicephalus	Brown-headed Gull	2to3	Ali & Ripley 1969, Roberts 1991
Larus maculipennis	Brown-hooded Gull	2.6	Burger 1974
Larus cirrocephalus	Grey-headed Gull	2.42	this study
Larus hartlaubii	Hartlaub's Gull	1.8	Hockey & Crawford 2005
Larus novaehollandiae	Silver Gull	2.1	Higgins & Davies 1996
Larus bulleri	Black-billed Gull	1.85	Higgins & Davies 1996

The high incidence of two-egg clutches in Lane Island, Lake St Lucia during this study may have been influenced by the effect of drought conditions on the availability of food to breeding Grey-headed Gulls. These conditions, prevalent since the estuary mouth closed off during June 2002, had adverse affects on juvenile fish stocks and marine crustaceans in the system (Cyrus *et al.* 2004). The egg-production hypothesis

(Lack 1968) suggests that clutch size is influenced by the parent's ability to allocate nutrient reserves to egg formation. This reasoning has been proposed for the strong correlations between clutch size and food availability which have been experimentally demonstrated for Lesser Black-backed Gull *Larus fuscus* (Bolton *et al.* 1992) and Nazca Booby *Sula granti* (Clifford & Anderson 2001) and may explain a reduction in average clutch size for Grey-headed Gulls at Lane Island. A compounding factor may have been the influence of predation by African Fish Eagles forcing Grey-headed Gulls to lay replacement clutches. Food availability has been shown to have significant influences on the size of replacement clutches, as compared to original clutch sizes, in Silver Gulls (Mills 1979).

Egg dimensions

Intra-clutch variation

There are two hypotheses that explain substantial variation in egg size within a clutch. The first hypothesis, based primarily on Lack's (1968) insight into the effects of asynchronous hatching, concerns the 'third-chick disadvantage' where the third and final egg in the laying sequence is the smallest egg in the clutch, a common occurrence in many gull species (for review see Pierotti & Bellrose 1986). Consequently, this third egg produces a smaller chick that hatches later than its siblings which ultimately reduces its chance of survival. This has been attributed to an adaptive strategy whereby adults deliberately reduce the survival probability of the 'third chick' by investing less in its energy reserves, during egg production, and by commencing incubation prior to the third egg being laid. The outcome is a chick that provides little competition to its siblings in times of unpredictable food shortage with the result that it starves, thereby relieving the parents of fulfilling an unattainable objective (Hahn 1981). Other authors have questioned this reasoning and have given evidence to suggest that variation in egg size is a facultative response to varying food availability, which is influenced by parental age and colony density (Mills 1979; Pierotti & Bellrose 1986; Sydeman & Emslie 1992). Both these hypotheses could explain the variation in egg size documented for clutches in this study. However, the lack of any significant differences in size between first-, second- and third-laid eggs suggests that a more facultative explanation is more convincing and would also explain the discrepancies in egg size between two and three-egg clutches. This is probably attributable to the variation in parental condition and age within and between sites as well as food availability and the influences of territoriality as is related to colony density. Clearly, this limited sample size would have to be bolstered for a more accurate interpretation.

Inter-clutch variation

A number of researchers have postulated, and sometimes demonstrated, the causal effects of the variation in inter-clutch egg sizes. Some of these factors are listed below:

1. Availability of food – egg production imposes a physiological stress on females which results in an increased demand for food, the quantity and nutritional status of which influences egg size and mass (Meathrel & Ryder 1987; Pons 1992; Kilpi *et al.* 1996 and references therein).
2. Difference in laying dates – gulls breeding earlier in the season tend to have larger eggs than those breeding later in the season (Mills 1979; Sydeman & Emslie 1992; Oro 2002).
3. Parental quality – generally egg size increases with female age to an asymptote after which egg size decreases (Mills 1979; Coulson *et al.* 1982; Sydeman & Emslie 1992); egg size has also been shown to be positively associated with the age of the male (Ryder 1975; Mills 1979); the influence of adult body weight on egg size has been shown to have a positive correlation (Mills 1979); and gulls that retain their pair bond between successive breeding years have been demonstrated to have larger eggs than those that do not (Mills 1979 and references therein).
4. Density of the colony – generally a decrease in colony density results in an increase in egg size (Schreiber *et al.* 1979; Coulson *et al.* 1982; Pierotti & Bellrose 1986).
5. Incidence of replacement clutches – depending on the prevailing conditions replacement eggs are known to differ in size when compared to original clutches (Mills 1979).

None of these factors are mutually exclusive. For instance, while food availability and abundance may be constant for a given colony, there may still be great variation within egg sizes between different clutches. This could be attributed to the quality of the parental birds, expressed by their foraging efficiency, which is largely influenced by their age and therefore experience. Mills (1979) was able to show that older Silver Gulls still produced large eggs at the beginning of the season despite a comparatively reduced food supply. These birds were efficient foragers able to exploit limited food supplies and thereby initiate breeding earlier than less experienced birds. He also demonstrated that these older birds laid larger eggs in replacement clutches (when compared to their original clutches) during peaks in food abundance. Furthermore, the amount of food available to each nesting pair is density dependent and will be influenced by the size of the breeding colony, which ultimately affects certain breeding parameters. Coulson *et al.* (1982) in their study of the influence of intensive culls on certain breeding parameters of the Herring Gull *Larus argentatus*, established that younger sub-adult birds that had previously been recorded with smaller eggs than their older counterparts, and that had now replaced these birds at lower breeding densities, started producing even larger eggs than was previously recorded for older birds. They attributed these findings to a decrease in competition for available food as well as a reduction in energy expended due to territorial confrontations commonly associated with dense colonies. These studies highlight the need to consider various factors in combination with one another when ascertaining causal relationships with egg size variability. They emphasize the overarching effects of food availability and the confounding nature of other variables that operate within these hypothetical boundaries.

The inter-clutch variation in egg measurements from this study showed some significant differences, especially between different sites studied during the same period. These included the comparatively larger egg sizes recorded at Modderfontein Pan and the significantly smaller egg sizes recorded at Lakefield Pan. The location of Modderfontein Pan is unique in the context of the distribution of Grey-headed Gull breeding sites in Gauteng. It is situated approximately 25 km from the nearest known breeding site and unlike the typical suburban habitat occupied by the majority of breeding birds, is surrounded by mostly agricultural land-uses. From what is known, Grey-headed Gulls bred for the first time at this site and in previous years this pan was mostly dry; water was artificially pumped into this pan for the first time during 2005 (D. Duvenaag pers. comm.). What then has deemed this site beneficial in terms of breeding success, as has been expressed in the comparatively large eggs that these birds produce? A notable characteristic of this colony, recorded during this study, was the significantly larger nearest neighbour distances probably influenced by the comparatively small number of breeding pairs at this site (Table 2.2). This site was also in close proximity to a chicken abattoir where Grey-headed Gulls were observed feeding on chicken off-cuts (Plate 4.3). Adult birds were also noted foraging within the dam adjacent to this abattoir on sub-surface invertebrates, probably Diptera (midge) larvae (see Chapter 4). The apparent abundance of more natural food items at this site together with a relatively small colony may have provided breeding birds with favourable conditions with reduced competition both for food and for nest sites. Ageing of these birds during this study was not possible and it is unknown whether these were older more experienced birds; I did not note any sub-adult birds here.

In contrast to this site, Lakefield Pan is situated within the core of the Grey-headed Gull breeding distribution and nests at this site were the most densely spaced of all sites recorded. Observations at this site also revealed the presence of a number of young birds, and even sub-adult birds, probably breeding for the first time; this was confirmed from re-sightings of colour-ringed known-age birds (see Chapter 5). At the time of my observations at Lakefield Pan, there were four additional Grey-headed Gull breeding colonies within 8 km of this site (Figure 2.1). Re-sightings of colour-ringed birds from these colonies, including Lakefield Pan, have confirmed, that at least in part, these birds utilize the surrounding landfill sites for feeding purposes. Lakefield Pan birds were therefore likely to have experienced increased levels of competition for food at these landfills during this time, which would have been compounded by the relative inexperience of some of these birds. Furthermore, the high densities of birds at this site would have induced extra demands on energy reserves due to territorial confrontations. In summary, the circumstances of Grey-headed Gulls breeding at Lakefield Pan during 2005, viz. under high densities, of relatively low. parental quality, in a densely populated region, would have been conducive to the production of eggs of comparatively smaller dimensions.

A comparison of Grey-headed Gull egg dimensions for all sites during this study with other samples is shown in Table 3.9. These results show eggs from this study to be smaller than those of all other samples. Interestingly, egg dimensions recorded by

James (1970), a large proportion of which were from eggs at Lake St Lucia, were larger than those recorded at the same site during this study and this suggests that conditions during these historical times were more favourable. This implies that the drought conditions during 2004 may have not only affected clutch size but also average egg sizes. The availability of food resources is known to influence both of these parameters in other species, although there are conflicting ideas as to which

Table 3.9. Comparative Grey-headed Gull oometric data from various localities within southern and East Africa including data from this study.

		Length			Breadth			
Locality	**No. eggs**	**min**	**max**	**mean**	**min**	**max**	**mean**	**Reference**
South Africa	793	41.9	58.5	51.4	29.9	40	36.7	This study
East African lakes	100	49.2	60.6	53.9	32.3	41.4	37.3	Britton & Brown 1974
Southern Africa, 86% St Lucia	22	49.8	58	53.6	35.5	40.7	37.9	James 1970
South Africa, Brandvlei	9	50.9	57.6	54.1	36.8	39.2	38.2	McLachlan 1955
Zimbabwe, Lake Kariba	20	50.4	56.3	53.9	33	39.1	37.1	Worsley & Worsley 1986

parameter is affected first (Mills 1979; Coulson & Horobin 1986; Kilpi *et al.* 1996). Like Lake St Lucia, all other localities where oometric data were recorded are situated in more natural areas, and with the exception of the east African sites, had comparatively smaller populations than those recorded in Gauteng during this study. This may reflect a similar situation as was suggested for Modderfontein Pan where an alleviation in competition for resources together with potentially more favourable (natural) food items and reduced competition for space at the breeding colony, would have benefited breeding adults during egg production.

The general tendency for eggs from two-egg clutches to have higher volumes than eggs from three-egg clutches mirrors the findings of Mills (1979) with Silver Gulls. This author likened this phenomenon to the ability of females to determine whether a third egg was to be laid during the production of the second egg, i.e a comparatively smaller second egg was produced if a three-egg clutch was anticipated.

Incubation

The incubation period for Grey-headed Gulls, recorded during this study, is similar to that of Hartlaub's Gull, i.e. 25 days (Williams 1990); molecular techniques have revealed these two species to be each others closest relatives (Given *et al.* 2005). The proportion of time that each sex contributes to incubation varies between different gull species. Great Black-backed Gull *Larus marinus* females are known to invest significantly more time in incubation than males (Butler & Janes-Butler 1983), whereas Sabine's *Larus sabini* (Stenhouse *et al.* 2003), Slaty-backed *Larus schistisagus* (Watanuki 1992) and Black-headed (Cramp & Simmons 1983) gulls separate incubation duties in almost equal proportions. Grey-headed Gulls would appear to be similar to the latter group. All observations during this study took place during the first half of the day, i.e. from sunrise to just after noon, and the small discrepancy between male/female incubation shifts can probably be accounted for by the bias associated with observation periods. The high incidence of female birds incubating at first light and the short duration of their incubation shifts before changeover, suggests that they may have fulfilled incubation duties during the evening. In both the Silver and Black-billed *Larus bulleri* gulls only one adult, in a pair, takes on the responsibility of incubating through the evening (Higgins & Davies 1996). If the same were true for the Grey-headed Gull (a close relative of these masked gull species) then birds incubating during the evening would be expected to want to feed as early as possible the following day, after expending large energy reserves during this long and cold incubation shift while not being able to feed. This would explain the absence of females for extended periods after first shift relief as their feeding requirements were probably of the highest magnitude during this time.

The high incidence of aggressive encounters, especially by male Grey-headed Gulls, was probably related to the high nesting density at this site (see discussion above). In other gull species, males usually take on the dominant role in territorial disputes (e.g. Stenhouse *et al.* 2003 and references therein; Butler & Janes-Butler 1983). This could also explain the longer periods of time males spent attending nests while females incubated.

Egg survival

Various methods have been proposed for calculating daily nest survival. These have included: the traditional Mayfield method (Mayfield 1961), the first to take into account the influence of exposure days; variations and improvements of the Mayfield method (e.g. Johnson 1979; Hensler & Nichols 1981; Bart & Robson 1982; Hazler 2004); and methods that incorporate modelling techniques that allow for the influence of certain variables to be assessed (e.g. White & Burnham 1999; Stanley 2000; Dinsmore *et al.* 2002; Shaffer 2004). General linear models that use information-theoretic methods based on AIC have the advantage over other methods in determining which variables and in which combination and form to use in the best-fit model; they avoid subjective bias in determining which variables to include and therefore facilitate comparisons between studies that would otherwise result in uncertainty in model selection (Shaffer 2004).

In this study the final model with the best fit, as determined by the AIC values, included all variables other than 'colony' (Table 3.7). This was because 'sub-colony' accounted for more of the variability in daily egg survival rates than did 'colony' which may be related to varying degrees of overall fitness of birds between strongly cohesive sub-colony groups. For instance, more experienced sub-colonies could occupy more favourable breeding sites thereby preventing excessive egg loss due to rising water levels. Within each sub-colony Grey-headed Gulls laying later than the mean laying date had lower daily egg survival rates than those laying earlier. This phenomenon is probably related to the variation in adult quality with older, more experienced birds laying earlier on in the season and being better equipped to look after their eggs than younger less experienced birds (e.g. Mills 1979). The pronounced effect of this variable at Lake St Lucia was influenced by the high incidence of predation towards the end of the laying period. The slight decline in daily egg survival rates for Grey-headed Gulls in Gauteng towards the end of the incubation period may be related to these birds abandoning or removing infertile or damaged eggs once the outcome of these eggs was confirmed, i.e. after a critical period of incubation investment. It is unlikely that these eggs would have hatched as there was no sign of either chicks or egg-shell fragments at or in the vicinity of these nests. Lane Island was the only site that differed significantly from all other sites in terms of daily egg survival and this was undoubtedly due to the high levels of predation by African Fish Eagles. There was little evidence of egg predation at Gauteng sites and daily egg survival rates for all sites were high.

Conclusion

Important life-history information coming out of this chapter includes the incubation period, the first time it has been determined for this species, as well as differential parental investment during the incubation period. The most compelling difference between the two largest South African breeding populations of Grey-headed Gulls, Gauteng and Lake St Lucia, was the high level of synchronicity in laying dates shown by the latter colony and further research at this site could elucidate if this was an unusual incident influenced by the high levels of African Fish Eagle predation. This chapter has highlighted significant intraspecific differences in oometric data between Grey-headed Gulls at different colonies in Gauteng. The smaller egg sizes of birds breeding in the large 'core' colonies in the suburban areas of the East Rand in Gauteng, compared with the smaller, peripheral and rural Modderfontein Pan site, suggest that density dependent factors may be operating at the former colonies. This study has also provided important insights into factors that limit the daily egg-survival rates of the Grey-headed Gull, such as the relative timing of egg laying and differences at a sub-colony level. The robustness of the model produced for this purpose has ensured that future research into survival rates of this species can be directly compared to the findings of this study. This information is important as it is directly associated with breeding success and hence population dynamics.

Chapter 4

Breeding Biology of the Grey-headed Gull *Larus cirrocephalus* in Gauteng Province, South Africa – the chick stage

Summary

The chick stage of the Grey-headed Gull's *Larus cirrocephalus* breeding biology was studied at three sites in Gauteng, Bonaero Park, Lakefield Pan and Modderfontein Pan, between May and July 2005. Repeat measurements of 326 chicks from 168 nests were used to generate empirical growth curves for measurements of mass, wing, head, culmen, tarsus and foot. A comparison with Swift Tern *Sterna bergii* chicks (Le Roux 2006), the only other species for which this empirical approach to generating growth curves has been used, reveals similar patterns of chick development, other than for culmen growth. Standardized growth rates (z-scores) were calculated to compare differences between Grey-headed Gull chicks from different colonies, between chicks of different hatching order both within and between colonies, and between chicks from different laying dates. Growth rates differed significantly between chicks from different colonies in foot and wing measurements but not in mass. The fastest-growing chicks were from Modderfontein Pan, a relatively small colony situated in agricultural land on the periphery of their core breeding range, and the slowest-growing chicks were from Lakefield Pan, a larger colony situated in suburbia within their core breeding range. Last-hatched chicks grew consistently slower than their siblings throughout their development period at all sites, with the exception of Modderfontein Pan, where last-hatched chicks were apparently able to match the growth of their older siblings in the latter period of development as expressed by growth of wing length. The advantages of Modderfontein Pan to enhanced chick development were related to the close proximity of a chicken abattoir and associated dam, as well as the relatively small size of this colony. There were no significant differences between the growth rates of chicks from different laying dates. A sample of 100 regurgitated pellets from 57 nests are compared and related to the differential growth rates between three age groups of chicks from the three sites. For Bonaero

Park and Modderfontein Pan, invertebrates were more prevalent in chick diets during the early stages of development but were gradually replaced, to varying degrees, by other food items as the chicks got older. There was a larger proportion of anthropogenic discards in the diets of chicks from Bonaero Park and Lakefield Pan than at Modderfontein Pan and this is associated with slower growth rates at these sites. The fledgling rate of artificially penned chicks from Modderfontein Pan was 73% compared to 66% for chicks from Bonaero Park. Predation of Grey-headed Gull chicks was only recorded at Modderfontein Pan and this factor is likely to have affected the energy expended, and the concomitant growth rate in mass of these chicks.

Introduction

The chick (i.e. pre-fledging) stage in bird reproduction is a demanding and vulnerable period during which risks of predation and deficiencies in factors associated with parental care, e.g. food provisioning and thermoregulation, often lead to mortality (O'Connor 1984). An important measurement during the chick stage is the rate at which chicks grow, viz. chick growth rates. Lack (1968) hypothesised that the different fledgling periods, i.e. from hatching to flight, between different bird species were influenced by different levels of vulnerability and implied that increased chick growth rates reduced this period of vulnerability of the young. Similarly, Case (1978) accredited juvenile mortality, mainly from predators, and the ability of parents to provision their young as the key factors in determining different growth rates between terrestrial vertebrate species. Ricklefs (1968) showed that both adult body size and precocity of development were important factors in determining growth rates in birds. By using fitted growth rate equations, i.e. where the form, rate and magnitude of the growth pattern can be described quantitatively by the constants of equations which can be fitted to the growth curves, this author was able to compare the growth rates of different species in more detail and concluded that the rate of development of mature function was an important influence in determining overall growth rates. Despite the advances put forward by Ricklefs (1967, 1968, 1973) in describing patterns of growth in birds, the use of growth equations, such as the Gompertz and logistic equations, used by this author in fitting growth curves have certain limitations (e.g. Smith & Diem 1972; Arendt 1997), especially for semiprecocial species whose growth rates are too irregular to be fitted to standard equations (Ricklefs 1968). This is because the data have to be modified in order to fit a standardized growth curve with the result that certain information is lost. This becomes especially relevant when one wishes to compare the growth rates of closely related species, or between different populations of the same species, where all growth data becomes important in interpreting subtle differences.

Growth rates can be used as a measure of intraspecific differences in breeding success. This is because variations in growth rates produce phenotypic variations in measures of fledgling linear body size and mass with a corresponding influence on post-fledgling fitness and survival (Hunt 1972; Alatalo & Lundberg 1986; Richner 1989).

In this chapter I investigate the growth rates of semiprecocial Grey-headed Gull chicks in Gauteng, South Africa, using an empirical approach to generating growth curves, i.e. where the growth curve is fitted to the data rather than the other way around. This is the same method as was used by Le Roux (2006) on Swift Tern and the growth curves generated for Grey-headed Gull chicks in this study are compared to those of that species.

Standardized growth rate values are generated to compare intraspecific differences in growth rates, such as between those of different populations and chicks from different hatch order. I used these values to compare differences in chick growth rates between three sites in Gauteng: Bonaero Park, Lakefield Pan and Modderfontein Pan. Two of these sites, Bonaero Park and Lakefield Pan are situated within suburbia, while Modderfontein Pan is situated in an agricultural area. I also compared the differences in growth rates of chicks from different hatch order, as well as chicks from different laying dates. Causative factors for these differences are discussed, especially with regard to the prevailing environmental conditions and the locations of these sites. I also compare the diet of chicks at all three sites by analysing the contents of chick pellets, regurgitated whilst being measured in the field. Information coming from this dietary analysis is then related to the comparative growth rates at all three sites. Finally, the survival of chicks from a small sample of chicks, enclosed in pens, is compared between Bonaero Park and Modderfontein Pan.

Methods

Grey-headed Gull breeding colonies were studied at three sites: Bonaero Park, Lakefield Pan and Modderfontein Pan in Gauteng Province between 13 May and 15 July 2005.

The same nests that were studied at the egg stage during 2005 at these sites (Chapter 3) were used during this study. Successive nest visits were conducted every two to five days. All chicks from these nests were initially marked with coloured permanent non-toxic ink under the wing until they were approximately three days old after which they were fitted with standard (SAFRING) stainless steel rings. Where possible, hatching order was recorded. The following measurements were taken from all chicks:

1. Mass – each bird was placed in bag and weighed with an Ohaus spring balance to the nearest gram and then the mass of the empty bag was deducted.
2. Wing – measured with a wing rule (with back-stop) as the flattened chord from the carpal joint to the tip of the longest primary, to the nearest mm.
3. Culmen – measured with dial callipers from the tip of the upper mandible to where the rhamphotheca meets with the skin, to the nearest 0.1 mm.
4. Head – measured with wing rule (with back-stop) as the straight line from the occiput (rear of the skull) to the tip of the upper mandible, to the nearest mm.
5. Tarsus - measured with dial callipers from the notch on the posterior side of the tibiotarsal joint to the anterior distal edge of the flexed tarsus, to the nearest 0.1 mm.
6. Foot - measured with wing rule (with back-stop) from the proximal end of the tarsometatarsus to the end of the longest toe (excluding nail) of the flattened foot, to the nearest mm.

Due to the increasing absence of chicks from the vicinity of their nests as they got older and the concomitant difficulty in locating them during subsequent visits, it was decided to erect enclosed pens around a sample of nests from both Bonaero Park and Modderfontein Pan. Both of these sites had nests that were situated in marshy vegetation which exacerbated the problem of finding chicks while, at the same time, providing suitable and unobtrusive habitat for erecting pens. It was decided against using this method at Lakefield Pan due to the exposed substrate on which birds nested at this site, i.e. open shoreline, and the potential for terrestrial predation and disturbance (see Chapter 3). Pens were constructed of wire mesh with a 5 cm inner mesh diameter. These were laid out in 60 cm high strips that were secured to anchored steel droppers situated around the nest(s). Pens were large enough to incorporate the nest area and an area of adjacent hygrophilous vegetation that afforded them some concealment from predators as well as shelter from the elements (Plate 4.1a). Large pens were erected around a number of nests when the distances between these nests were two small to allow for individual pens. A total of nine pens incorporating 31 nests was erected at Bonaero Park and a total of 15 pens incorporating 16 nests was erected at Modderfontein Pan. In order to calculate relative chick survival, all mortalities of chicks enclosed in pens were recorded and, where possible, the reason for this mortality was determined.

Regurgitated pellets were collected incidentally during the study and were preserved in containers with 70% ethanol solution. These pellets were later analysed in the laboratory.

Data analysis

Growth rates

The data analysis for growth rates followed the approach pioneered by le Roux (2006), and applied by her to the growth of Swift Tern chicks. A full description of the method is contained in Underhill & Le Roux (in prep.). The following paragraphs summarize this non-parametric approach to the fitting of growth curves; as for Le Roux's (2006) Swift Tern chicks, the most frequently fitted growth models, the logistic curve and the Gompertz curve, provided poor fits to the data.

Growth rates, for all measurements, were calculated for all chicks captured more than once. The first two values to be calculated were: growth rate g between successive visits:

$$g\text{=(change in size)/(time period)=}(m_t\text{-}m_u)/(t\text{-}u),$$

where m_t and m_u represent masses at different times t and u; and the average of each pair of measurements a where $a=(m_t+m_u)/2$. All pairs of values a and g for all measurements were plotted in 'growth-rate vs size' plots.

Using mass as an example (the same was done for all measurements), a set of masses at small increments between hatching and fledging were used to estimate the average growth rate at the masses. This was achieved by using weighted regression. To estimate the growth rate at a target mass, weights for all the pairs of observations (a,g) were calculated so that values close to the target mass had large weights and values further away had increasingly smaller weights. If the target mass was m^*, then the weight w attached to observation (a, g) was:

$$w=\exp(-((a-m^*)/\sigma)^2),$$

where σ was chosen to be 8 g. This is about 3% of the average adult mass (c. 280 g; Crawford & Hockey 2005). With this choice of σ, the weights attached to observations 8 g distant from the target mass are substantial (weight 0.37), weight at 12 g distant is small (0.105), and at 16 g distant the weight is tiny (0.018). Observations more than 16 g distant from the target mass thus have negligible weights to the regression calculations.The weighted linear regression was fitted to predict growth rate from mass using these weights, and the regression line was used to predict the growth rate g* at the target mass. The estimated growth rate depends on observed growth rates in the neighbourhood of the target mass. The size of the neighbourhood can be modified by varying σ. A compromise needs to be met between low and high values of σ to avoid unstable estimates and biases. As has been used in moving average smoothing (Silverman 1986) visual inspection of the results was used to choose σ; however the results do not depend critically on the choice of a particular value for σ. Experimentation showed that had a value twice as large or half as small been chosen, the results would have been nearly identical.

To estimate an approximate standard deviation at each target mass, a weighted standard deviation s_{m^*}, based on the same weights used in the regression, was used. The formula used was:

$$s_{m^*}=(1/\sum w)((w(g-g^*)^2)$$

In order to provide a measure of variability, an approximate coefficient of variation was calculated for each target mass as:

$$\mathrm{CV}^*= 100 \times (s_{m^*}/m^*).$$

The estimated growth rates at each target mass were plotted and the points were linked using an interpolated line. In a similar fashion lower and upper confidence limits were also plotted. A normal distribution was assumed, so that the lower and upper confidence limits were g*-1.96 s_{m^*} and g*+1.96 s_{m^*}, respectively.

For each successive pair of measurements of a chick, the observed and expected growth rates were compared. The expected growth rate was calculated at the average of the two measurements and the approximate standard deviation was calculated as described above. A standardized growth rate z was computed from the following formula:

$$z=(g-g^*)/s,$$

where g and g^* represent the observed and expected growth rates, respectively, and s represents the standard deviation. These values provide an index of the extent to which growth is above or below the expected and are therefore independent of the stage of growth.

If the analyst is prepared to make the assumption of normality (which to a first approximation is probably reasonable), the magnitudes of z-scores can be expected to be in keeping with the standard normal distribution.

Because the index is independent of growth stage, it becomes possible to compare different growth rates. I compared differences between the three sites, Bonaero Park, Lakefield Pan and Modderfontein Pan and chicks from different hatching orders, i.e. A- (first-hatched), B- (second-hatched) and C- (third-hatched) chicks, within and between sites. I used analysis of variance (ANOVA) to compare these differences. I also used these standardized growth rates to regress the influence of laying dates on chick growth rates using data obtained during the analysis phase of Chapter 3.

Regurgitated pellets

For each pellet, numbers and the wet mass of all prey items were determined in the laboratory. Prey items were weighed using an Ohaus electronic scale to the nearest 0.001 grams. All natural food items were identified under a microscope and were classified to the nearest known taxon using the taxonomic keys of Scholtz & Holm (1985). Samples of Diptera larvae, pupae and adults were sent to the Natal Museum, Pietermaritzburg for identification. Food items originating from anthropogenic waste were classified into three broad categories:

1. Animal - consisting of butcher products (beef, pork and mutton);
2. Chicken waste - consisting of feathers and chicken off-cuts observed in the local chicken abattoir near Modderfontein Pan;
3. Grain and vegetable – consisting of vegetables and grains including processed material e.g. maize meal and bread.

Chick survival

For the purpose of determining relative chick survival, chicks surviving to 30 days and older were presumed to have fledged. The survival rate was calculated as the proportion of these chicks surviving relative to the total number of chicks present when the pens were erected. A Chi-squared test was used to test if there were any significant differences between these fledgling rates.

Results

A total of 326 chicks from 168 nests was measured at three sites during 2005 in Gauteng. These comprised 149 chicks from 78 nests at Bonaero Park, 94 chicks from 47 nests at Lakefield Pan, and 83 chicks form 43 nests at Modderfontein Pan (Table 4.1). A large proportion of chicks at both Bonaero Park and Modderfontein Pan were recaptured on subsequent visits (89% and 84%, respectively), while only 56% of chicks at Lakefield Pan were recaptured. Recaptured chicks at both Bonaero Park and Modderfontein Pan were caught on average six times with the maximum number of recaptures for any chicks being 17 and 15 times for Bonaero Park and Modderfontein Pan, respectively. The mean number of recaptures for chicks at Lakefield Pan was 2.7 with the maximum number of recaptures for a chick being six times.

Table 4.1. Sample sizes of all chicks caught and recaptured at three sites: Bonaero Park, Lakefield Pan and Modderfontein Pan during 2005 in Gauteng.

	Total		Recaptures				
					no. of recaptures/chick		
Site	nests	chicks	nests	chicks	mean	sd	range
Bonaero Park	78	149	75	132	6.1	4.3	2 - 17
Lakefield Pan	47	94	28	53	2.7	0.9	2 - 6
Modderfontein Pan	43	83	36	70	6.4	4.6	2 - 15
Totals	168	326	139	255			

Measurements of 32 hatchlings are shown in Table 4.2. Only chicks that had just hatched, i.e. were wet and/or were observed emerging from the egg, were used in this analysis. Mass was the most variable of all measurements with a coefficient of variation of 9.6%, followed by culmen (CV=7.9%), wing (CV=7.5%), foot (CV=4.6%), tarsus (CV=4.5%) and head (CV=3%).

Table 4.2. Summary of 32 Grey-headed Gull hatchling measurements from chicks caught at three sites: Bonaero Park, Lakefield Pan and Modderfontein Pan during 2005 in Gauteng. Q1 – lower quartile; Q3 – upper quartile.

	Mean	SD	Min	Q1	median	Q3	Max	n
mass	25.9	2.5	20.5	24.4	26	28	30	32
wing	18	1.4	15	17	18	19	20	32
head	36.2	1.1	34	35.8	36	37	38	32
bill	13	1	11.6	12.5	12.9	13.3	17.8	32
tarsus	19.7	0.9	18.1	19	19.8	20.3	21.3	32
foot	43.6	2	40	42	43.5	45	49	32

Measurements of 82 fledged juveniles trapped at landfill sites in Gauteng during 2004 and 2005 are shown in Table 4.3 (for comparisons between juvenile and adult morphometrics see Chapter 5). These measurements were used as the guidelines for the upper limits of the growth rate plots and the empirical growth curves (Figures 4.1 – 4.6). Likewise the measurements coming from the hatchlings were used as the starting points for these graphs.

Table 4.3. Summary of Grey-headed Gull fledgling measurements of birds trapped at landfill sites in Gauteng during 2004 and 2005. Q1 – lower quartile; Q3 – upper quartile.

	Mean	SD	Min	Q1	Median	Q3	Max	n
mass	312.2	43.3	210	285	307.5	340	420	82
wing	297.3	10.8	276	289.3	297.5	304.8	322	82
head	82.6	3.8	76	80	82	86	90	81
bill	34.8	2.6	30	32.9	34.6	36.2	41	81
tarsus	48.9	2.5	43.5	47.3	49.2	50.8	57.7	82
foot	96.7	3.8	89	94	97	100	105	82

Growth rates and empirical growth curves

Growth rate vs size plots and empirical growth curves for all measurements are illustrated in Figures 4.1 – 4.6.

The growth rate for mass increased fairly rapidly from hatchling to approximately seven days old. Chicks between 74.7 g and 165.1 g (c. seven to 16 days old) maintained a constantly high mean growth rate of >10 g/day with a peak in mean growth rate of 11.3 g/day at 132 g (c. 13 days old) (Table 4.4). There was a steady to moderate decline in the growth rate after this period to fledgling. Variation of the mean growth rate for mass was positively correlated with chick development; this result was highly significant (R_2=0.531, P<0.0001).

The growth rate for wing was lowest at hatchling to approximately 12 days when the wing was between 16 mm and 36.5 mm long. Growth rate increased rapidly after this stage to when the chicks were approximately 18 days old. When the wing was between 80.6 mm and 145.1 mm long (c. 18 to 25 days old), a constantly high mean growth rate of >8 mm/day was maintained with a peak in growth rate of 8.6 mm/day being reached when the wing was 101 mm long (c. 20 days old) (Table 4.4). Thereafter, the growth rate declined steadily but was still growing at 4.5 mm/day towards the end of the fledgling period (c. 35 days old) when the wing was 227 mm long. The variation of the growth rate for wing was greatest from hatchling to approximately 10 days old when the wing was 30.7 mm (CV range=53.5% - 128%). The least variance was evident just after peak growth when the wing was between 127.5 mm and 142.2 mm long (CV range=10.1% – 12.6%). Comparing variation in growth rate for all measurements during peak growth rate, wing was the least variable (CV=15%) (Table 4.4).

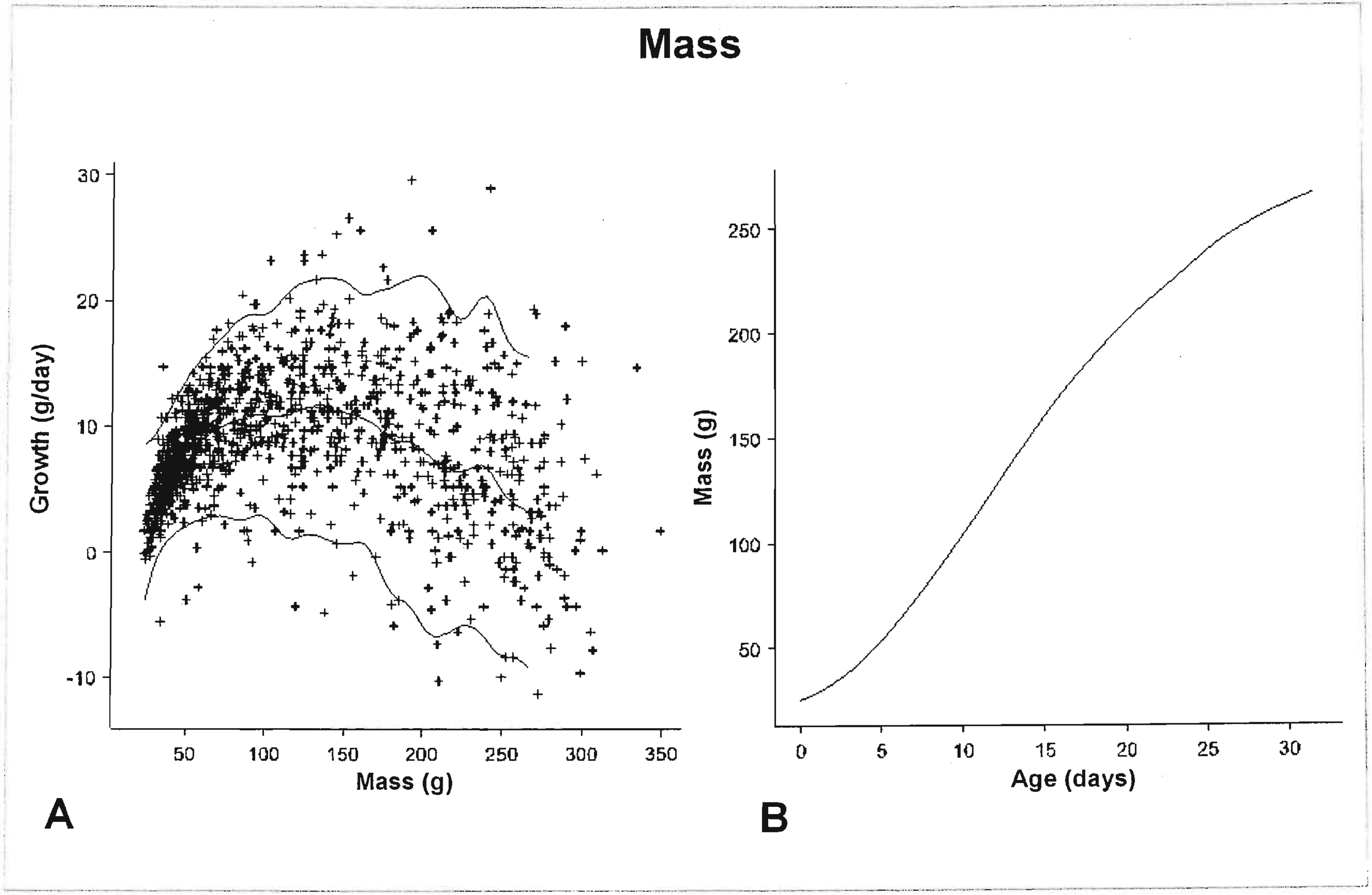


Figure 4.1. A: Growth rates (g/day) of the mass (g) of Grey-headed Gull chicks caught in Gauteng during 2005. Smoothed curve gives the trajectory of the mean, and upper and lower 95% confidence intervals are shown. **B**: Growth curve of mass (g) of Grey-headed Gull chicks in relation to age (days), transformed from the trajectory of the mean in A. using the hatching mass from Table 4.2 as the mass on day 0.

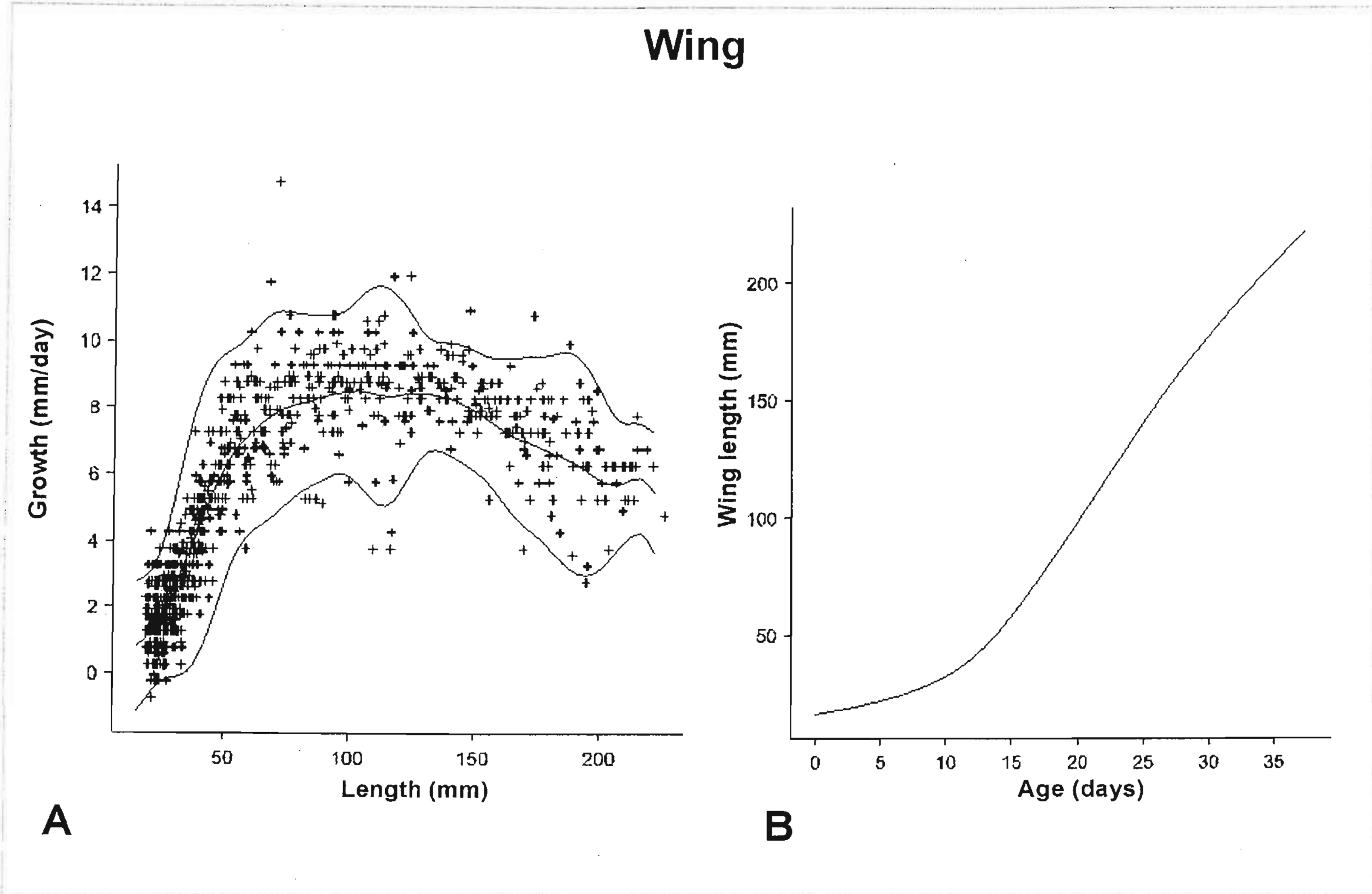


Figure 4.2. A: Growth rates (mm/day) of the wing length (mm) of Grey-headed Gull chicks caught in Gauteng during 2005. Smoothed curve gives the trajectory of the mean, and upper and lower 95% confidence intervals are shown. **B**: Growth curve of wing length (mm) of Grey-headed Gull chicks in relation to age (days), transformed from the trajectory of the mean in A. using the hatching wing length from Table 4.2 as the length of wing on day 0.

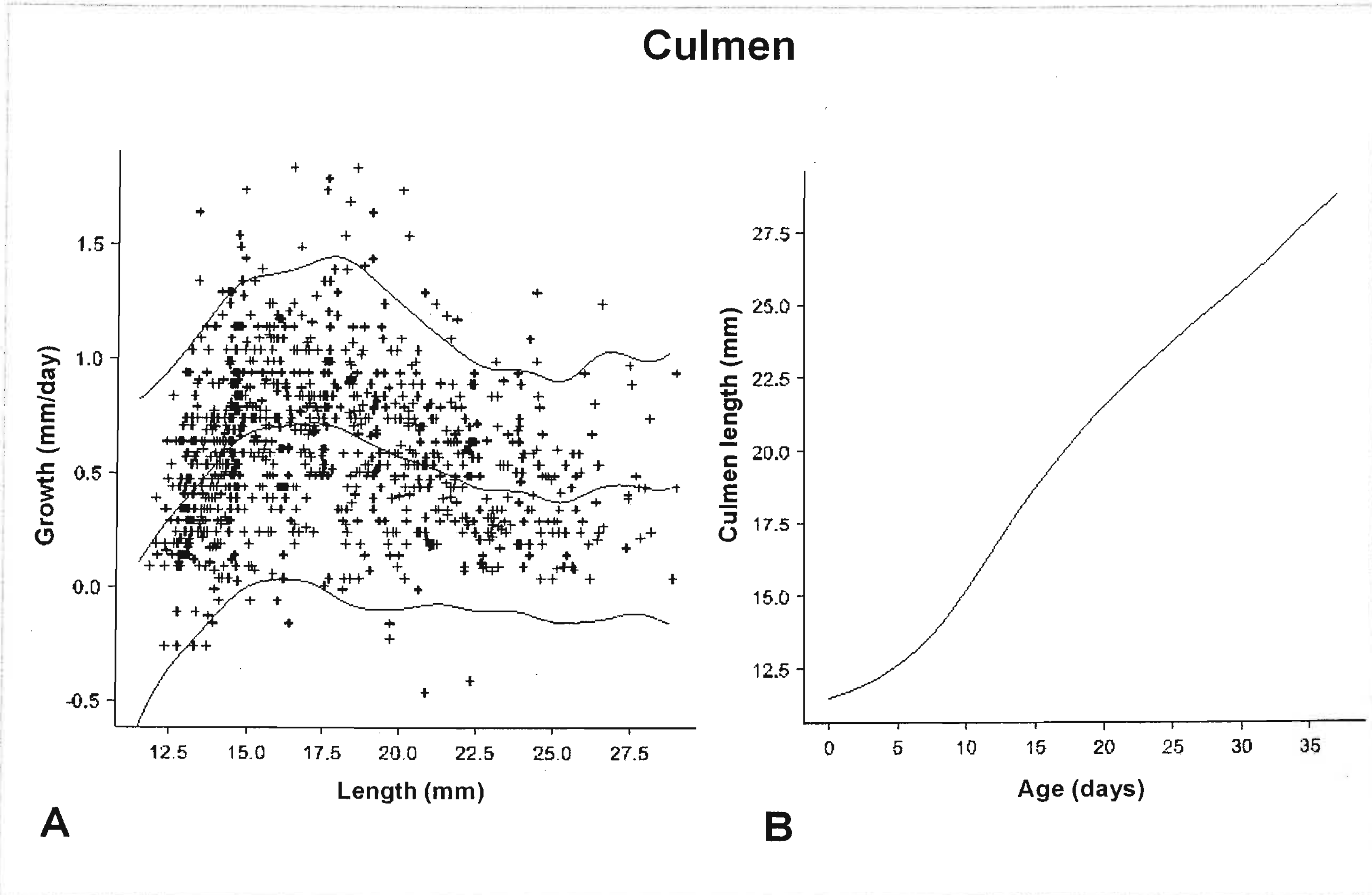


Figure 4.3. A: Growth rates (mm/day) of the culmen length (mm) of Grey-headed Gull chicks caught in Gauteng during 2005. Smoothed curve gives the trajectory of the mean, and upper and lower 95% confidence intervals are shown. **B**: Growth curve of culmen length (mm) of Grey-headed Gull chicks in relation to age (days), transformed from the trajectory of the mean in A. using the hatching culmen length from Table 4.2 as the length of culmen on day 0.

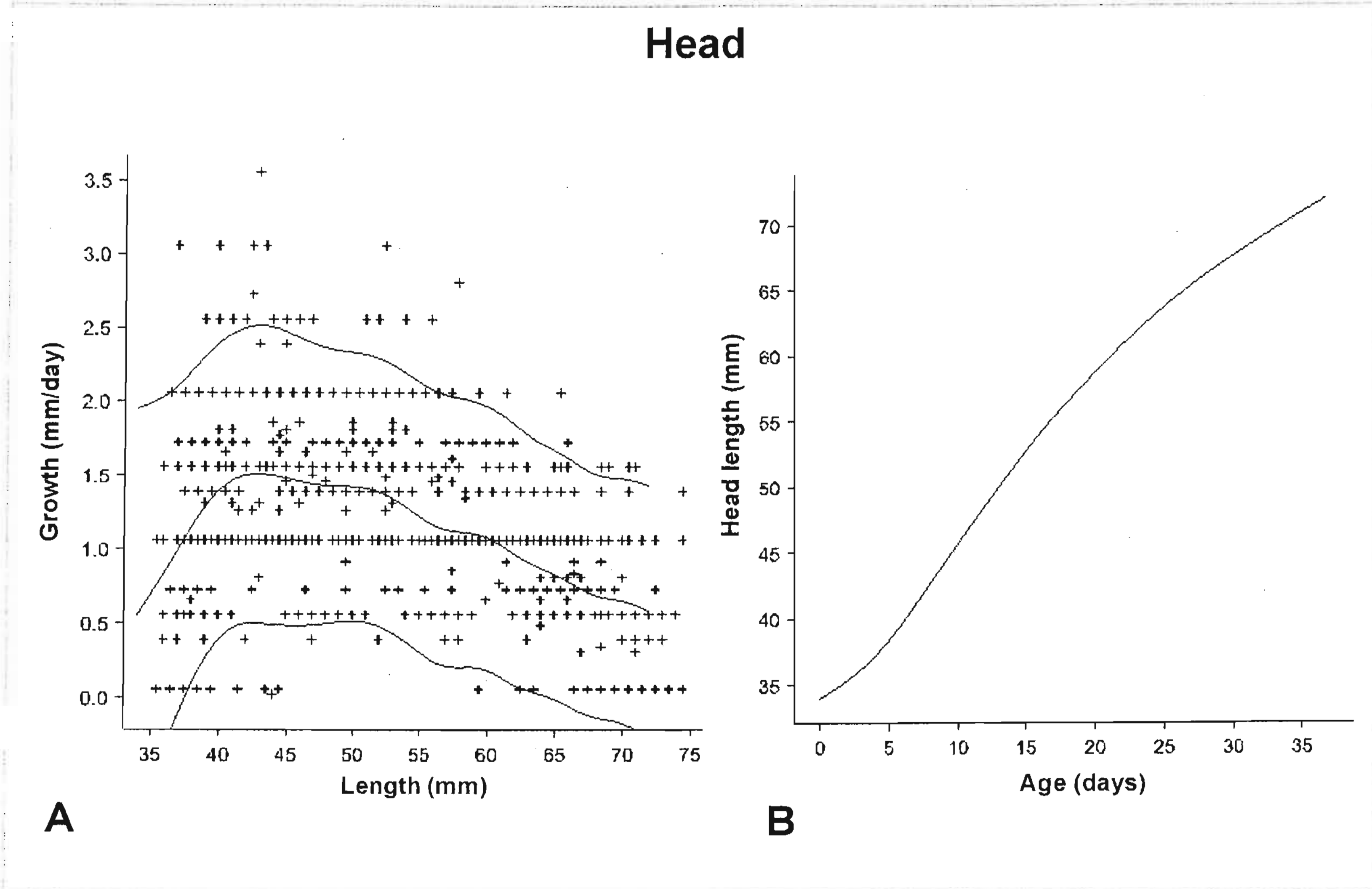


Figure 4.4. **A**: Growth rates (mm/day) of the head length (mm) of Grey-headed Gull chicks caught in Gauteng during 2005. Smoothed curve gives the trajectory of the mean, and upper and lower 95% confidence intervals are shown. **B**: Growth curve of head length (mm) of Grey-headed Gull chicks in relation to age (days), transformed from the trajectory of the mean in A. using the hatching head length from Table 4.2 as the length of head on day 0.

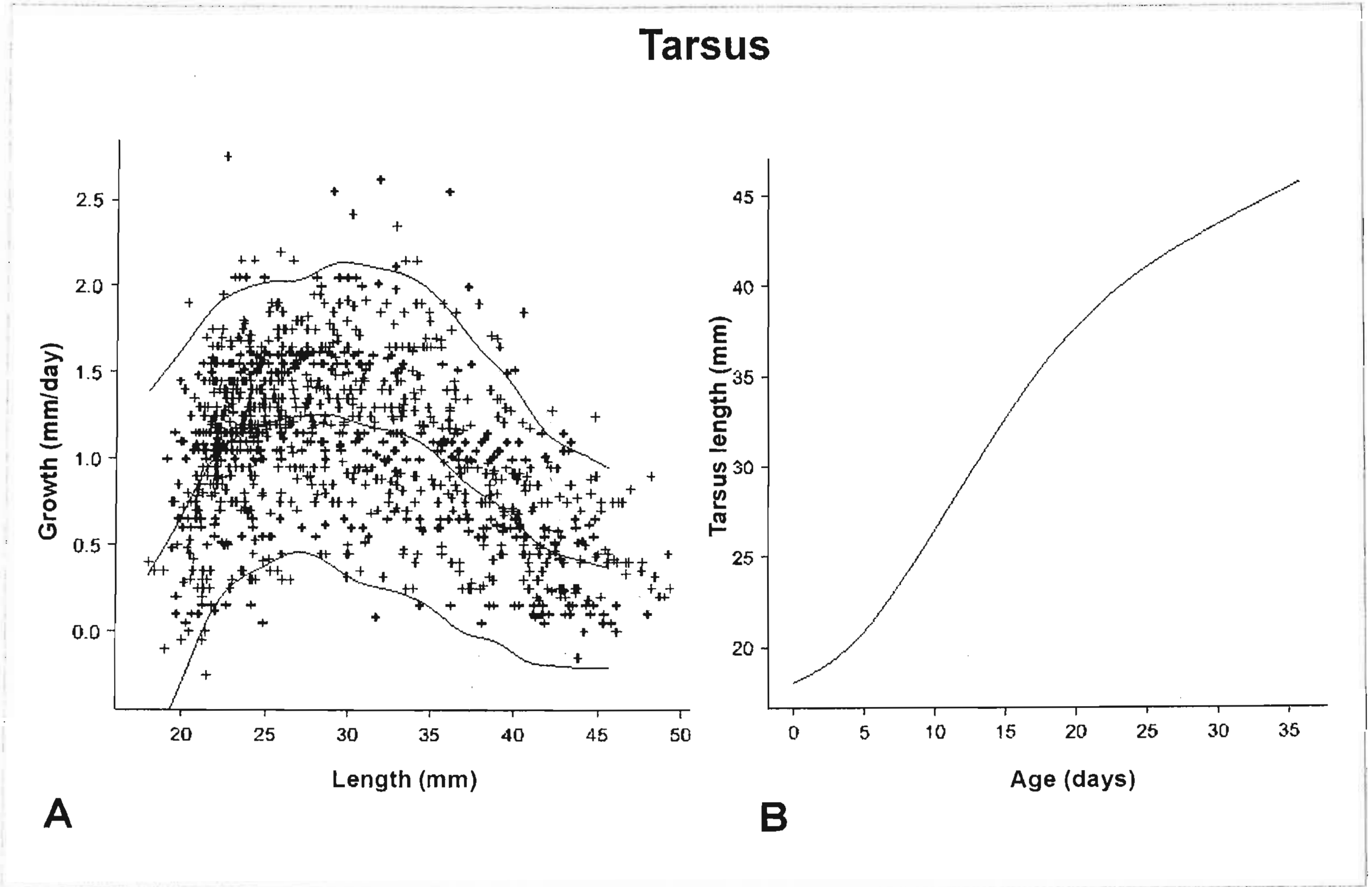


Figure 4.5. A. Growth rates (mm/day) of the tarsus length (mm) of Grey-headed Gull chicks caught in Gauteng during 2005. Smoothed curve gives the trajectory of the mean, and upper and lower 95% confidence intervals are shown. **B**: Growth curve of tarsus length (mm) of Grey-headed Gull chicks in relation to age (days), transformed from the trajectory of the mean in A. using the hatching tarsus length from Table 2 as the length of length on day 0.

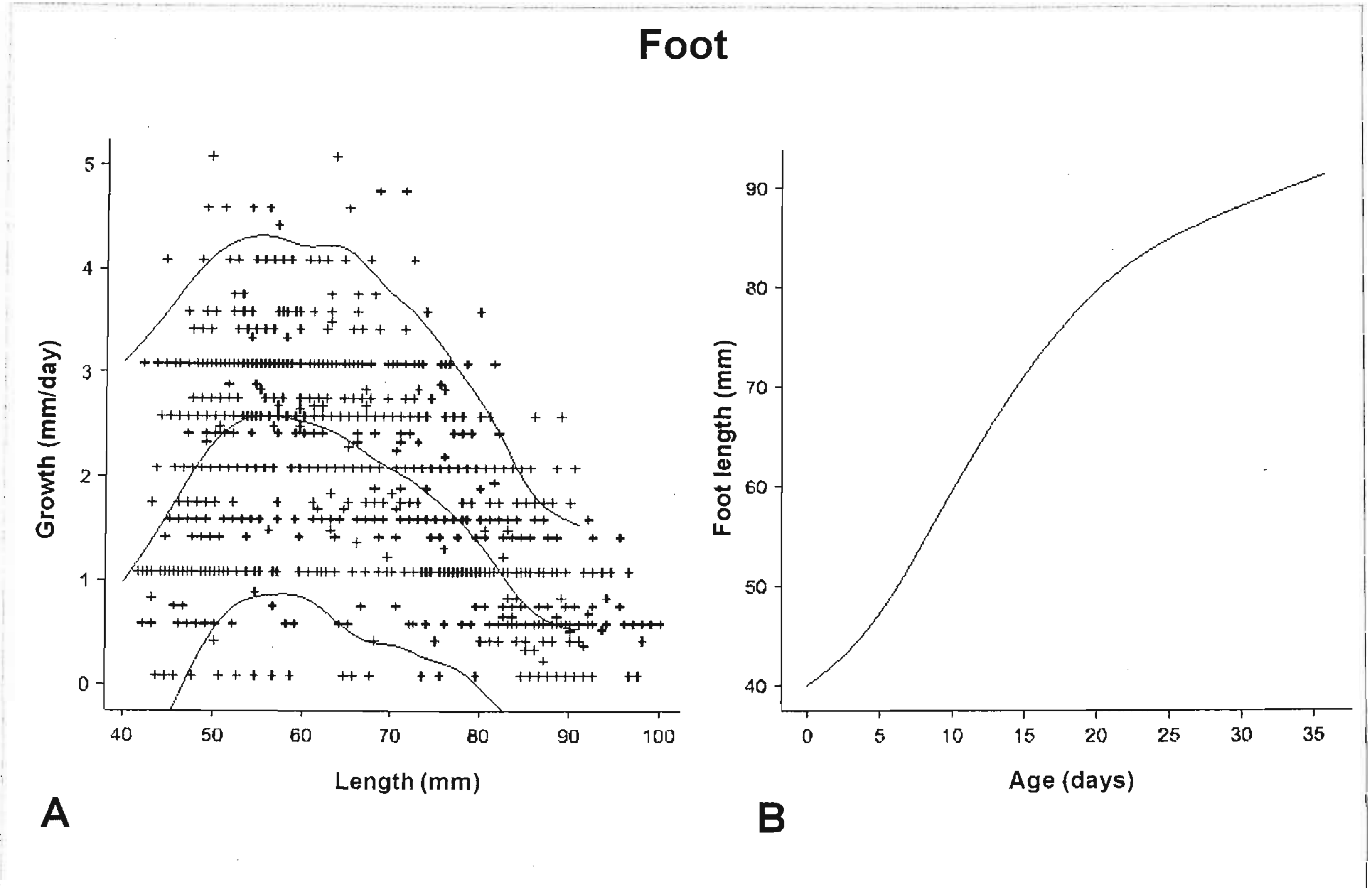


Figure 4.6. A: Growth rates (mm/day) of the foot length (mm) of Grey-headed Gull chicks caught in Gauteng during 2005. Smoothed curve gives the trajectory of the mean, and upper and lower 95% confidence intervals are shown. **B**: Growth curve of foot length (mm) of Grey-headed Gull chicks in relation to age (days), transformed from the trajectory of the mean in A. using the hatching foot length from Table 2 as the length of foot on day 0.

Table 4.4. Measurements of Grey-headed Gull chicks at their maximum growth rates for all measurements. The proportion of their adult size at this stage of development is shown, as well as the comparative variability of each measurement at this stage.

	Maximum growth rate (g/day, mm/day))	Length (mm)/mass (g) at max growth rate	Adult size	% of adult size	CV (%) of the growth rate
mass	11.3	132	300	44	46
wing	8.6	101	313	32	15
culmen	0.68	16.8	37	45	53
head	1.5	43	84	51	34
tarsus	1.27	29	49	60	35
foot	2.6	56	97	58	34

The growth rate for culmen was lowest during the first five days of development when the culmen was between 11.5 mm and 12.84 mm. The growth rate increased moderately after this stage to approximately nine days. When the culmen was between 15 mm and 19.3 mm long (c. nine to 16 days old), a constantly high mean growth rate of >0.4 mm/day was maintained with a peak in growth rate of 0.68 mm/day being reached when the culmen was 16.8 mm long (c.12 days old) (Table 4.4). There was considerable variation in growth rate values for culmen. Variability was greatest (CV=328%) during the early stages of development when the rate of growth for culmen was lowest, i.e. up to five days old. The least variation occurred when the chicks were approximately 14 days old, just after peak growth when the culmen was 16.8 mm long (CV=53%). Comparing variation in growth rate for all measurements during peak growth rate, culmen was the most variable (CV=53%) (Table 4.4).

The growth rate for head was lowest at both the hatchling period and at the final fledgling period, where the mean growth rates were 0.55 mm/day and 0.4 mm/day at 34 mm and 76 mm, respectively. The growth rate increased moderately from approximately three to six days. When the head was between 40.3 and 51.3 mm (c. six to 14 days old), a constantly high mean growth rate of >1.4 mm/day was maintained with a peak in mean growth rate of 1.5 mm/day being reached when the head was 43 mm long (c. eight to nine days) (Table 4.4). Thereafter there was a steady decline in the growth rate to fledging. The greatest variability in growth rate was associated with the initial (CV=130% at 34 mm long) and final stages (CV=194% at 76 mm long) of development when the growth rate was lowest. Variability of growth rate was lowest just after the peak in growth rate when the head was 50.1 mm long (CV=33%).

The growth rate for tarsus was lowest at both the hatchling period and the final fledgling period, where the mean growth rates were 0.3 mm/day and 0.2 mm/day at 18 mm and 49 mm, respectively. Shortly after the hatchling period, at approximately three days old, the growth rate increased fairly rapidly until when the chicks were approximately eight days old. When the tarsus was between 25.2 mm and 30.7 mm long (c. eight to 13 days old), a constantly high mean growth rate of >1.2 mm/day was maintained with a peak in growth rate of 1.27 mm/day being reached when the tarsus was 28.6 mm long (c. 12 to 13 days old) (Table 4.4). There was a steady to moderate decline in growth rate after this period. The greatest variation in the growth rate for foot was during the initial stages of growth, from hatchling to approximately three days old (CV range=79% - 156%) when the growth rate was low. Variability was lowest when the tarsus was 26.9 mm long (CV=32%) just before the peak growth rate.

The growth rate for foot was initially slow, but increased fairly rapidly after the chicks were approximately three days old when the foot was 43.3 mm long. When the foot was between 52 mm and 61 mm long (c. seven to 11 days old), a constantly high growth rate of >2.5 mm/day was maintained and a peak growth rate of 2.6 mm/day was reached when the foot was 56 mm long (c. eight days old) (Table 4.4). The growth rate of foot declined moderately to fairly rapidly after this period and reached a low of 0.25 mm/day towards the end of the fledgling period when the foot was 100 mm long. Variation in growth rate for foot was highest towards the end of the fledgling period at approximately 31 to 35 days when the foot was between 89 mm and 92 mm long (CV range=95% - 104%). Variability was lowest when the foot was between 57 mm and 60 mm long (CV range=33% - 34%) just after the peak growth rate.

Standardized growth rate comparisons

Clutch size differences

For all measurements at all sites there was no significant difference between the average growth rates of Grey-headed Gull chicks from different clutch sizes (Table 4.5).

Table 4.5. Tests for significance between mean standardized growth rates of chicks from different clutch sizes. All results not significant.

	Clutch size no.s			ANOVA F=values			
Site	**1**	**2**	**3**	**Mass**	**Wing**	**Head**	**Foot**
Bonaero Park	1	11	25	0.263	0.049	0.936	1.116
Lakefield Pan	0	8	10	0.6	0.172	1.279	0.709
Modderfontein Pan	0	5	11	0.082	0.001	0.615	2.772

Between sites

A total of 72 A-chicks, from all clutch sizes, from the three sites in Gauteng was used in this analysis. These comprised 37 chicks from Bonaero Park, 19 chicks from Lakefield Pan and 16 chicks from Modderfontein Pan. Each chick was recaptured on average six times for both Bonaero Park and Modderfontein Pan, but was only recaptured on average two times for Lakefield Pan.

Standardized growth rate values (z values) for four measurements, mass, wing, head and foot, were used to compare growth rates of A-chicks between the three different sites (Table 4.6, Figure 7 a - d). Only the most repeatable measurements, i.e. features measured with a wing rule (with back-stop) as opposed to features measured with callipers, were used in this analysis. For all measurements, the mean standardized growth rate values for Modderfontein Pan and Lakefield Pan were the highest and lowest of all sites, respectively. The difference between standardized growth rates of wing length, between the three sites, was statistically significant (ANOVA $F_{2,337}$=5.879, P<0.005). Standardized growth rates for wing length at Modderfontein

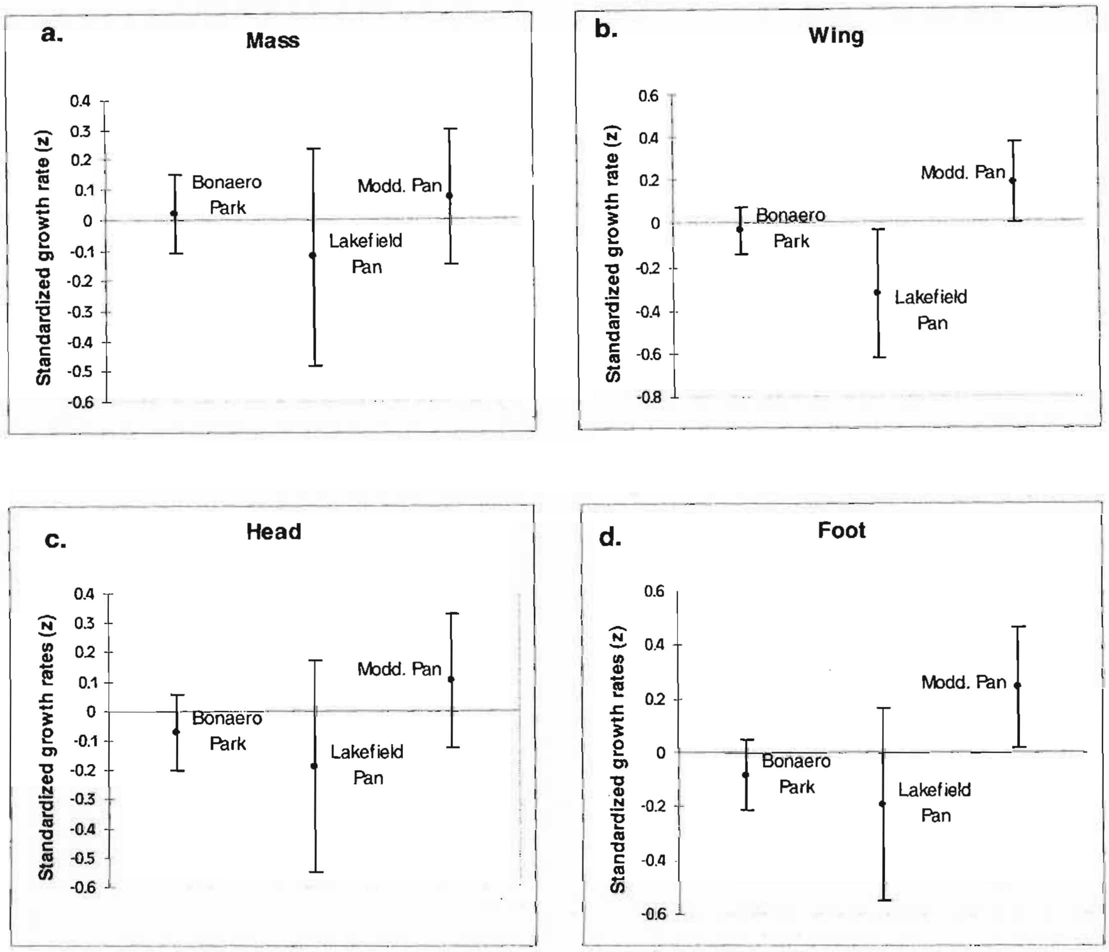


Figure 4.7. Standardized growth rate comparisons between mass (**a**.), wing (**b**.), head (**c**.) and foot (**d**.) growth rates of Grey-headed Gull A-chicks from three sites: Bonaero Park, Lakefield Pan and Modderfontein Pan (Modd. Pan) during 2005 in Gauteng.

Table 4.6. Standardized growth rate (means and standard deviations) comparisons for four measurements of Grey-headed Gull A-chicks for three sites: Bonaero Park, Lakefield Pan and Modderfontein Pan during 2005 in Gauteng.

Site	Mass			Wing			Head			Foot		
	n	mean	sd	n	mean	sd	n	mean	sd	n	mean	sd
Bonaero Park	209	0.02	0.99	207	-0.03	0.87	209	-0.07	1	203	-0.08	0.97
Lakefield Pan	31	-0.12	-0.91	31	-0.32	0.68	31	-0.19	1.05	31	-0.19	1.07
Modderfontein Pan	102	0.07	0.88	102	0.19*	0.58	102	0.1	0.82	102	0.24**	0.83

* ANOVA, P<0.05
** ANOVA, P<0.01

Pan were on average 0.22 higher than those of Bonaero Park (t=2.337, P=0.02) and the standardized growth rates for Lakefield Pan were on average 0.295 lower than those of Bonaero Park (t=1.97, P=0,05) (Figure 4.7b). The difference between the standardized growth rates of foot length, between the three sites, was statistically significant (ANOVA $F=4.731_{2,333}$, $P<0.01$). Standardized growth rate for foot at Modderfontein Pan were on average 0.32 higher than those of Bonaero Park ($t=2.818$, $P=0.005$) (Figure 4.7d). For all measurements used, Lakefield Pan had the greatest variation in standardized growth rate values, followed by Modderfontein Pan and Bonaero Park (Figures 4.7 a - d).

Between A-, B-, C-chicks (hatch order)

A total of 160 chicks from three different hatch orders, i.e. A-, B- and C-chicks, for three sites in Gauteng was used in this analysis. Details of sample sizes including mean numbers of recaptures are shown in Table 4.7. Sample sizes for C-chicks were lower than those of A- and B-chicks for all sites and the mean number of recaptures for C-chicks was lower than those of A- and B-chicks at Bonaero Park and Lakefield Pan, but not at Modderfontein Pan.

Table 4.7. Sample sizes of all chicks from known hatch order (A-, B-, C-chicks) caught and recaptured at Bonaero Park, Lakefield Pan and Modderfontein Pan during 2005 in Gauteng.

Site	Hatch order	Total chicks	No. of recaptures/chick mean	sd	max
Bonaero Park	A	37	5.6	4.2	15
	B	27	5.0	4.2	14
	C	13	3.1	3.4	13
Lakefield Pan	A	19	1.6	0.7	3
	B	16	1.6	1.1	4
	C	5	1.2	0.4	2
Modderfontein Pan	A	16	6.4	4.9	14
	B	17	5.6	4.4	13
	C	10	6.6	4.9	13

Standardized growth rate values (z values) for four measurements, mass, wing, head and foot, were used to compare the growth rates of A-, B- and C-chicks at and between the three different sites (Table 4.8, Figures 4.8 a - d).

For most measurements at all sites, the mean standardized growth rates for C-chicks were lower than both A- and B-chicks. There were two exceptions: the mean standardized growth rate for head measurement of C-chicks at Bonaero Park was higher than those of both A- and B-chicks; and the mean standardized growth rate for wing measurement of C-chicks at Modderfontein Pan was higher than that of B-

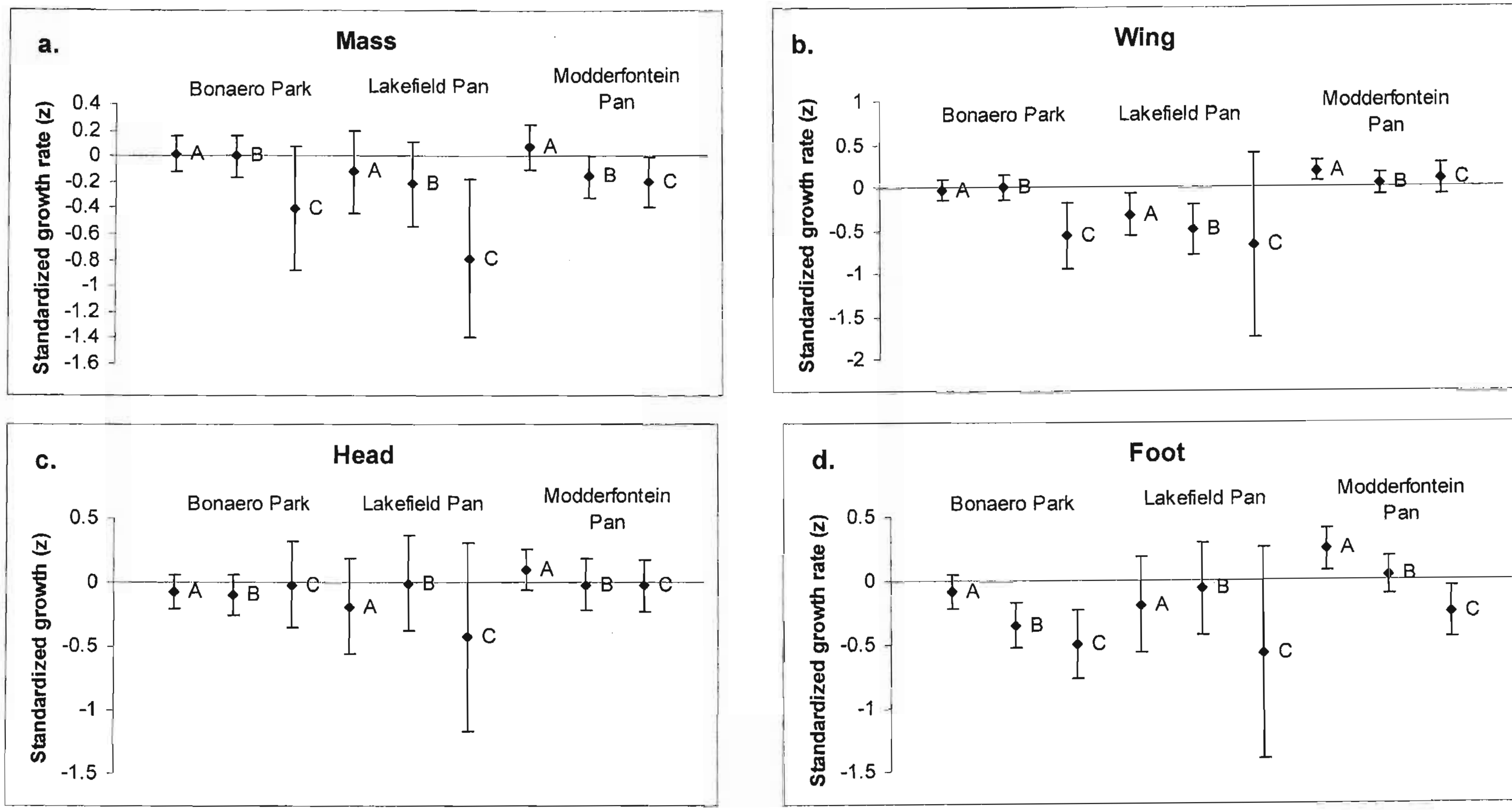


Figure 4.8. Standardized growth rate comparisons between mass (a.), wing (b.), head (c.) and foot (d.) growth rates of Grey-headed Gull chicks from different hatch orders (A-, B-, C-chicks) for three sites: Bonaero Park, Lakefield Pan and Modderfontein Pan during 2005 in Gauteng.

Table 4.8. Standardized growth rate (means and standard deviations) comparisons for four measurements of Grey-headed Gull chicks from different hatch orders (A-, B-, C-chicks) for three sites: Bonaero Park, Lakefield Pan and Modderfontein Pan (Modd. Pan) during 2005 in Gauteng.

Site	Chick	Mass n	Mass mean	Mass sd	Wing n	Wing mean	Wing sd	Head n	Head mean	Head sd	Foot n	Foot mean	Foot sd
Bonaero Park	A	209	0.02	0.99	207	-0.03	0.87	209	-0.07	1.00	203	-0.08	0.97
	B	134	0.00	0.96	134	-0.001	0.87	134	-0.10	0.95	134	-0.35*	1.05
	C	40	-0.40	1.54	40	-0.57***	1.23	38	-0.02	1.06	40	-0.5*	0.85
Lakefield Pan	A	31	-0.12	0.91	31	-0.32	0.68	31	-0.19	1.05	31	-0.19	1.07
	B	26	-0.22	0.84	26	-0.49	0.74	26	-0.01	0.98	26	-0.06	0.93
	C	6	-0.79	0.76	6	-0.67	1.34	6	-0.43	0.92	6	-0.57	1.03
Modd. Pan	A	102	0.07	0.88	102	0.19	0.58	102	0.10	0.82	102	0.24**	0.83
	B	95	-0.16	0.80	94	0.04	0.65	95	-0.02	1.02	95	0.04	0.71
	C	66	-0.20	0.80	66	0.10	0.75	66	-0.03	0.84	66	-0.25***	0.82

*ANOVA, P<0.05
**ANOVA, P<0.001
***ANOVA, P<0.0001

chicks. Comparing the standardized growth rates between chicks of different hatch order at Bonaero Park, there was a highly significant statistical difference between the growth rates of wing lengths (ANOVA $F_{2,378}$=7.11, P<0.001) and a statistically significant difference between the growth rates of foot lengths (ANOVA $F_{2,374}$=4.799, P<0.01). Standardized growth rate values of wing length for C-chicks were on average 0.537 lower than those of A-chicks (t=3.398, P<0.0001) (Figure 4.8b). The standardized growth rates of foot length for B and C-chicks were on average 0.269 and 0.421 lower than those of A-chicks, respectively (B-chicks t=2.448, P=0.015; C-chicks t=2.462, P=0.014) (Figure 4.8d). At Modderfontein Pan there was a statistically highly significant difference between the standardized growth rates of chicks of different hatch order for foot length (ANOVA $F_{2,260}$=7.73, P<0.001). The standardized growth rates of foot length for A-chicks were on average 0.203 higher than those of B-chicks (t=3.092, P=0.002), while those of C-chicks were on average 0.487 lower than those of A-chicks (t=3.93, P,0.001) (Figure 4.8d). The variation in standardized growth rate values for C-chicks was higher than both A and B-chicks for all measurements at all sites, other than head length at Modderfontein where variation in B- and C-chicks were almost identical (Figures 4.8 a - d). There was little difference between the variation in standardized growth rates for A and B-chicks for all measurements at all sites (Figures 4.8 a - d).

Two-way ANOVAs were used to check if there were any significant differences between the standardized growth rates between all A-, B- and C-chicks between all sites, for all measurements. Statistically significant differences were found for mass (ANOVA $F_{8,700}$=1.963, P<0.05), and statistically highly significant differences were found for wing (ANOVA $F_{8,697}$=5.526, P<0.0001) and foot (ANOVA $F_{8,694}$=4.639, P<0.0001). For mass, C-chicks from Bonaero Park and Lakefield Pan accounted for most of the difference in variation (t=2.559, P=0.011 and t=2.036, P=0.042, respectively). For wing length, C-chicks from Bonaero Park, B-chicks from Lakefield Pan and A-chicks from Modderfontein Pan accounted for most of the difference in variation (t=3.814, P<0.001; t=2.709, P=0.007; and t=2.225, P=0.026, respectively). For foot length, B- and C-chicks from Bonaero Park, and A-chicks from Modderfontein Pan accounted for most of the difference in variation (t=2.63, P=0.009; t=2.646, P=0.008; and t=2.878, P=0.004, respectively).

Comparison with laying dates

Laying dates for 63 nests from three sites were compared to the average standardized growth rate values for mass of A-chicks for each corresponding nest. These comprised 34 nests from Bonaero Park, 18 nests from Lakefield Pan, and 11 nests from Modderfontein Pan.

For all sites there were weak negative associations between laying dates and mean standardized growth rates, (i.e. the earlier the laying date the faster the growth of chicks): Bonaero Park, r=-0.091; Lakefield Pan, r=-0.162; and Modderfontein Pan, r=-0.259 (Figures 4.9 – 4.11).

Chick diet

A total of 100 regurgitated pellets coming from 71 chicks from 57 nests from the three sites was used in this analysis. These comprised 51 pellets from 35 chicks from 28 nests at Bonaero Park; 14 pellets from 13 chicks from 13 nests at Lakefield Pan; 35 pellets from 23 chicks from 17 nests at Modderfontein Pan. These represented 36%, 28% and 40% of the total number of sampled nests from Bonaero Park, Lakefield Pan and Modderfontein Pan, respectively. Summaries of the % contribution to the diet of

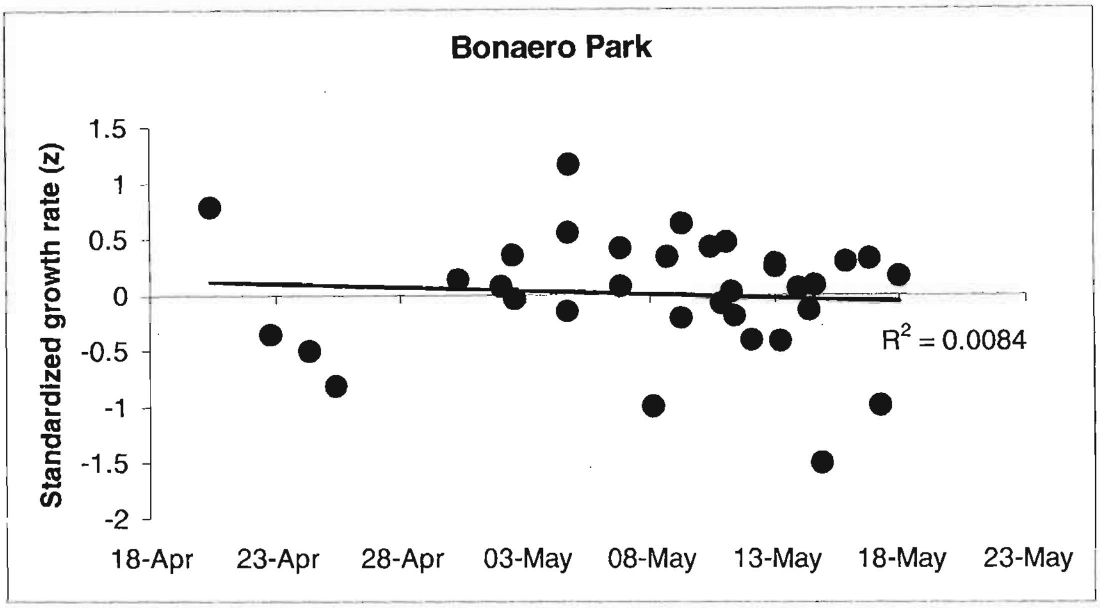


Figure 4.9. Relationship between laying dates of eggs of A-chicks and their corresponding standardized growth rates at Bonaero Park. Line fitted by simple linear regression.

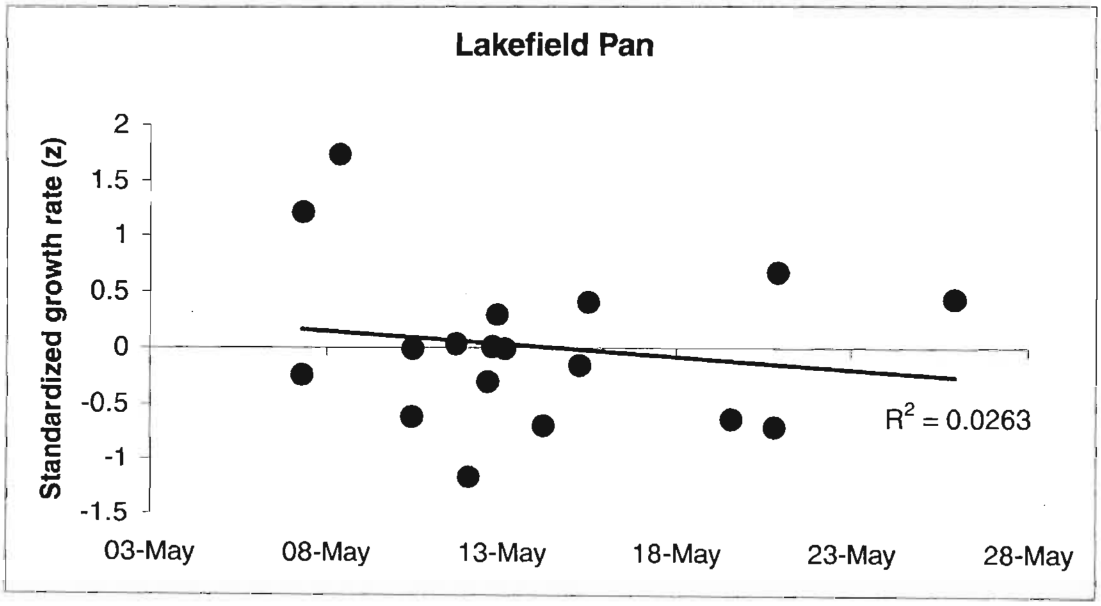


Figure 4.10. Relationship between laying dates of eggs of A-chicks and their corresponding standardized growth rates at Lakefield Pan. Line fitted by simple linear regression.

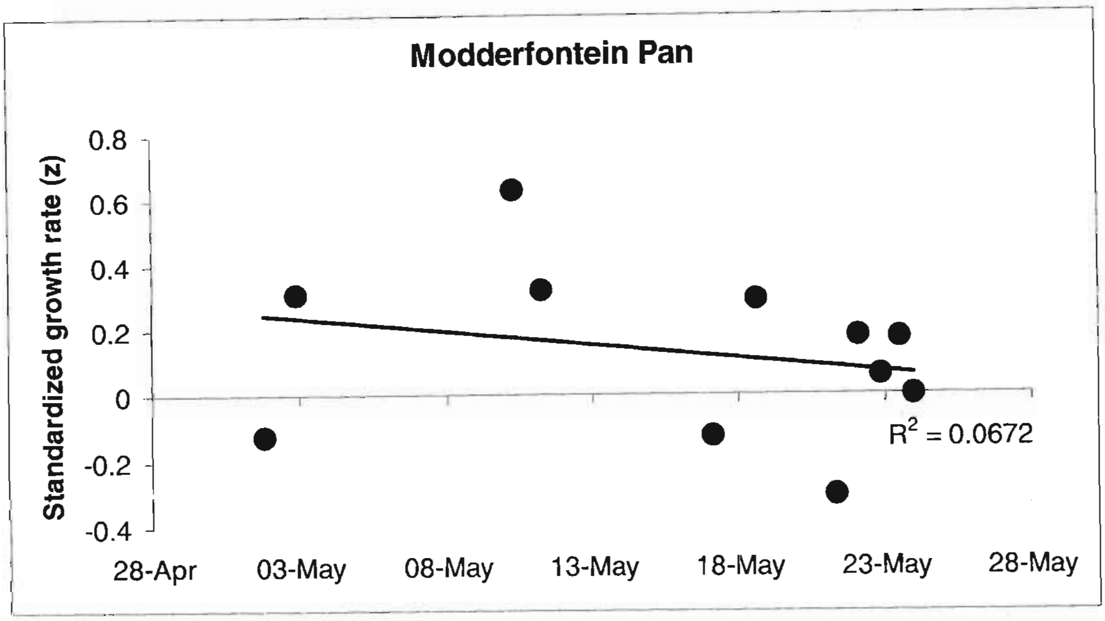


Figure 4.11. Relationship between laying dates of eggs of A-chicks and their corresponding standardized growth rates at Modderfontein Pan. Line fitted by simple linear regression.

different prey items, by frequency of occurrence, mass and number, are shown in Table 4.9.

Invertebrates and anthropogenic discards featured prominently in Grey-headed Gull chick diets for all sites sampled, constituting 45% and 44% of the frequency occurrence in diet, respectively (Figure 4.12a, Table 4.9). Anthropogenic discards contributed 64% of the overall mass of pellets sampled, with invertebrates and vertebrates contributing 27% and 8%, respectively. The majority of individual prey items from all pellets sampled were invertebrates (94%) while anthropogenic discards made up only 5% of this total (Figure 4.12a, Table 4.9).

At Bonaero Park, the most regularly encountered food groups in chick pellets were invertebrates (63% frequency) and anthropogenic discards (61% frequency) (Figure 4.12b, Table 4.9). A large proportion (74%) of the overall mass of different food groups was comprised of anthropogenic discards, while invertebrates only contributed 23% of this mass. Conversely, invertebrates made up the majority (95%) of individual prey items of all pellets at this site, while anthropogenic discards made up only 4% of this total. There was greater variety of food items in pellets at this site when compared to the other sites (Table 4.9). This was especially evident in the Arthropoda, where a

Table.4.9. Frequency, mass and numbers of different food items and food groups in regurgitated pellets of Grey-headed Gull chicks from three sites in Gauteng: Bonaero Park, Lakefield Pan and Modderfontein.

	Bonaero Park						Lakefield Pan						Modderfontein Pan					
Food type	**freq.**	**%**	**mass**	**%**	**nos**	**%**	**freq.**	**%**	**mass**	**%**	**no.s**	**%**	**freq.**	**%**	**mass**	**%**	**nos**	**%**
Invertebrates	32	62.7	25.7	22.7	2158	94.8	8	57.1	4.7	46.3	335	87.7	29	82.9	21.2	31.30	3811	94.5
Gastropoda (snails)	2	3.9	0.2	0.1	4	0.2	-	-	-	-	-	-	-	-	-	-	-	-
Oligochaeta (earthworms)	2	3.9	1.3	1.1	9	0.4	-	-	-	-	-	-	2	5.7	0.5	0.7	4	0.1
Arthropoda (insects)	31	60.8	24.2	21.3	2145	94.2	8	57.1	4.7	46.3	335	87.7	28	80	20.7	30.6	3807	94.4
Blattodea	1	2.0	0.1	0.1	1	0.04	-	-	-	-	-	-	-	-	-	-	-	-
Coleoptera	4	7.8	1.9	1.7	225	9.9	1	7.1	0.1	1	2	0.5	1	2.9	0.2	0.3	1	0.02
larvae	4	7.8	1.9	1.7	225	9.9	-	-	-	-	-	-	-	-	-	-	-	-
adults	-	-	-	-	-	-	1	7.1	0.1	1	2	0.5	1	2.9	0.2	0.3	1	0.02
Diptera	23	45.1	18.6	16.5	1834	80.6	2	14.3	0.8	8	250	65.4	21	60	20.5	30.3	3806	94.3
unknown adults	4	7.8	0.6	0.5	23	1	-	-	-	-	-	-	-	-	-	-	-	-
Chironomidae	17	33.3	17	15	1661	73	-	-	-	-	-	-	12	34.3	8.2	12.1	1092	27.1
larvae	14	27.5	14.8	13.1	1336	58.7	-	-	-	-	-	-	11	31.4	7.1	10.5	817	20.3
pupae	5	9.8	1.6	1.4	211	9.3	-	-	-	-	-	-	-	-	-	-	-	-
all stages	3	5.9	0.6	0.5	114	5	-	-	-	-	-	-	2	5.7	1.1	1.6	275	6.8
Muscidae larvae	2	3.9	0.4	0.4	17	0.7	-	-	-	-	-	-	5	14.3	1.7	2.5	92	2.3
Psychodidae larvae	-	-	-	-	-	-	2	14.3	0.8	8	250	65.4	7	20	9.4	13.9	2618	64.9
Syrphidae larvae	-	-	-	-	-	-	-	-	-	-	-	-	1	2.9	1.2	1.8	4	0.1
Tipulidae pupae & adults	3	5.9	0.7	0.6	133	5.8	-	-	-	-	-	-	-	-	-	-	-	-
Isoptera - *Hodotermes mossambicus*	5	9.8	3.4	3	81	3.6	6	42.9	3	29.9	74	19.4	-	-	-	-	-	-
unknown	2	3.9	0.1	0.1	4	0.2	1	7.1	0.8	7.5	9	2.4	-	-	-	-	-	-
Vertebrates	3	5.9	4	3.5	15	0.7	-	-	-	-	-	-	9	25.7	11.9	17.6	9	0.2
Osteichthyes (fish)	1	2.0	0.8	0.7	13	0.6	-	-	-	-	-	-	-	-	-	-	-	-
Amphibia (frogs)	-	-	-	-	-	-	-	-	-	-	-	-	2	5.7	1.7	2.5	2	0.05
Mammalia (mammals)	2	3.9	3.2	2.8	2	0.1	-	-	-	-	-	-	7	20	10.2	15.1	7	0.2
Rodentia	1	2.0	3	2.6	1	0.04	-	-	-	-	-	-	6	17.1	10.2	15.1	6	0.1
unknown	1	2.0	0.2	0.2	1	0.04	-	-	-	-	-	-	1	2.9	0.02	0.03	1	0.02
Plant material	3	5.9	0.4	0.4	15	0.7	1	7.1	0.1	1	10	2.6	1	2.9	0.02	0.03	5	0.1
Human discards	31	60.8	83.2	73.5	88	3.9	11	78.6	5.3	52.7	37	9.7	20	57.1	34.6	51.1	209	5.2
animal	24	47.1	70	61.8	64	2.8	8	57.1	4	39.8	16	4.2	1	2.9	1.1	1.6	4	0.1
chicken waste (abbatoir)	-	-	-	-	-	-	-	-	-	-	-	-	17	48.6	29.2	43.1	201	5
[illegible]	[illegible]	[illegible]	[illegible]	11.7	24	1.1	3	21.4	1.3	12.9	21	5.5	2	5.7	4.3	6.3	4	0.1

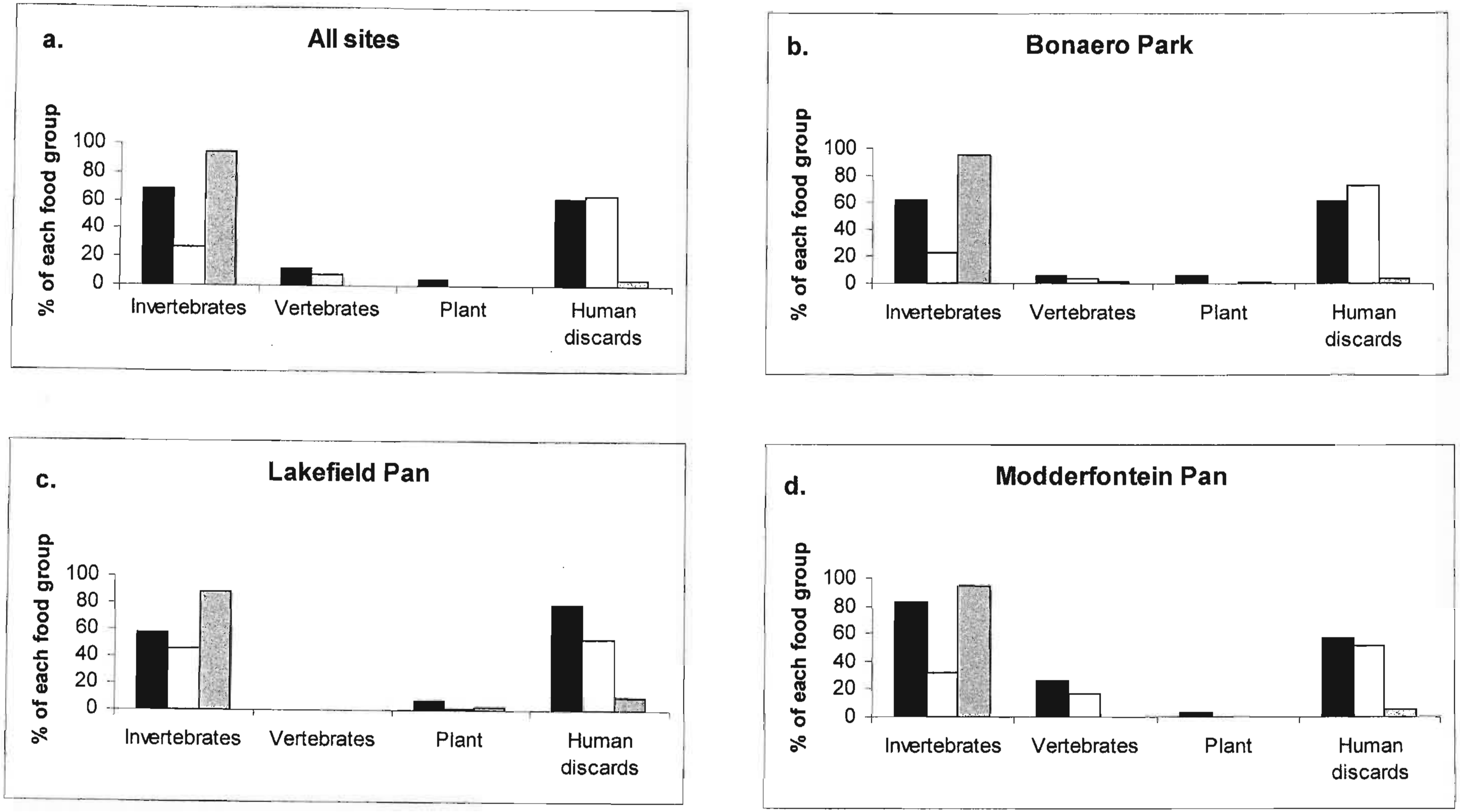


Figure 4.12. Frequency (black bars), mass (white bars) and numbers (grey bars) of different food groups from regurgitated pellets of Grey-headed Gull chicks from: all Gauteng sites combined (**a**.), Bonaero Park (**b**.), Lakefield Pan (**c**.) and Modderfontein Pan (**d**.) .

variety of species from four insect orders, cockroaches (Blattodea), beetles (Coleoptera), flies (Diptera) and termites (Isoptera) were represented. The majority of insects selected were flies, especially bloodworms (Chironomidae larvae). Anthropogenic discards comprised mostly food items of animal origin, including cooked chicken and beef flesh and, to a lesser extent, grains and vegetables, especially maize meal and bread. The only vertebrates found in pellets at this site included 13 small fish fry (Osteichthyes) coming from one pellet and rodent (Mammalia) remains in another pellet.

At Lakefield Pan, anthropogenic discards occurred more frequently in pellets (79%) than did invertebrates (57%), but were almost equally represented in terms of overall mass (46% and 53% for invertebrates and human discards, respectively) (Figure 4.12c, Table 4.9). This site had the least diversity of prey items in chick pellets when compared to the other sites. Insects that featured prominently in the diet included termites and fly larvae (Psychodidae). Anthropogenic discards were comprised of similar items, and in similar proportions, to those found at Bonaero Park.

At Modderfontein Pan, the most commonly occurring food group in chick pellets was invertebrates (83% frequency), followed by anthropogenic discards (57%) and vertebrates (26%) (Figure 4.12d, Table 4.9). Anthropogenic discards contributed the largest proportion (51%) of food mass followed by invertebrates (31%) and vertebrates (18%). As in the Bonaero Park sample, the majority (94%) of individual prey items constituted invertebrates, which comprised mostly fly larvae, especially bloodworms. Psychodidae larvae were also fairly prevalent, occurring in 20% of all pellets sampled. Anthropogenic discards comprised mostly chicken feathers and raw chicken pieces, including intestines and feet. Vertebrate food items included six rodents and two frogs (Amphibia).

Comparisons between different age groups

The composition of regurgitated pellet samples was quantified according to three chick age groups: hatchling to five-days old, five- to ten-days old, and ten- to 20-days old. The proportion (% frequency and % mass) of each major food group for each of these categories for the three sites are illustrated in Figures 4.13 and 4.14.

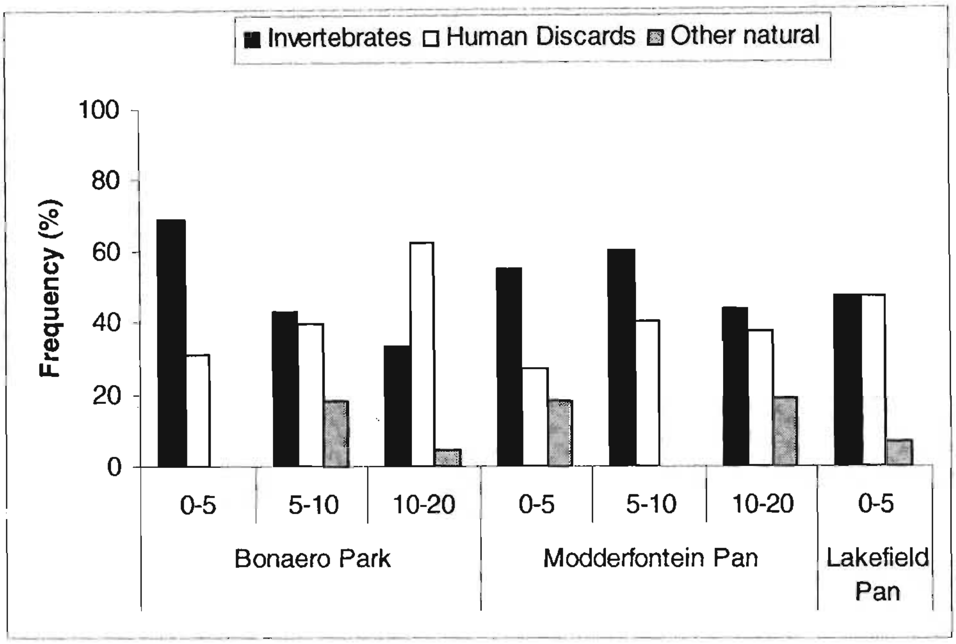


Figure 4.13. Relative age-related frequencies of different food groups found in regurgitated pellets of Grey-headed chicks at three sites in Gauteng: Bonaero Park, Lakefield Pan and Modderfontein Pan. Pellets were only collected from 0 to 5 days old chicks at Lakefield Pan. X-axis: age in days.

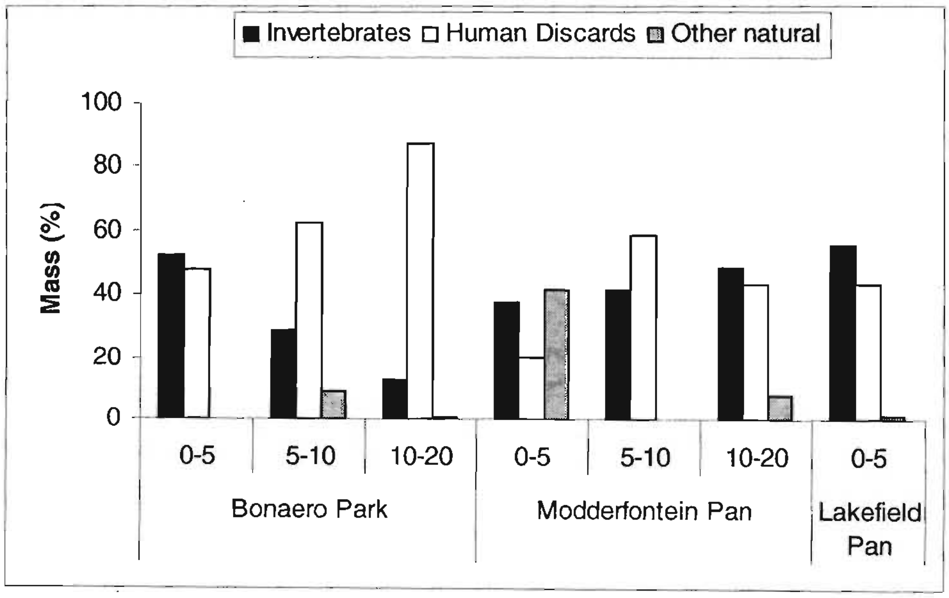


Figure 4.14. Relative age-related mass proportions of different food groups found in regurgitated pellets of Grey-headed chicks at three sites in Gauteng: Bonaero Park, Lakefield Pan and Modderfontein Pan. Pellets were only collected from 0 to 5 days old chicks at Lakefield Pan. X-axis: age in days.

The frequency of invertebrates in pellets of chicks, aged 0- to 5-days, was almost double that of anthropogenic discards at both Bonaero Park and Modderfontein Pan. Invertebrates also contributed to the largest proportion of mass of food items of chicks at this age. Pellets of chicks at Lakefield Pan contained almost equal proportions (frequency and mass) of invertebrates and anthropogenic discards. Pellets of birds, aged five- to ten-days old, at Bonaero Park contained higher proportions of anthropogenic discards, especially in terms of mass, than those of Modderfontein Pan, which retained insects as their primary food item. The composition of pellets of chicks, aged ten- to 20-days old, was predominantly anthropogenic discards at Bonaero Park, but at Modderfontein Pan pellets contained almost equal proportions of both, with invertebrates being slighter greater. Therefore, for both Bonaero Park and Modderfontein, invertebrates were more frequent in chick diets during the early stages of development but were gradually replaced, in varying degrees, by other food items as the chicks got older.

Comparative chick survival

A comparison between the survival rates of chicks at Bonaero Park and Modderfontein Pan was made possible by observations on penned chicks at both of these sites. Because pens were only erected around certain nests after chicks had already hatched and had managed to survive for a few a days, these results are not a true reflection of the fledgling/survival rates of Grey-headed Gull chicks in Gauteng. They are only useful in comparing the relative survival rates of these sites.

Fledging rates were higher at Modderfontein Pan with 73% of all chicks in pens surviving to 30 days old compared to 66% at Bonaero Park (Table 4.10); these differences were not statistically significant (χ^2=3.59, df=1, P=0.058). A similar number of chicks were found dead in pens at both sites during the course of the study. The cause of death for all chicks at Bonaero Park was undetermined, as there were no visible wounds or any signs of struggle or predation. In contrast to that site, the six chicks found dead at Modderfontein Pan had noticeable wounds and it was clear that they had been killed by a predator (Plate 4.1b). Owing to the nature of the wounds, i.e. flesh had clearly been torn from the carcasses; the most likely predators were Marsh Owls *Asio capensis*. I flushed three pairs of this species while conducting a peripheral

Table 4.10. Comparison of fledgling (survival) rates of Grey-headed Gull chicks enclosed in pens at Bonaero Park and Modderfontein Pan including reasons for chick mortalities.

	Bonaero Park	Modderfontein Pan
Total nests	15	8
Total no. chicks	35	22
No. chicks fledged	23	16
Fledging rate (%)	66	73
Chick mortality:	7	6
predated	0	6
unknown	7	0

walk of the pan (Plate 4.2a); one of these pairs was accompanied by a fully-fledged juvenile. These birds were immediately mobbed by Grey-headed Gulls after they were flushed. Two other species that were observed in the vicinity of the nests were Grey Herons *Ardea cinerea* and Sacred Ibis *Threskiornis aethiopicus*. Both of these species were also mobbed by Grey-headed Gulls (Plate 4.2 b & c, respectively).

Discussion

Differential growth rates

Grey-headed Gull chicks, like those of most Larids, show fastest growth initially in their lower extremities, i.e. foot and tarsus, while the greatest investment in wing growth only occurs in the latter stages of development (O'Connor 1984). This growth strategy is said to have evolved as an adaptation to avoid predation (Ricklefs 1973). According to this author, interspecific differences in growth rates are strongly influenced by the timing of development of flight capabilities. This is especially relevant for gulls whose proportionate requirements, in terms of overall body weight, necessary for wing development far exceed those required for tarsus and foot, i.e. the difference in associated muscle mass. The semiprecocial mode of development of gulls allows them to gain weight relatively fast compared to most other non-altricial species because wing development is stunted until later on in the growth period. In this context it is interesting to note that a general decline in peak growth rates of mass for Grey-headed Gull chicks was followed by a corresponding increase in the growth rate of wing. This is undoubtedly influenced by the general increase in energy requirements of gull chicks during development. In a study on the energetics of the

Kittiwake *Rissa tridactyla*, a gull species of similar size to the Grey-headed Gull, Gabrielsen *et al.* (1992) showed that overall energy requirements of chicks increased as development advanced. A large portion of this energy was allocated to resting metabolism (53%) and only a small proportion (24%) was deposited as tissue during development. Energy allocated to activity was especially evident from approximately 16 days until fledging, during which time it contributed 22% of the total metabolisable energy intake. This period corresponds with the period of maximal growth for wing and the corresponding increase in flapping activity and would explain the concomitant increase in growth rate for wing with a general decrease in growth rate for mass of Grey-headed Gull chicks (Figures 4.1 & 4.2).

The increase in the variability in growth rates for mass of Grey-headed Gull chicks with age is probably also related to this increase in demand for energy. This is because as the fledgling period advances, more pressure is placed on adults to meet the increased demand for food by the developing chicks, which may even result in a facultative adjustment in parental provisioning behaviour (e.g. Morbey & Ydenberg 1997). The ability of adults to meet these requirements will depend on their foraging efficiency, which will likely vary between pairs.

For all measurements other than mass, there was a higher variation in average growth rates during the lowest growth rate periods, while the least variation occurred just after peak growth rates. For wing, culmen and head measurements this was evident just after hatching and was probably influenced by the variation in embryonic development associated with parental investment at the egg production stage. Advanced embryonic development has been shown to favour accelerated growth in gull hatchlings (Risch & Rohwer 2000 and references therein) and the great variety in egg sizes within and between the three sites sampled (see Chapter 2) could therefore have influenced rates of chick development, especially during the hatchling period. This would also have been compounded by the so-called 'third-chick disadvantage' (for review see Pierotti & Bellrose 1986) and would explain why certain hatchlings had negative growth rates in mass; this would have ultimately affected the variation in growth rates.

The decrease in variation during peak growth rate periods was probably influenced by an upper limit on physiological growth rates as defined by the Grey-headed Gulls' genotype (Drent *et al.* 1992; Arendt 1997). It also suggests that environmental conditions, notably food availability, for chicks at all sites during the course of this study were adequate to allow most chicks to reach their optimal growth rates. The discrepancy in variation of average growth rates for bill was probably influenced by the method employed in measuring the culmen, i.e. the difficulties associated with determining the point at which the rhamphotheca meets the skin.

Empirical growth curves

The advantage of using empirical growth curves is exemplified by the growth curve for mass of Grey-headed Gull chicks (Figure 4.1B). Both the Gompertz and logistic growth curves cannot accommodate for the approximately linear growth of chicks when growing at their fastest, i.e. between seven and 16 days old. The empirical approach allows one to analyse fluctuations in growth at a finer scale. For example, when comparing the growth curves of mass, wing and foot (Figures 4.1B, 4.2B and 4.6B), it is evident that the peak period for growth rate in mass exceeds that of foot by approximately four days which suggests that once the chicks are sufficiently mobile there is still a period of peak growth in mass that doesn't correspond to either leg or wing development. This can probably be attributed to the growth of other body structures, e.g. digestive organs (O'Connor 1984).

One of the advantages of using growth curves to analyse chick development is that they facilitate comparisons between different species (Ricklefs 1967, 1968). The only other bird species for which empirical growth curves have been generated in the fashion pursued here is that of the Swift Tern *Sterna bergii* (Le Roux 2006) (Appendix 4.1). Comparing the empirical growth curves of Grey-headed Gull chicks (Figures 4.1 – 4.6) with this species, their development appears to be very similar. An exception is the growth curves of culmen, which is more sigmoidal in the Grey-headed Gull. Swift Tern chicks grow their culmen evenly from hatching up to 20 days whereas Grey-headed Gulls chicks accelerate growth in this region after approximately eight days old. The average bill length of Swift Tern adults (63.6mm, Le Roux 2006) is almost double that of the Grey-headed Gull (36.7mm, Table 5.7) which suits their mode of feeding, viz. plunge diving for, mostly, pelagic fish just below the water surface (Crawford & Hockey 2005). Other fish-eating tern species, e.g. Common *Sterna hirundo* and Sandwich *Sterna sandvicensis* terns, feed their chicks fish (Klaasen *et al.* 1992) and it is reasonable to assume that Swift Terns do the same. It would therefore be advantageous for Swift Tern chicks to grow their bill rapidly at the onset of development so as to handle their food more efficiently and thereby avoid kleptoparasitism. Presumably it is less important for Grey-headed Gull chicks to grow this area of the integument initially as most food items require less specialised handling techniques, e.g. Diptera larvae (Table 4.9).

Chick diet

Feeding on anthropogenic discards by Grey-headed Gulls has been well documented in South Africa, particularly at refuse dumps (Waller 1961; Farkas 1962; Nicole 1982; Grond 1986) and picnic sites and fast-food outlets (Tarboton 1970; van Heerden 1983; Uys 1986). Many of these accounts come from Gauteng. Invertebrates have also been regularly documented as food items for Grey-headed Gulls, and these include: termite alates (Milstein 1970; van Heerden 1983; Grond 1986; Berruti 1990; Kok & Hewitt 1990), unidentified insects (Farkas 1962; Underhill 1987), and prawns (Cyrus 1982). Other food items recorded include: small rodents unearthed by ploughing (Farkas 1962), fish (Brooke 1968, 1971; Hustler 1986), and frogs (van Heerden 1983). Results from this study have elaborated on this variety, especially where it concerns the reproductive stage in the Grey-headed Gulls' life cycle. Of interest was the ubiquity of Diptera larvae in the diets of chicks at all sites, and in particular, Chironomid (bloodworms) and Psychodidae larvae. Chironomids are common inhabitants of fresh-water systems (Scholtz & Holm 1985) and are known to favour organically polluted water, such as the permanent and ephemeral wetland systems in Gauteng (e.g. Bonaero Park and Lakefield Pan) that receive nitrate- and phosphate-rich run-off from surrounding residential and industrial land-uses (Arthur Harrison pers. comm.). All stages of the life cycles of these flies frequently occur in large densities (Scholtz & Holm 1985). Depending on the species, Psychodidae larvae are also known to complete the larval stage of their life cycle in moist conditions, such as wetlands, moist soil, compost heaps and nutrient rich water bodies, e.g. sewage filter beds and septic tanks (Scholtz & Holm 1985).

In addition to the situations in which Grey-headed Gulls have been recorded feeding on anthropogenic discards (mentioned above), we recorded Grey-headed Gulls feeding on chicken off-cuts at the Daybreak Farms Chicken Abattoir (Plate 3 a & b) in close proximity to Modderfontein Pan; these off-cuts constituted a large proportion of the chick diets at this breeding colony. Highly nutrified run-off, containing waste material from this abattoir, was discharged into the adjacent dam (pers. obs.) and this probably caused favourable conditions for Diptera larvae, especially bloodworms. Large numbers of adult Grey-headed Gulls were observed surface-feeding on small prey items just below the surface of this dam (Plate 3c). The water at Modderfontein Pan originates from this dam and biological water conditions are likely to be similar at this site. The relatively high incidence of vertebrates in the diet of chicks at this site is probably directly related to the surrounding agricultural land use. Most of these prey items were rodents and unfortunately we were not able to identify them to species level. However, all of them appear to be the same species (based on overall size and colour) and probably constitute a common species in the area either associated with the cultivated fields (mostly maize) or the many chicken hatcheries and associated industries in the area.

The diet of Grey-headed Gulls is similar to other hooded gull species for which information on dietary composition is available: Slender-billed *Larus genei* and Black-headed *Larus ridibundus* gulls (del Hoyo *et al.* 1996); Silver and Black-billed gulls (Higgins & Davies 1996); and Hartlaub's Gull *Larus hartlaubii* (Hockey & Crawford 2005). Both Slender-billed and Black-billed gulls do not appear to utilise human refuse, with the former concentrating more on fish. It would seem, therefore, that the Grey-headed Gull is more similar to Silver and Black-headed gulls with regards to its catholic diet; all food types recorded of Grey-headed Gull chicks during this study have also been recorded for these species. Despite the wide range of prey items selected for, during chick-rearing Black-headed Gulls have been known to feed their chicks predominantly invertebrates, especially earthworms, and Silver Gulls have been known to feed their chicks predominantly insects especially in the earlier stages of chick development. This suggests that the availability of certain invertebrate food types has had an important influence on the evolution of the reproductive life history of certain hooded gull species. Some of these life history traits probably include selection of breeding sites, timing of breeding and overall colony size limitations.

Growth rate comparisons

For all morphological traits, chicks at Modderfontein Pan had the fastest growth rates and chicks at Lakefield Pan had the slowest growth rates. This was particularly evident for foot and wing measurements and less so for the other measurements. The lack of any significant differences between mass growth rates suggests that chicks from all sites were sufficiently nourished to achieve fledging; this would negate any influence of serious limitations on food resources for chick development at all sites studied in Gauteng. However, the differences between chicks of different hatch order are significant at all sites. These differences are apparent for both young chicks, viz. as expressed through foot development, and older chicks, viz. as expressed through wing development, at Bonaero Park but are only apparent for young chicks at Modderfontein Pan. Unfortunately, there were not many older chicks measured at Lakefield Pan and they will therefore be omitted from the present discussion. Not only did the overall growth rate of chicks at Modderfontein Pan exceed those of Bonaero Park, but C-chicks at the former site expressed marked ‘catch-up growth’, and even exceeded wing growth rates of B-chicks. Conditions would therefore seem favourable for chicks at this site throughout the chick-rearing period. There are number of possible reasons for this:

1. Oometric differences – positive correlations between egg volume and corresponding chick growth rates have been recorded for Slaty-backed Gulls *Larus schistisagus* (Watanuki 1992), Thick-billed Murre *Murre lomvia* (Hipfner & Gaston 1999), and Razorbill *Alca torda* (Hipfner 2000). All but the study on Slaty-backed Gulls were experimentally controlled for confounding influences of parental quality and showed that wing growth rates were significantly influenced by egg volume. These authors attribute this association to the benefits that increased availability of sulphur amino acids in the egg, which the chick uses to grow its feathers. Although there is clear adaptive significance of this association in Thick-billed Murres and Razorbills, the same can only be postulated for gulls in general. What is clear from the literature, however, is that egg volume has a

definite influence on the size of chicks at hatching (Hipfner 2000 and references therein).

2. Food quality and quantity – tissue growth and associated growth rates are influenced by available nutrients (Ricklefs 1973). Different food types vary with respect to their nutrient content with the result that chick growth rates vary according to quality of diet, e.g. Slaty-backed Gull (Watanuki 1992), Herring Gulls *Larus argentatus* (Bukacinska *et al.* 1996), and Pigeon Guillemots *Cepphus columba* (Golet *et al.* 2000). The quantity of food brought to the chick will be influenced both by the size of individual prey items as well as the frequency of foraging bouts and has an important influence on chick growth rates, e.g. for Herring Gulls (Hunt 1972) and for Arctic Terns (Monaghan *et al.* 1989).
3. Proximity to feeding grounds – various studies have attributed the proximity of feeding areas to breeding sites as important in influencing various breeding parameters such as chick growth rates, e.g. for Herring Gulls (Hunt 1972), for California Gulls *Larus californicus* (Smith 1972), and review by Golet *et al.* (2000). This would affect provisioning rates as well as the time spent guarding the chicks.
4. Parent quality – parental quality includes parent age and therefore experience, as well as the general condition of the adults during breeding. This has important implications for feeding efficiency, as high quality gulls are usually more efficient in securing sufficient nutrients for chicks, e.g. for Herring Gulls (Bukacinska *et al.* 1996; Risch & Rohwer 2000).
5. Predation and disturbance – an increase in both of these inter-related factors may result in increased energy expenditure in chicks as well as higher attendance rates of adults, the latter phenomenon having indirect influences on provisioning rates. These factors have been suggested by Morbey & Ydenberg (1997) to influence the growth rates of Cassin's Auklets *Ptychoramphus aleuticus* growing in high disturbance/predation regimes.
6. Colony size and density – this refers to density dependent implications (as was discussed in Chapter 2) influencing activity budgets of chicks as well as increased competition for food at feeding grounds, e.g. for Herring Gulls (Spaans *et al.* 1987).

Although egg volumes were significantly larger for Grey-headed Gulls breeding at Modderfontein Pan (Chapter 2), it is unlikely that there was a direct influence of this parameter on chick growth rates. The effects of parental quality, which would likely be expressed during both the egg stage and the chick rearing stage, were probably more important than the intrinsic effects of egg volume. This suggests that prevailing environmental conditions were more favourable for birds at this site during both stages of reproduction when compared to the other sites. I do not have data on parental age but other authors have suggested that parental condition is more likely to be influenced by environmental conditions rather than the actual age of the bird (Bukacinska *et al.* 1996; Risch & Rohwer 2000). This would be especially relevant if food was readily available in good quantities, of good quality and in close proximity to the breeding ground. This was certainly true for the Modderfontein Pan situation as chicken off-cuts and insect larvae were readily available in large quantities only *ca* 1.8 km away (Figure 2.1). This availability of food was also probably more sustainable for this relatively small colony and competition for this resource was expected to be small. Further evidence for these favourable conditions benefiting chick growth rates is expressed in the fast ‘catch-up growth’ of the C-chicks at Modderfontein. Pierotti & Bellrose (1986) in a study on the Western Gull *Larus occidentalis* showed that good feeding conditions (i.e. abundant good quality food in close proximity to their breeding colony) resulted in an absence of the so-called ‘third-chick disadvantage’. C-chicks at Modderfontein Pan had significantly smaller foot growth rates than A- or B-chicks, which suggests that feeding conditions may have improved during the course of chick development. The increased use of chicken off-cuts as the chicks got older (Figures 4.13 and 4.14) probably influenced this catch-up growth.

The slower growth rates of C-chicks at Bonaero Park throughout their development period could have been influenced by density dependent factors such as food acquisition and disturbance of chicks at the colony. This may have been compounded by the poorer nutritional value of anthropogenic discards brought to chicks, especially in the latter stages of development (Figures 4.13 and 4.14). Belant *et al.* (1993) in a study on the importance of landfills to nesting Herring Gulls concluded that landfills were unimportant when alternate, high-quality food sources were available. Similarly, Pierotti & Annett (1987) suggested that ‘garbage’ is a low-quality food when compared to other more 'natural' food items. The above-mentioned factors proposed as influencing chick growth rates at Bonaero Park could equally be applied to chicks at Lakefield Pan, which were similarly situated. However, the circumstances here may have been worsened by the presence of inexperienced adults (see Chapter 3) as well as increased disturbance due to construction activity. Chicks were frequently observed scattering to the adjacent reedbed shoreline for cover when any workers from the construction site approached the colony (pers. obs.). On their return to their nest sites, 'intruding' chicks were regularly attacked by neighbouring adults, which may have placed excessive demands on their energy requirements. This would explain the relatively slow and variable growth rates of all chicks at this site.

As discussed earlier, a significant proportion of energy utilised by chicks during their development is allocated to activity, especially during the latter stages of development, i.e. at the onset of accelerated wing development. One would expect that energy budgets for chicks being reared in colonies with higher predation levels would impose greater demands on their energy requirements related to activity. This may explain the absence of any significant differences between mass growth rates between the sites despite there being significant differences in growth rates of locomotary body structures. Modderfontein Pan was the only site where chick predation was evident and it is possible that chicks, at this site, exhausted a large amount of energy on activity associated with escaping or concealing themselves from potential predation.

Conclusion

This study is the first on the growth and development of Grey-headed Gull chicks. The empirical approach to growth rates used, while only available for one other species, provides an accurate interpretation of the growth of this species and the growth curves generated from this method should make for interesting comparisons between the only other two South African breeding gull species, viz. Hartlaub's *Larus hartlaubii* and Kelp *Larus dominicanus* gulls, as well as other Laridae species. The lack of any significant differences between growth rates in mass between the three study sites suggests that qualitative inter-colony differences are slight. However, the significant differences in wing and foot development, and the relative disadvantages of last-hatched chicks between sites, paints a finer picture of the suitability of each breeding site. Interestingly, Modderfontein Pan, a site on the edge of the Grey-headed Gull's core breeding population, was the most suitable in terms of growth rates, which is further evidence in support of limiting density dependent factors operating within the more centrally located sites (as was the case for the egg stage). This chapter also presents the first detailed study of the diet of the Grey-headed Gull during the breeding season. An interesting finding was the preference for invertebrates during the early stages of chick development, even at Bonaero Park, a site in close proximity to landfill sites, where one would expect anthropogenic discards to be the most commonly exploited food item. Results of the dietary analysis show that the adults from all sites preferred to feed their chicks food of anthropogenic origin during the latter stages of development, but that the nutritional quality of these items, i.e. chicken offal versus general human discards, likely differed between sites. More intensive study is required to verify this hypothesis and food quality could have an important bearing on the breeding success of this species in Gauteng.

Appendix 4.1. Empirical growth curves for Swift Tern *Larus bergii* chicks for five measurements: mass, wing, culmen, head and foot (Le Roux 2006).

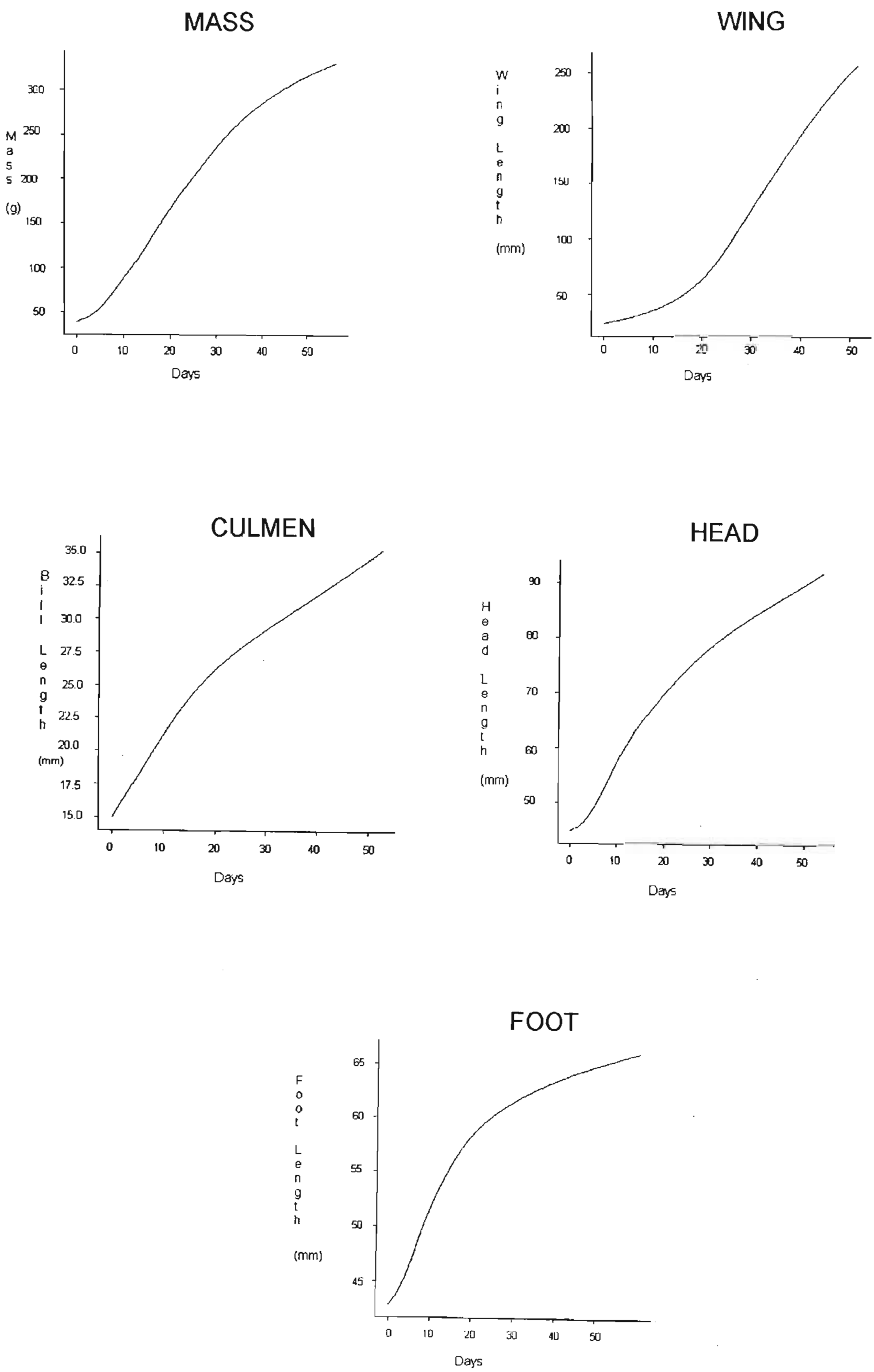
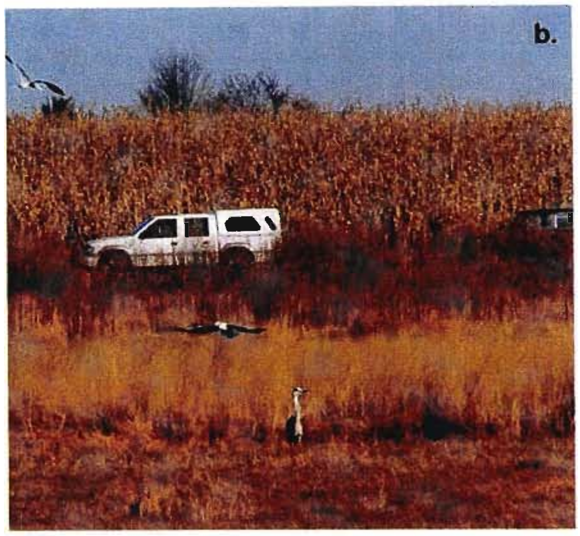


Plate 4.1. a. Wire-mesh pen erected around Grey-headed Gull nest at Modderfontein Pan, Gauteng. **b.** Remains of predated Grey-headed Gull chick at Modderfontein Pan.



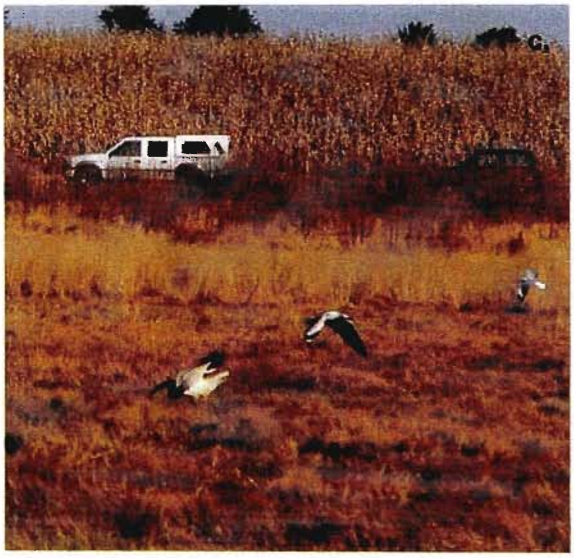


Plate 4.2. a. Marsh Owls *Asio capensis* flushed at Modderfontein Pan. **b.** Grey Heron *Ardea cinerea* being mobbed by Grey-headed Gulls at Modderfontein Pan. **c.** Sacred Ibis *Threskiornis aethiopicus* being mobbed by Grey-headed Gulls at Modderfontein Pan.

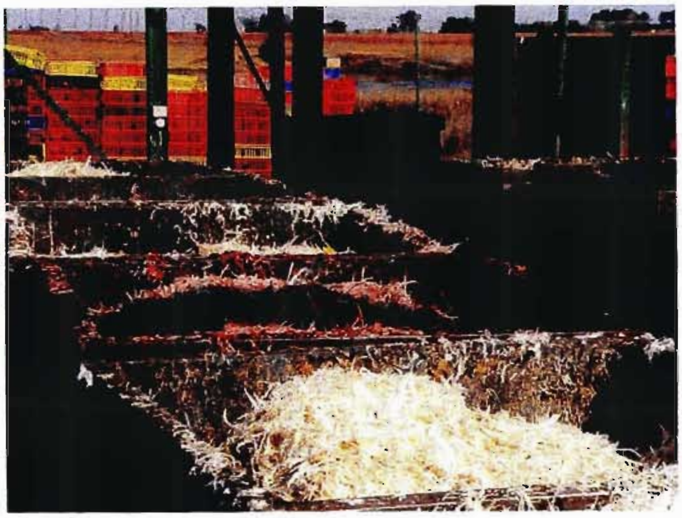


Plate 4.3. a. Contents of disposal bins at Daybreak Farms Chicken Abattoir. b. Grey-headed Gulls feeding on contents of bins at Daybreak Farms Chicken Abattoir. c. Grey-headed Gulls surface-feeding on dam adjacent Daybreak Farms Chicken Abattoir.

Chapter 5

Ageing, sexing and moult of the Grey-headed Gull *Larus cirrocephalus* in South Africa

Summary

Plumage and bare-part characteristics of 263 adults, 80 immatures and 28 juvenile Grey-headed Gulls *Larus cirrocephalus*, trapped in Gauteng and Durban between April 2004 and July 2005, suggested that Grey-headed Gulls can be divided into six discrete age classes. Re-sightings of ten individually recognisable (colour-ringed) birds of known age were used to validate this classification. Differences between my results and previous age classifications include: a more detailed account of the variability in bare-parts colouration of adult birds; the potential for first-summer birds to have pale-greyish eyes; and the potential for second-winter birds to have little or no contrast between the upper secondaries and the remainder of the upper-wing. Age-related morphometric differences revealed juveniles to be significantly heavier than adults and this is probably related to the breeding condition of adults and the relative advantage of landfill sites to juveniles. The morphometrics of 48 sexed adults were used to generate a discrimant function to sex Grey-headed Gulls. The most important variables used in this discriminant function were head, followed by culmen, foot and wing measurements, with all measurement values being significantly greater for males. Mean primary moult duration of adults, using the percentage of feather mass grown, was calculated as 136 days between 12 October (mean starting date) and 24 January (mean completion date) and mostly occurring during their non-breeding season. The timing of primary moult in immatures was more variable than adults. In both adults and immatures, the timing of moult in the outermost secondaries (S1 – S10) coincided approximately with the moulting of the central primaries. This was followed by a second wave of moult in the innermost secondaries. Tail moult was mostly associated with the early stages of primary moult for both age groups, and head moult in adults occurred in November and December (into the non-breeding condition) and again between March and May (into the breeding hood).

Introduction

In population and ecological studies it is often necessary to age and/or sex individual study animals (Goodman 1980; Newton 1998). Many bird species are dimorphic in plumage and can be sexed in the field with relative ease, e.g. in the Charadriiformes: phalaropes and Painted Snipe *Rostratula benghalensis* (del Hoyo *et al.* 1996). Monomorphic birds, however, such as gulls, provide the field worker with a challenge when trying to determine their sex (Coulson *et al.* 1983). Age determination in long-lived species poses similar problems (Olsen & Larsson 2003).

The Grey-headed Gull is one of ten species in the 'masked' gull species group; relatively small gulls that invariably possess a contrasting hood during the breeding season (Crochet *et al.* 2000; Given *et al.* 2005). Some of these species are extremely similar to each other in appearance; especially in non-breeding plumage (Grant 1978; Chandler 1989; Olsen & Larsson 2003). The long-lived nature of these birds, like all gull species, is reflected in their delayed maturity and in a variety of age classes, evident in different plumages and colouration of the bare-parts. These age classes are usually defined by season as it relates to the timing of breeding and the subsequent influence on the timing of moult. While juveniles, and non-breeding and breeding adults are usually readily distinguishable within a species, immature stages may be less easily assigned to any definitive age-class, owing largely to the variety of intermediate plumages (Grant 1978). The most recent, detailed account describing the identification of various age-classes of the Grey-headed Gull is by Olsen & Larsson (2003) and is summarised as follows:

1. Adults – head with grey hood (breeding season) and white with grey ear-spots (non-breeding season); hindneck white (breeding) and pale-grey (non-breeding), saddle and upper-wing coverts grey; white mirrors on outer primaries P10, P9 and sometimes P8; bill and legs red; eyes yellow/white; and orbital ring red/orange.
2. Juveniles – head white with greyish-brown shading; mantle and scapulars scaled brown; upper-wing coverts grey-brown, no primary mirrors, black subterminal tail-bar; bill and legs pale flesh to yellowish-flesh; eye brown; and orbital ring reddish/brown.

3. First-winter – head usually white with eye and ear spots; hindneck pale-grey; mantle and scapulars grey sometimes with a few retained juvenile features; tail as juvenile; bill with reddish-brown base and legs dark orange-brown; eye sometimes pale brown.
4. First-summer – some acquire adult-like hood and lose pale grey on hindneck; dark juvenile feathers become faded; and tail disappears with wear.
5. Second-winter – similar to non-breeding adult except: darker secondaries; small mirrors usually only on P10, sometimes on P9; tail white; bill, legs and orbital ring dull flesh to reddish- or orange-brown; eye usually pale, sometimes intermediate between juvenile and adult.
6. Second-summer – similar to adult summer, but generally with more black on wing-tip, darker terial centres and often darkish eye.

Sexing of gulls in the field is extremely difficult and can only be accomplished through close observation of known pairs (e.g. Rodriguez & Pugesek 1996) or by the analysis of morphometrics, e.g. through the use of discriminant functions (e.g. Coulson *et al.* 1983; Allaine & Lebreton 1990; Bosch 1996; Rodriguez & Pugesek 1996).

The literature on moult in masked gulls is extensive and is summarised by Dwight (1925) for all gull species, Cramp & Simmons (1983) and Olsen & Larsson (2003) for Palearctic and north American species (including Grey-headed Gull), and by Higgins & Davies (1996) for Australian and New Zealand species. Information on moult in Hartlaub's Gull *Larus hartlaubii* has been described by Crawford & Underhill (2003). To date, most moult studies have been concerned with the primaries and there is little information published on secondary moult, especially for the northern hemisphere species.

The first part of this chapter aims to provide guidelines for the ageing of Grey-headed Gulls, with special reference to the immature stages. In the second part, I provide a discriminant function for the sexing of Grey-headed Gulls and compare the morphometrics of the various age-classes. In the last section I deal with various aspects of moult in this species, including the timing and duration of primary moult, as well as describing the secondary moult process.

Methods

Capture techniques and procedure

All birds were trapped using a spear-gun driven net (McInnes *et al.* 2005b, Appendix 5.1). The trap was employed on landfill sites in Gauteng and on beaches in Durban. Grey-headed Gulls were lured within range of the net by baiting them with restaurant discards in Gauteng and with fishing bait (pilchards) in Durban. All birds caught were temporarily stored in ventilated cardboard boxes until processed. Each bird was weighed, ringed with both an individually engraved colour ring and a metal ring. Each bird was then measured and the moult was assessed.

Age classification

Grey-headed Gulls that were observed or caught in the field were assigned to the following basic age categories based on plumage and bare-part characteristics (Grant 1978; Olsen & Larsson 2003) and the season in which they were trapped. Adult features, as described by these authors, were confirmed by observations of actively breeding birds in Gauteng and Lake St Lucia, viz. breeding adults, and by re-sightings of colour-ringed birds, originally ringed as chicks at Lake St Lucia, that were known to be older than five years, viz. non-breeding adults. Likewise, juvenile features, as described by these authors, were confirmed from following the progression of marked chicks to fledging during the breeding study in Gauteng (see Chapter 4):

1. Breeding adult – pale eye, grey hood, white mirrors on outer primaries, and observed between May and August.
2. Non-breeding adult – pale eye, usually pale hood, white mirrors on outer primaries, and observed between October and March.
3. Juvenile – extensive brown and dusky markings in plumage (notably wing feathers and coverts), black terminal bar to the tail, dark eye.
4. Immature – all birds that could not be clearly identified as either juvenile or adult.

For adults, only those features that were not used in their classification, i.e. all plumage and bare part features other than head, primary mirrors and eye colour, were analysed in the results. All immature Grey-headed Gulls, used in the analysis, were divided into the same seasonal categories as adults, i.e. breeding and non-breeding.

We used Olsen & Larssons' (2003) age-categories for the immature stages in our discussion: first-winter (birds in their first non-breeding season); first-summer (birds in their second breeding season); second-winter (birds in their second non-breeding season); and second-summer (birds in their third breeding season).

Plumage & bare parts

The following topographically defined plumage sections were assigned a specific code related to their general appearance: head, greater primary coverts, primary mirrors, secondaries, greater, median and lesser coverts, mantle, scapulars, hindneck, and tail. Similarly, the following bare parts were assigned specific codes: bill, legs, eye and orbital ring. These codes are listed in Appendix 5.2 and illustrated in Plates 5.1 – 5.4.

Morphometrics

All Grey-headed Gulls caught were subjected to the following measurements:

1. Mass – each bird was placed in bag and weighed with an Ohaus spring balance to the nearest gram. The weight of the bag was subtracted from the total mass of the bird and bag.
2. Wing – taken with a wing rule (with back-stop) and measured as the flattened chord from the carpal joint to the tip of the longest primary, to the nearest mm. Wing measurements taken from birds in active primary moult in their outer primaries were discarded from the analysis.
3. Tail – taken with standard steel ruler and measured from point of insertion between two central retrices to tip of longest retrix, to the nearest mm.
4. Culmen – taken with dial callipers and measured from the tip of the upper mandible to where the rhamphotheca meets with the skin, to the nearest 0.1 mm.
5. Bill depth – taken with dial callipers and measured as the depth of the closed bill at the proximal edge of the nares, to the nearest 0.1 mm.

6. Head – taken with wing rule (with back-stop) and measured as a straight line from the occiput (rear of the skull) to the tip of the upper mandible, to the nearest mm.
7. Tarsus – taken with dial callipers and measured from the notch on the posterior side of the tibiotarsal joint to the anterior distal edge of the flexed tarsus, to the nearest 0.1 mm.
8. Foot – taken with wing rule (with back-stop) and measured from the proximal end of the tarsometatarsus to the end of the longest toe (excluding nail) of the flattened foot, to the nearest mm.

Sexing

A sample of sexed individuals was obtained by the following means:

1. Dissection (specimens) - dead Grey-headed Gulls were collected in the field, either found incidentally while conducting other related field work (only freshly dead specimens were collected), or those that died during capture. These birds were stored in a cooler-box with ice-bricks at around 6˚C for between two and seven hours before being frozen. Frozen specimens were allowed to thaw before being subjected to the same measurements, plumage and bare part analysis as mentioned previously. In addition to these measurements, the birds were dissected and their gonads examined to determine sex (a rough sketch was drawn to illustrate the size and extent of the gonads). The mass values of these birds were excluded from this analysis.

2. DNA - blood samples were taken from a number of Grey-headed Gulls, all captured on Gauteng's landfills, and were subjected to molecular analysis (Molecular Diagnostic Services Pty Ltd).

3. Observations - while conducting behavioural observations on Grey-headed Gulls at Lakefield Pan, Gauteng, certain colour-ringed individuals that were seen with their mates were scrutinized for any apparent indications of sex. Factors that determined this discrimination were based on previous studies of other gull species (e.g. see review by Rodriguez & Pugesek 1996) and included the overall size of the bird (i.e. larger/bulkier or slighter) when compared to its mate, the more or less aggressive role taken on by an individual in territorial confrontations, and the sex-related role in pre-copulation (e.g. courtship feeding) and copulation activities.

Moult

Each Grey-headed Gull trapped (or found dead, etc.) was examined for active moult in the primaries and tail. If active moult in the primaries was evident, then secondary moult was also examined. A standard moult scoring system (Ginn & Melville 1983) was used to record the stage of moult for each primary, secondary and tail feather. Details of moult scores are listed in Appendix 5.2 and the numbered positions of each feather are illustrated in Figure 5.1. In order to calculate percentage feather mass grown (PFMG), all primary feathers of four Grey-headed Gull wings, coming from four specimens collected as freshly dead in Gauteng, were weighed to the nearest 0.01 g using an Ohaus electronic balance. Further moult data on the primaries were extracted from the following sources and were included in this analysis: 21 adult specimens from Durban Natural Science Museum, and ringing data coming from SAFRING cards. Information on the timing of head moult in adults was taken from monthly waterbird counts conducted in Durban Bay during 2004 and 2005 (see Chapter 2).

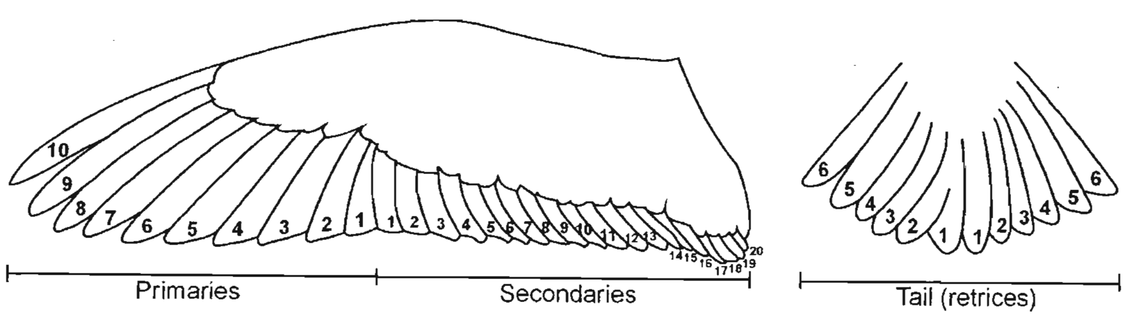


Figure 5.1. Numbered positions of primary, secondary and tail feathers of the Grey-headed Gull as used in the moult analysis.

Data analysis

Ageing

Summary statistics were tabulated for all measurements to compare the three age classes: adults, immatures and juveniles. One-way ANOVAs were applied to each of these measurements to identify any significant differences between the ages.

Sexing

A five-number table was created for all measurements and Student's t-tests were applied to all variables to search for significant differences between sexes. A Principal Component Analysis (PCA) was conducted on all morphometric variables other than bill depth and mass. Bill depth was excluded from the PCA due to the potential for it to continue increasing through adulthood; Coulson *et al.* (1983) recorded an increase in bill-depth measurements in Herring Gulls *Larus argentatus* until about nine years. Mass was excluded from the PCA due to the naturally fluctuating nature of this variable (Murphy 1996). The PCA was used to identify any outliers and to illustrate the relationship between the variables. A bivariate analysis was conducted on the two most independent variables that accounted for the most variation; this was for comparison purposes with the PCA. The same variables used in the PCA were used in the discriminant analysis.

Moult

Estimates of the duration of primary moult and start and finish dates were obtained using the model of (Underhill & Zucchini 1988). This method takes into account the PFMG as the governing protocol for estimating the stage of progression through primary moult. We used this method's "data type 2" moult index which includes all birds sampled, i.e. not just birds actively moulting.

Results

Ageing

Birds trapped

A total of 485 Grey-headed Gulls was trapped between April 2004 and July 2005 (Table 5.1). A large proportion of these birds (91%) was trapped at Gauteng's landfill sites, while a small proportion (9%) was trapped on Durban's beachfront and harbour. Of these birds, only those Grey-headed Gulls that had data for all plumage and bare part categories were used in the analysis and these comprised 263 adults, 80 immatures and 28 juveniles. A summary of the frequencies of plumage and bare part characteristics for all age groups of Grey-headed Gulls trapped in Gauteng and Durban are shown in Tables 5.2 – 5.5.

Table 5.1. Origin and numbers of Grey-headed Gulls trapped or collected as specimens in Gauteng and Durban, KwaZulu-Natal between April 2004 and July 2005.

			No. trapped			Specimens taken	
Locality	**Lat./Long.**	**Province**	**Ads**	**Imms**	**Juvs**	**Ads**	**Imms**
Korsman's Bird Sanctuary	2611S 2818E	Gauteng	-	-	-	3	-
Linbro Park Landfill	2605S 2807E	Gauteng	1	-	-	-	-
Rooikraal Landfill	2618S 2815E	Gauteng	92	20	48	-	-
Simmer & Jack Landfill	2612S 2808E	Gauteng	48	8	2	-	-
Steward's Pan	2612S 2817E	Gauteng	-	-	-	1	-
Weltevreden Landfill	2612S 2821E	Gauteng	202	8	13	3	-
Gauteng totals			**343**	**36**	**63**	**7**	
Blue Lagoon	2948S 3202E	KwaZulu-Natal	15	8	19	-	-
Fish Wharf	2951S 3100E	KwaZulu-Natal	-	-	1	-	-
South Africa totals			**358**	**44**	**83**	**7**	

Table 5.2. Numbers and % frequencies of head and saddle plumage characteristics for different age categories (A – adults, I – immatures, J – juveniles) of Grey-headed Gulls trapped in Gauteng and Durban between April 2004 and July 2005. Adults and immatures are seperated into the seasons in which they were trapped (B - Breeding season; N - non-breeding season). Plumaged codes are described in Appendix 5.2.

Age	Season		n	Head 1	Head 2	Head 3	Hind-neck 1	Hind-neck 2	Hind-neck 3	Mantle 1	Mantle 2	Mantle 3	Scapulars 1	Scapulars 2	Scapulars 3	Scapulars 4
A	B.	no.	251	0	0	251	251	0	0	0	0	251	0	0	0	251
		%		0	0	100	100	0	0	0	0	100	0	0	0	100
	N	no.	12	0	10	2	7	5	0	0	0	12	0	0	0	12
		%		0	83	17	58	42	0	0	0	100	0	0	0	100
I	B	no.	53	0	1	52	51	2	0	0	0	53	0	0	0	53
		%		0	2	98	96	4	0	0	0	100	0	0	0	100
	N	no.	27	4	22	1	0	25	2	0	3	24	0	1	5	21
		%		15	81	4	0	93	7	0	11	89	0	4	19	78
J	B	no.	28	28	0	0	28	0	0	16	12	0	7	16	5	0
		%		100	0	0	100	0	0	57	43	0	25	57	18	0

Table 5.3. Numbers and % frequencies of wing covert plumage characteristics for different age categories (A – adults, I – immatures, J – juveniles) of Grey-headed Gulls trapped in Gauteng and Durban between April 2004 and July 2005. Adults and immatures are seperated into the seasons in which they were trapped (B - Breeding season; N - non-breeding season). Plumaged codes are described in Appendix 5.2.

Age	Season		n	Upper wing coverts: Lesser coverts 1	Lesser coverts 2	Lesser coverts 3	Median coverts 1	Median coverts 2	Median coverts 3	Median coverts 4	Greater secondary coverts 1	Greater secondary coverts 2	Greater secondary coverts 3	Greater primary coverts 1	Greater primary coverts 2
A	B	no.	251	0	0	251	0	0	0	251	0	0	251	251	0
		%		0	0	100	0	0	0	100	0	0	100	100	0
	N	no.	12	0	0	12	0	0	0	12	0	0	12	12	0
		%		0	0	100	0	0	0	100	0	0	100	100	0
I	B	no.	53	0	2	51	0	0	2	51	0	1	52	46	7
		%		0	4	96	0	0	4	96	0	2	98	87	13
	N	no.	27	8	12	7	5	11	6	5	3	13	11	2	25
		%		30	44	26	19	41	22	19	11	48	41	7	93
J	B	no.	28	1	27	0	27	1	0	0	0	27	1	0	28
		%		4	96	0	96	4	0	0	0	96	4	0	100

Table 5.4. Numbers and % frequencies of wing and tail plumage characteristics for different age categories (A – adults, I – immatures, J – juveniles) of Grey-headed Gulls trapped in Gauteng and Durban between April 2004 and July 2005. Adults and immatures are seperated into the seasons in which they were trapped (B - Breeding season; N - non-breeding season). Plumaged codes are described in Appendix 5.2.

				Secondaries		**Primary mirrors**							**Tail bar**		
Age	**Season**		**n**	**1**	**2**	**0**	**1s**	**2s**	**2m**	**3m**	**2l**	**3l**	**1**	**2**	**0**
A	**B**	**no.**	251	250	1	0	5	32	127	80	1	6	0	0	251
		%		99	1	0	2	13	51	32	0	2	0	0	100
	N	**no.**	12	12	0	0	0	1	6	0	5	0	0	0	12
		%		100	0	0	0	8	50	0	42	0	0	0	100
I	**B**	**no.**	53	47	6	10	6	12	17	0	8	0	51	0	2
		%		89	11	19	11	23	32	0	15	0	96	0	4
	N	**no.**	27	4	23	26	0	1	0	0	0	0	6	16	5
		%		15	85	96	0	4	0	0	0	0	22	59	19
J	**B**	**no.**	28	0	28	28	0	0	0	0	0	0	27	1	0
		%		0	100	100	0	0	0	0	0	0	96	4	0

Table 5.5. Numbers and % frequencies of bare part characteristics for different age categories (A – adults, I – immatures, J – juveniles) of Grey-headed Gulls trapped in Gauteng and Durban between April 2004 and July 2005. Adults and immatures are seperated into the seasons in which they were trapped (B - Breeding season; N - non-breeding season). Bare part codes are described in Appendix 5.2.

				Bill colour								Leg colour								Eye colour				Orbital ring	
Age	Season		n	bro	bh	db	dr	fh	o	ob	rob	bro	bh	db	dr	fh	o	ob	rob	1	2	3	4	1	2
A	B	no.	251	52	0	3	26	0	1	48	121	78	0	0	2	3	28	42	98	251	0	0	0	251	0
		%		21	0	1	10	0	0	19	48	31	0	0	1	1	11	17	39	100	0	0	0	100	0
	N	no.	12	6	0	0	0	0	2	1	3	8	0	0	0	0	2	0	2	12	0	0	0	12	0
		%		50	0	0	0	0	17	8	25	67	0	0	0	0	17	0	17	100	0	0	0	100	0
I	B	no.	53	1	0	6	2	1	0	21	22	1	1	6	0	1	3	23	18	1	31	16	5	51	2
		%		2	0	11	4	2	0	40	42	2	2	11	0	2	6	43	34	2	58	30	9	96	4
	N	no.	27	0	3	1	0	22	1	0	0	0	4	3	0	18	1	1	0	0	2	3	22	2	25
		%		0	11	4	0	81	4	0	0	0	15	11	0	67	4	4	0	0	7	11	81	7	93
J	B	no.	28	0	24	0	0	4	0	0	0	0	10	1	0	17	0	0	0	0	0	0	28	0	28
		%		0	86	0	0	14	0	0	0	0	36	4	0	61	0	0	0	0	0	0	100	0	100

Table 5.6. Plumage and bare part characteristics of re-sighted Grey-headed Gulls trapped and re-sighted in Gauteng and Durban between May 2004 and September 2005. Ages: C – chick; J – juvenile; 1W – first winter; I – immature.

										Coverts							Bare parts					
	ID	Date (ddmmyy)	Time elapsed (days)	Locality	Age	Head	Hind-neck	Mantle	Scapulars	Lesser	Median	Greater secondary	Greater primary	Secondaries	Mirrors	Tail bar	Bill colour	Leg colour	Eye	Orbital ring	No. photos	Plate ref.
ringed	A3	28/01/2005		Blue Lagoon	I	2	2	3	3	2	2	2	2	2	0	2	fh	fh	4	2	2	5.5a
re-sighted	A3	25/02/2005	27	Battery Beach	I	2	2	3	4	3	3	3	2	2	0	2	fh	fh	-	2	2	5.5b
re-sighted	A3	30/09/2005	244	Battery Beach	I	3	1	3	4	3	4	3	1	1	0	0	rob	ob	3	-	4	5.5c, d
ringed	AL	19/11/2004		Blue Lagoon	I	2	2	3	4	1	2	1	2	2	0	1	fh	fh	4	2	0	-
re-sighted	AL	5/03/2005	105	Vetjies Beach	I	2	-	3	4	3	4	3	-	-	0	-	fh	fh	-	-	1	-
ringed	B7	24/11/2004		Blue Lagoon	I	1	2	3	4	1	2	2	2	2	0	1	db	db	4	2	1	-
re-sighted	B7	18/03/2005	113	Bay Beach	I	2	2	3	4	3	4	3	-	-	0	0	fh	fh	3	2	4	-
ringed	C6	26/11/2004		Blue Lagoon	I	2	2	3	4	1	3	2	2	2	0	1	fh	bh	4	2	1	-
re-sighted	C6	18/2/2005	83	Snake Park Beach	I	2	2	3	4	3	4	3	-	-	0	0	fh	fh	3	-	2	-
ringed	C7	1/12/2004		Blue Lagoon	I	2	2	3	4	1	3	3	2	2	0	1	fh	fh	4	2	1	-
re-sighted	C7	5/3/2005	93	Battery Beach	I	2	-	3	4	3	4	3	-	-	0	0	fh	fh	2	1	2	5.5e
ringed	EJ	29/12/2004		Blue Lagoon	I	1	2	2	3	1	1	1	2	2	0	1	fh	fh	4	2	0	-
re-sighted	EJ	9/09/2005	253	Addington Beach	I	2	1	3	4	3	4	3	1	-	2s	0	fh	ob	3	-	6	5.5f
ringed*	5H34645	03/09/2004		Port Elizabeth	C	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0	-
re-captured	EP	5/01/2005	124	Blue Lagoon	1W	2	2	3	4	2	2	2	2	2	0	2	fh	fh	4	4	1	-
ringed	ER	19/05/2004		Rooikraal Landfill	I	3	1	3	4	3	4	3	1	1	2s	0	ob	db	3	1	0	-
re-sighted	ER	11/07/2005	417	Lakefield Pan	I	3	1	3	4	3	4	3	1	1	-	0	ob	rob	2	1	1	-
ringed	JK	6/07/2004		Rooikraal Landfill	J	1	3	1	2	2	1	2	2	2	0	1	bh	fh	4	2	0	-
re-sighted	JK	9/06/2005	337	Lakefield Pan	I	3	1	3	4	3	4	3	-	-	2m	0	ob	rob	2	1	3	-
ringed	KL	6/07/2004		Rooikraal Landfill	I	3	1	3	4	3	4	3	1	1	2s	0	ob	rob	3	1	0	-
re-sighted	KL	23/06/2005	351	Lakefield Pan	I	3	1	3	4	3	4	3	-	-	-	0	ob	rob	2	1	2	-
ringed	UD	14/07/2005		Simmer & Jack Landfill	J	1	3	3	2	2	2	1	2	2	0	1	fh	fh	4	4	2	-
re-sighted	UD	5/09/2005	53	Simmer & Jack Landfill	1W	1	3	3	3	2	2	2	-	-	0	2	fh	fh	4	-	3	-

Adults (Tables 2 – 5)

Breeding season

All breeding adults had white hindnecks, grey mantles, grey scapulars, grey secondary coverts, grey and white primary coverts, no terminal tail bars, and red/orange orbital rings. One adult had dark dusky-grey secondaries with pale white/grey tips; all other adults had grey secondaries. Bill and leg colours were dominated (80% and 71%, respectively) by red variants, i.e. bright red/orange, dark-red and red/orange/brown. The remaining proportions were dominated (19% and 34%, respectively) by orange variants, i.e. orange and orange/brown.

Non-breeding season

Just over half (58%) the number of non-breeding adults had white hindnecks; all these birds were trapped between November and December. The remaining 42% had pale-grey hindnecks and all of these birds were trapped between January and February. All other plumage features for non-breeding adults were the same as those described for breeding adults. Bill and leg colours were dominated (75% and 84%, respectively) by red variants, i.e. bright red/orange, dark-red and red/orange/brown. The remaining proportions were dominated (25% and 17%, respectively) by orange variants, i.e. orange and orange/brown.

Immatures (Tables 2 – 5)

Breeding season

The majority of these birds had grey hoods with white hindnecks (98% and 96%, respectively) while only one bird had a white head with dusky ear and eye patches and two birds were recorded with pale-grey hindnecks. All birds had grey mantles and scapulars and the majority of birds had grey lesser, median and greater secondary coverts (96%, 96% and 98%, respectively). Two birds had remnants of brown/dusky plumage in their lesser and median coverts and one bird had remnants of this plumage in its greater secondary coverts. The majority of birds (87%) had grey and white greater primary coverts, the remainder (13%) having grey and white greater primary coverts with black terminal tips. Six birds had dark contrasting dusky-grey secondaries with pale white/grey tips while all other birds had grey secondaries. Most birds (81%) had some form of white primary mirrors; 34% had small mirrors in one or both of the outer primaries and 47% had medium to large mirrors in both outer primaries. The remaining birds (19%) were without mirrors. The majority of birds (96%) were without a black terminal tail bar while two birds had reduced or faded tail bars. In the bare parts, bill and leg colour was dominated by orange/brown (40% and 43% for bill and leg colour, respectively) and red/orange/brown (42% and 32%, respectively). Most birds had light-brown (30%) to pale-greyish (58%) eyes while five birds had dark-brown eyes and one bird had pale-white/yellow eyes. The latter bird was without primary mirrors. The majority (96%) of birds had red/orange orbital rings, the remainder (2 birds) having brown orbital rings.

Of all the birds with remnants of brown/dusky plumage in their upper-wing coverts (n=6), four birds were without primary mirrors and two birds had one small mirror each on their outermost primaries. Five of these birds had black terminal tips to their greater primary coverts and dark contrasting dusky-grey secondaries with pale-white/grey tips. Bare part colouration for all these birds was variable. The only two birds with tail bars, both had black terminal tips to their greater primary coverts and dark contrasting dusky-grey secondaries with pale-white/grey tips. Both birds were without primary mirrors; one of these birds had no sign of brown/dusky plumage in its upper-wing coverts. Of all birds without primary mirrors (n=10), five birds had black terminal tips to their greater primary coverts and dark contrasting dusky-grey secondaries with pale-white/grey tips. Bare part colouration for all these birds was variable.

Non-breeding season

The majority of birds (96%) were without a grey hood and of these birds, 81% had white heads with dusky ear and eye patches and 15% had white heads with extensive dark markings. Most birds (93%) had pale-grey hindnecks while two birds had brown/dusky patches on their hindnecks. Of all birds in this category (n=27), three birds were without brown/dusky plumage in their upper-wing coverts while all other birds had some extent of this plumage in their upper-wing coverts. Two birds had grey and white greater primary coverts, the remainder (93%) having black terminal tips to these feathers. Twenty-three birds had dark contrasting dusky-grey secondaries with pale-white/grey tips while four birds had grey secondaries. Only one bird had primary mirrors. Most birds (81%) had some form of a tail bar while five birds were without a tail bar. In the bare parts, bill and leg colour was dominated by flesh/horn (81% and 67% for bill and leg colour, respectively) and to a lesser extent by brown/horn (11% and 15%, respectively) and dark-brown (4% and 11%, respectively). Eye colour was mostly light to dark-brown with only two birds having pale-greyish eyes. The latter two birds were also the only birds to have red/orange orbital rings; all other birds had brown orbital rings.

Of the three birds without brown/dusky plumage in their upper-wing coverts: all birds had grey secondaries and were without a tail bar; two birds had pale-greyish eyes with red/orange orbital rings; and one bird had light-brown eyes with brown orbital rings. One of these birds was the only bird in this category to have a grey hood, primary mirrors and orange bill and legs.

Juveniles (Tables 2 – 5)

All juveniles had extensive dark markings on their heads and all these birds had brown/dusky plumage in their hindnecks, mantles, scapulars and lesser and median and greater secondary coverts. All birds had dark terminal tips to their greater primary coverts and dark contrasting dusky/grey secondaries with pale-white/grey tips. All birds were without primary mirrors and most birds (96%) had a prominent dark terminal tail bar with only one bird having a reduced or faded tail bar. In the bare parts, bill and leg colour was dominated by brown/horn (86% and 36% for bill and leg colour, respectively) and flesh/horn (14% and 61%, respectively). All birds had dark-brown eyes and brown orbital rings.

Birds examined in the field (re-sightings)

Ten individually recognisable Grey-headed Gulls, with engraved colour rings, were observed and/or photographed in the field and these were compared to plumage and bare part information recorded when initially trapped. (Table 5.6, Plates 5.5 & 5.6). One Grey-headed Gull, initially ringed as a chick by Mr A Schultz in Port Elizabeth

(SAFRING data), was recaptured as a first winter bird in Durban; information of this bird's features is also noted in Table 5.6.

The re-sighting of "UD" and the re-capture of "EP" are the only confirmed first-winter birds in this sample. Both birds had some extent of brown/dusky plumage in the upper-wing coverts, especially "UD" which was observed earlier in the season. Both of these birds had faded terminal tail bars and neither of them had any primary mirrors. "EP" had black terminal tips to its greater primary coverts and dark contrasting dusky-grey secondaries with pale-white/grey tips; unfortunately, these features were not recorded for "UD", due to poor visibility. Both birds had flesh/horn bill and legs and dark brown eyes. Only the orbital ring of "EP" was observed and this was brown.

Five Grey-headed Gulls were trapped at Blue Lagoon in Durban during the non-breeding season and were subsequently re-sighted within the same season between 27 and 113 days later. When ringed, all these birds had obvious brown/dusky plumage still evident in their upper-wing coverts and to a lesser extent in their mantle and scapular feathers. Their heads were mostly white with dusky ear and eye patches and their hindnecks were pale-grey. All these birds had a dark terminal tail bar and their bill and leg colour was mostly flesh/horn. Eye and orbital ring colour was dark-brown. The re-sighting of "A3" in February (Plate 5.5b), 27 days after capture, illustrates the fairly rapid replacement of brown/dusky coverts with mostly grey feathers, the only brown/dusky feathers still evident being the small amount visible in the median coverts. The dusky-grey secondaries and the tail bar still remained. "AL", "B7", "C6" and "C7" were re-sighted between 83 and 113 days after capture had no brown/dusky feathers evident in their plumage and the latter three had all lost their tail bar. The eye colour of "B7" and "C6" had changed to light-brown and that of "C7" had changed to pale greyish (Plate 5.5e).

Two birds, "A3" and "EJ", were re-sighted in the subsequent non-breeding season after initial capture. Comparing their plumage at this stage with their plumage in the previous non-breeding season, the head of "A3" had changed into a complete pale-grey hood (Plate 5.5d) while that of "EJ" remained white with dusky ear and eye patches. The hindneck colour in both birds had changed from pale grey to white and their greater primary coverts had lost their black terminal markings. "EJ" moulted into primaries with two small mirrors on P10 and P9 while "A3" was still without primary mirrors (Plate 5.5c). "A3"'s secondaries changed from dark contrasting dusky-grey with pale-white/grey tips to grey. Both birds had no sign of dusky/brown plumage and both were lacking a tail bar. Both birds' legs changed from flesh/horn to orange/brown. Bill colour for "EJ" remained the same while "A3" changed from flesh/horn to red/orange/brown. "EJ"'s orbital ring changed from brown to orange.

Three Grey-headed Gulls ("ER", "JK" and "KL") were re-sighted and photographed at Lakefield Pan, a Gauteng breeding locality, and their plumage and bare parts were compared to their appearance when ringed (Plate 5.6). "ER" and "KL" were immatures when ringed and "JK" was a juvenile when ringed. Re-sighted birds appeared almost identical to breeding adults except for their eye colour, which was pale-greyish. When ringed, "ER" and "KL" had small or reduced mirrors on their outer primaries as well as pale-brown eyes. The mirrors of "ER" and "KL" were not observed during the re-sightings but both birds' eyes had become paler (Plate 5.6 a & b). Both birds' bills had remained orange/brown while "ER"'s legs had changed from dark brown to red/orange/brown. Both "ER" and "KL" were confirmed breeding when re-sighted. "JK" had typical juvenile features when ringed: brown/dusky plumage showing in the wing coverts and saddle (mantle and scapulars), an extensively marked head, no primary mirrors, a prominent tail bar, horn-coloured bill and legs, and dark-brown eyes and orbital rings. When re-sighted 351 days later, it had completely transformed into a bird with mostly adult features; the only feature distinguishing it from a true breeding adult was the presence of grey in the eye (Plate 5.6c); the primary mirrors were not visible.

Morphometric variation

Summary statistics for all measurements for the three age classes are given in Table 5.7. All variables, other than the two leg measurements (foot and tarsus), showed highly significant differences between the age groups (ANOVA, mass, wing, tail, culmen, bill depth $P<0.001$; head $P<0.01$). Juveniles were significantly heavier than both immatures and adults, but were significantly smaller for wing, tail, head and culmen. Immatures weighed less than adults, had smaller wing and tail measurements

Table 5.7. Summary statistics for all Grey-headed Gull measurements showing the comparison between three age groups. One way ANOVAs were applied to each measurement to distinguish age-related differences (significant differences are indicated after adult means). Ages: A – adult; I – immature; J – juvenile. Q1 – lower quartile; Q2 – upper quartile.

	Age	Mean	SE	Min	Q1	Median	Q3	Max	n
Mass	A	300.3***	1.7	225	279.4	301	321.4	385	317
	I	293.3	4.3	228	275	290	308.8	370	44
	J	314.3	4.9	210	285	313.2	345	420	82
Wing	A	313.2***	0.6	280	306	313	321	341	325
	I	301.8	1.6	283	293	301.5	309	324	44
	J	297.8	1.2	276	290	298	305	325	82
Tail	A	121.9***	0.28	109	118	122	125	135	325
	I	117.95	0.74	108	115	117	122	128	44
	J	113.57	0.61	99	110	113	118	126	82
Culmen	A	36.72***	0.14	30.1	34.90	36.9	38.6	42.7	325
	I	36.92	0.39	30.6	35	37.1	38.55	43.3	44
	J	34.97	0.34	30	32.9	34.7	36.4	49.7	82
Bill depth	A	10.38	0.04	8.9	9.9	10.4	10.8	12.2	325
	I	10.03	0.08	8.8	9.7	10	10.35	11.3	44
	J	9.67	0.07	7.9	9.2	9.7	10.1	11.1	82
Head	A	84.45**	0.23	75	81	85	88	95	325
	I	84.11	0.7	77	81	83	88	99	44
	J	82.74	0.43	76	80	82	86	91	82
Tarsus	A	48.68	0.15	39.9	47.2	48.7	50.52	55.4	325
	I	48.6	0.37	43.1	47.2	48.55	50.35	53.7	44
	J	49.04	0.28	43.5	47.3	49.4	50.9	57.7	82
Foot	A	96.86	0.26	82	93	97	100	109	325
	I	96.41	0.62	88	94	96.5	100	106	44
	J	96.9	0.42	89	95	97	100	105	82

**ANOVA, P<0.01
***ANOVA, P<0.001

but were similar in size to all other variables when compared with adults. Tarsus and foot had similar results for all age classes and showed no significant differences. Standard error (se) values indicated that immatures were the most variable age class with regard to all measurements other than mass. Juveniles had the most variation for mass.

Sexing

The sample of sexed adult Grey-headed Gulls included 35 males and 16 females which comprised (according to the method employed):

1. Dissection - the seven dead Grey-headed Gulls dissected consisted of four birds found freshly dead on their breeding grounds (three from Korsman's Bird

Sanctuary and one from Stewards Pan, Gauteng) and three birds that died subsequent to being trapped on Weltevreden Landfill, Gauteng (Table 5.1). Sexing of these individuals revealed four males and three females;

2. DNA - blood samples were taken from 38 adult Grey-headed Gulls at Gauteng's landfills and molecular techniques revealed 28 males and 10 females;
3. Observations – the six birds sexed from behavioural observations at Lakefield Pan revealed three males and three females.

Morphometric variation

For all measurements, males were significantly larger than females (Table 5.8, mass and tail P<0.01, all other measurements P<0.001). Figure 5.2 (a – h) indicate tendencies toward bimodal distributions for all measurements, with head length showing the highest dimorphism and little overlap between the sexes.

Table 5.8. Five number summary table showing results of eight different morphometric variables for Grey-headed Gulls, including sexed sample. Two sample Student's T-tests were applied to all measurements to distinguish sex-based differences (significant differences are indicated after male means). Sex: M – male; F – female; ? – unknown. Q1 – lower quartile; Q3 – upper quartile.

	Sex	Mean	SD	Min	Q1	Median	Q3	Max	n
Mass	M	313.72**	25.74	278	293	313	321	372.5	29
	F	285.04	25.28	245	266	282.5	301	322.5	13
	?	299.57	30.24	225	275	300	322.5	385	275
Wing	M	318.85***	8.54	303	313	319	325	336	34
	F	306.86	7.03	290	304	306	312	317	14
	?	312.77	10.69	280	306	313	320	341	277
Tail	M	123.71**	4.47	114	121.25	123	126.5	132	34
	F	119.36	3.5	115	116.25	120	121	126	14
	?	121.81	5.16	109	118	122	125	135	277
Culmen	M	38.56***	1.55	35.3	37.63	38.7	39.4	42.3	34
	F	34.19	2.01	31.1	33.13	34.45	35.475	37.2	14
	?	36.62	2.45	30.1	34.8	36.9	38.5	42.7	277
Bill depth	M	10.61***	0.52	9.2	10.3	10.6	10.8	11.8	34
	F	9.86	0.35	8.9	9.73	9.9	10	10.4	14
	?	10.38	0.64	8.9	9.9	10.4	10.8	12.2	277
Head	M	87.35***	2.36	83	86	86.5	89	92	34
	F	80.29	1.9	76	80	80.5	81.75	83	14
	?	84.3	4.08	75	81	85	88	95	277
Tarsus	M	49.56***	2.04	45.5	48.15	49.3	51.28	53.5	34
	F	46.81	2.89	39.9	46.7	47.1	48.35	51.7	14
	?	48.67	2.65	40.9	47.2	48.8	50.5	55.4	277
Foot	M	99.24***	3.49	92	97.25	99	102	106	34
	F	93.36	4.43	82	92.25	94.5	96	100	14
	?	96.75	4.66	82	93	97	100	109	277

** T-test, P<0.01
*** T-test, P<0.001

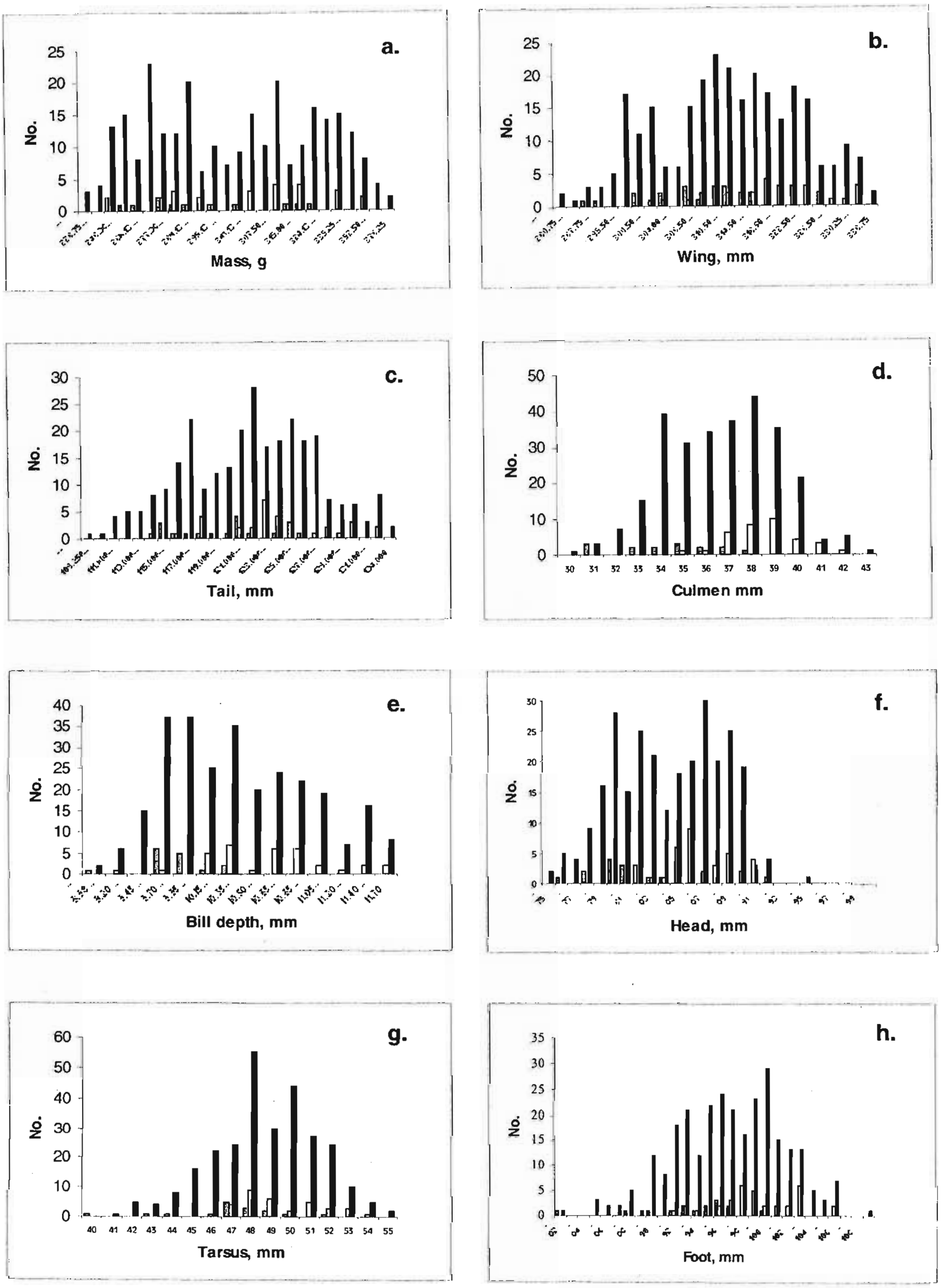


Figure 5.2. Histograms of eight different Grey-headed Gull morphometrics including males (white columns), females (striped columns) and unsexed individuals (black columns).

The initial PCA conducted on all variables of all sexed individuals found three outliers. One female had been incorrectly aged and was eliminated for the subsequent PCA analysis. The other two outliers consisted of a male and a female, both of which were correctly entered and were probably just exceptionally small individuals. The second PCA (Figure 5.3) showed the following paired variables to be highly correlated: wing and tail, head and culmen, and tarsus and foot. The measurements of wing, head and foot accounted for the majority of the variability. Wing and foot were located at right angles to each other, indicating independence of these variables. However, a bivariate analysis of just these two variables (Figure 5.4) does not give a clear seperation between the sexes and the advantage of using more variables is therefore emphasized.

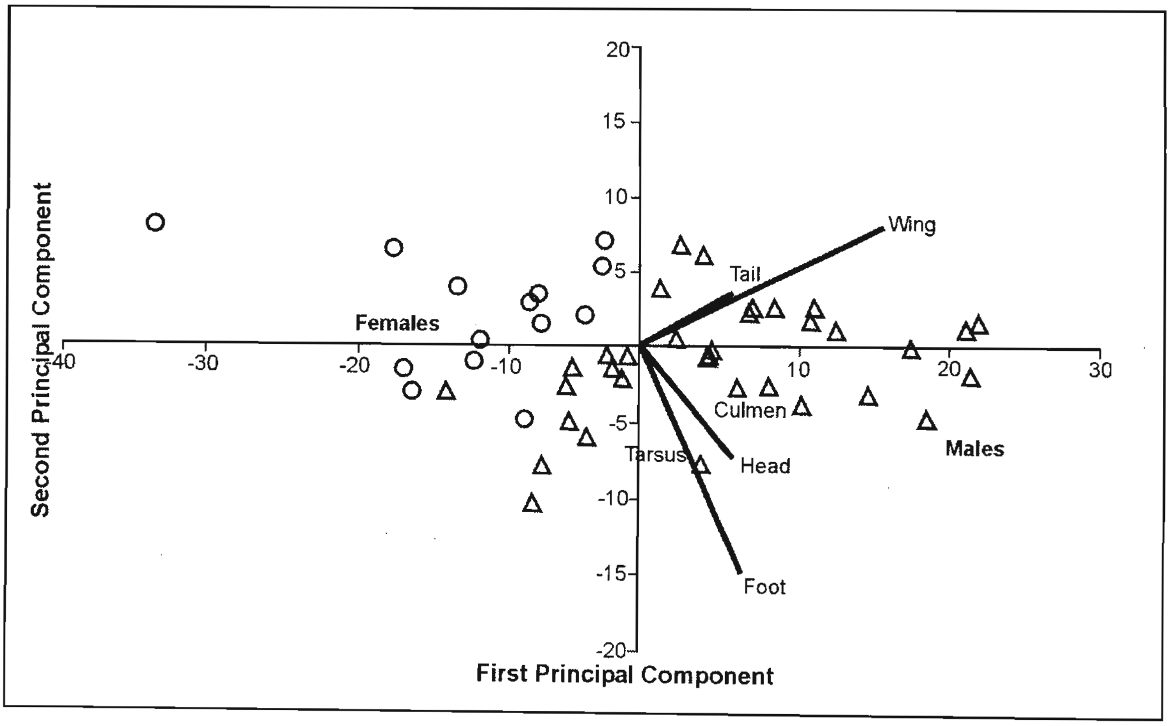


Figure 5.3. Principal Component Analysis for six morphometric variables of sexed adult Grey-headed Gulls (circles - females, triangles - males).

In the discriminant analysis, correlations of data variates and discriminant functions showed head to be the most important variable in separating males from females, followed by culmen, foot and wing (Table 5.9). The resulting combined discriminant function was:

$$DF = -0.2088*culmen - 0.0849*foot - 0.3371*head - 0.0256*tail + 0.1199*tarsus + 0.0221*wing,$$

where negative values were indicative of males and positive values were indicative of females (mean ♂ = -0.966; mean ♀ = 2.346).

The resultant discriminant function produced one error in 48 (2%) when applied to all sexed Grey-headed Gulls, the error coming from an exceptionally large female.

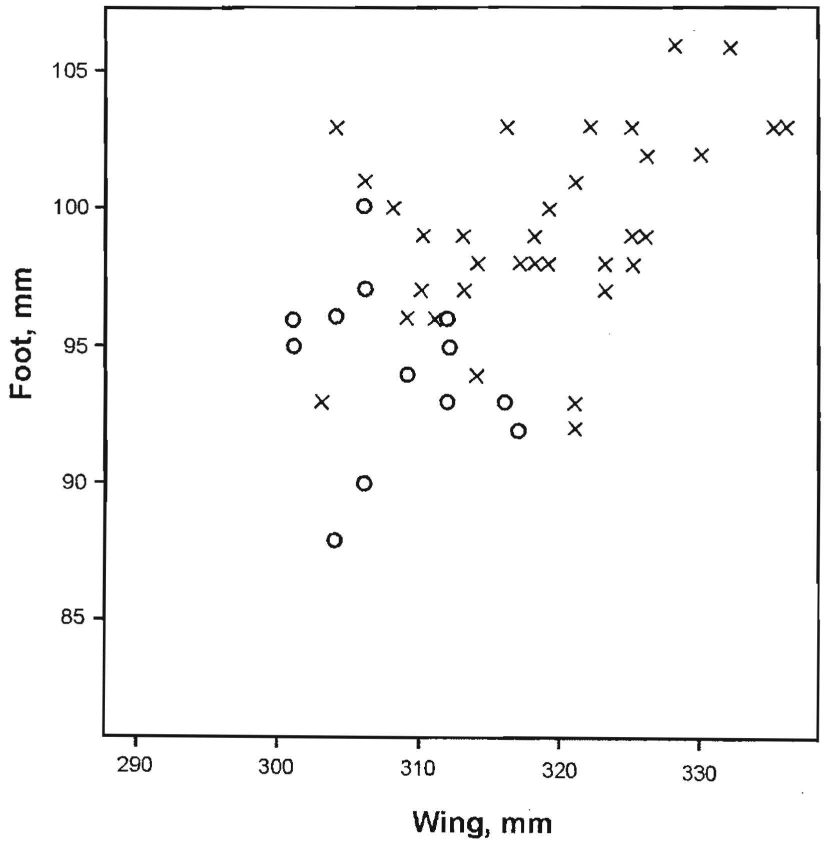


Figure 5.4. Bivariate scatterplot showing relationship of wing versus foot measurements for adult male (crosses) and female (circles) Grey-headed Gulls.

Table 5.9. Correlations between data variates and discriminant functions, ranked in order of importance.

Measurement	Value	Rank
head	-0.9531	1
culmen	-0.7808	2
foot	-0.4695	3
wing	-0.4448	4
tarsus	-0.3596	5
tail	-0.3113	6

Moult

Adults

The average weight of each primary feather and the proportionate mass of each feather to the total mass of all primaries are given in Table 5.10. The mean mass of all 10 primaries was 2.6 g. The outermost primary (P10) was on average 4.4 times heavier than the innermost primary (P1). The estimated mean starting date for Grey-headed Gull primary moult was 12 October and the estimated mean completion date was 24 January with a mean estimated duration of 136 days (Table 5.11). The standard deviation of the mean starting date was 25 days with a standard error of 4 days. It is therefore estimated that 95% of Grey-headed Gulls, coming from the population sampled, initiated primary moult between 24 August and 2 December. The 95% confidence limits for completion dates span a longer period and more sampling towards the final stages of moult are needed to gain more accuracy here.

Table 5.10. Mass (in gramms) and proportionate mass (%) of primary feathers taken from one wing each of four Grey-headed Gulls collected in Gauteng during June 2004.

Primary no.	Mass1	Mass2	Mass3	Mass4	Mean	%Total mass
10	0.39	0.41	0.47	0.48	0.44	16.83
9	0.36	0.38	0.45	0.45	0.41	15.77
8	0.32	0.34	0.4	0.43	0.37	14.33
7	0.27	0.29	0.33	0.37	0.32	12.12
6	0.24	0.26	0.29	0.32	0.28	10.67
5	0.21	0.22	0.25	0.26	0.24	9.04
4	0.16	0.17	0.2	0.2	0.18	7.02
3	0.13	0.14	0.16	0.17	0.15	5.77
2	0.11	0.12	0.13	0.13	0.12	4.71
1	0.08	0.1	0.11	0.11	0.10	3.85
Total	2.27	2.43	2.79	2.92	2.60	100.00

Table 5.11. Timing and duration of primary moult in the Grey-headed Gull calculated from percentage feather mass grown.

Mean starting date	Mean Duration	Mean completion date	SD	95% CI for mean starting date
12 October	136 days	24 January	25	24 August – 2 December

The chronology of the sample effort and the number of adult Grey-headed Gulls recorded in active primary moult during the study period are illustrated in Figure 5.5. Twenty-one birds (of the 315 sampled) were in active primary moult. Most Grey-headed Gulls were sampled during the breeding season, in all months between May and August, and of these birds, only a small proportion (9.7%) were in active primary moult. All of these birds (n=6) were trapped in late August. All Grey-headed Gulls trapped between November 2004 and February 2005 (n=15), during their non-breeding season, were recorded with active primary moult. Six adult Grey-headed Gulls, which had not initiated primary moult yet, had active moult in their inner tail feathers. These birds were trapped between May and August 2004.

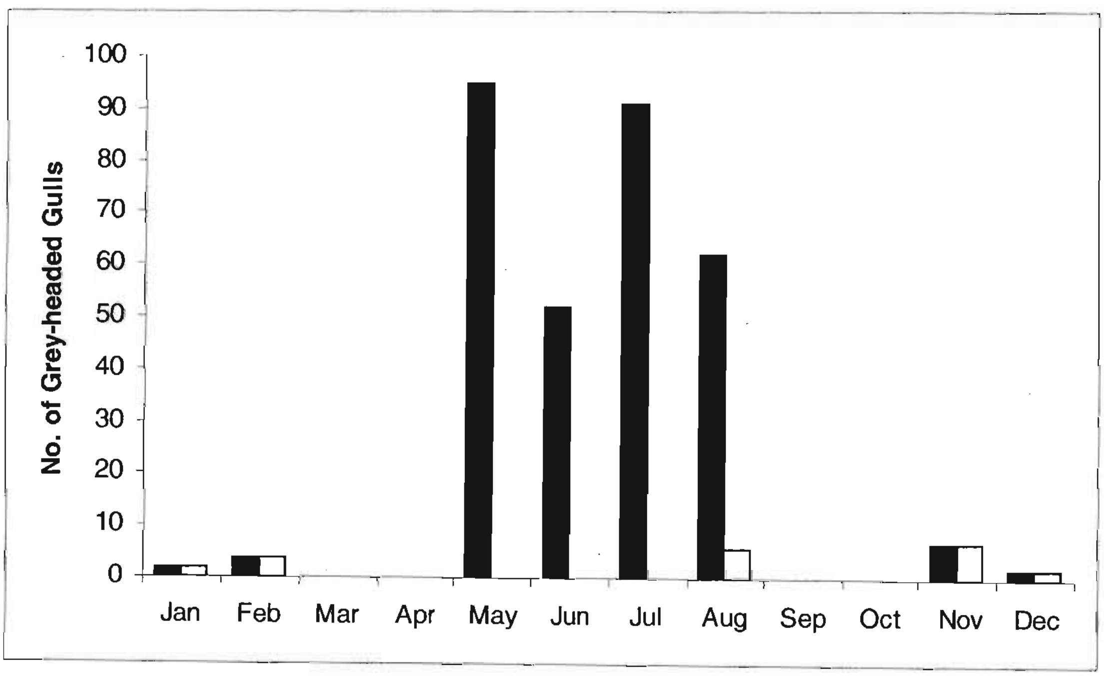


Figure 5.5. Total monthly numbers of adult Grey-headed Gulls sampled in Gauteng and Durban between April 2004 and July 2005 (black bars) and total number of adult Grey-headed Gulls recorded in active primary moult (white bars).

Two birds trapped in December and January, that were in the final stages of primary moult, i.e. moulting P8 – P10, were simultaneously moulting one inner primary each (P2 and P3, respectively).

Although no adult Grey-headed Gulls were observed actively moulting their outermost ten secondaries (S1-S10), all birds sampled between December and

February had these feathers newly replaced. This moult was therefore estimated to occur between the end of November and the middle of December, at which stage these birds would have been moulting their central primaries. During January and February, four of the six gulls sampled were moulting their proximal secondaries (S11-S14) inwardly (ascending), during the final stages of primary moult. Active moult at S17 was evident in all months between November and February, except December. In all months sampled, between 20% and 86% of all moulting birds had some degree of moult in the innermost three secondaries (S18 – S20).

Of all Grey-headed Gulls recorded in active primary moult, birds were only recorded in tail moult during November (six of seven) and December (one of two). The pattern of moult here generally started with the innermost retrices and ended with the outermost retrices being mostly synchronous but sometimes irregular, as was shown by one gull that had all of its retrices moulting simultaneously. The limited sample suggests that the timing of tail moult was somewhere within the first half of the primary moult period.

The timing of head moult for Grey-headed Gulls counted (and categorised into non-breeding and breeding adults) in all months in Durban Bay is illustrated in Figure 5.6.

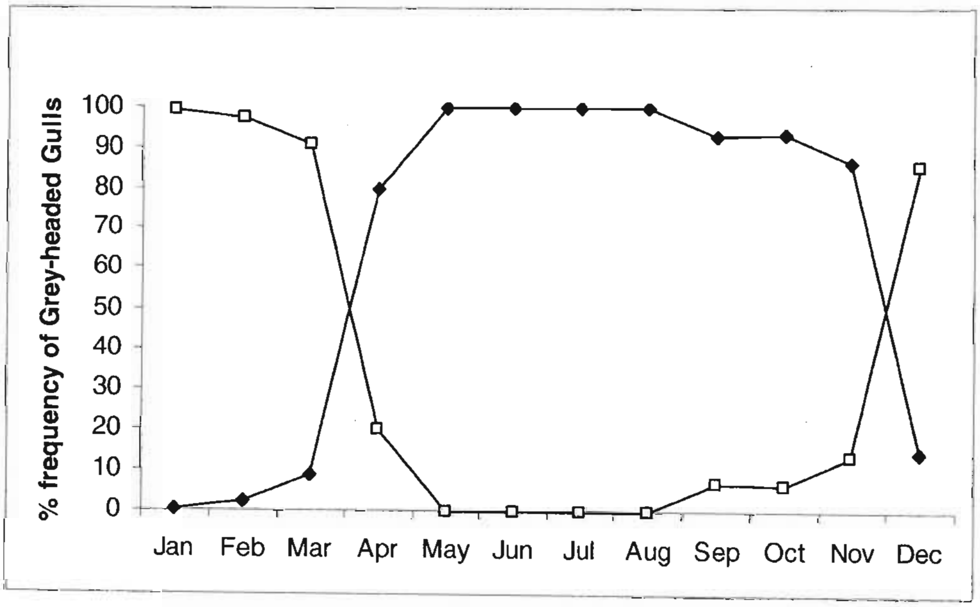


Figure 5.6. Percentage frequencies of adult Grey-headed Gulls with (black diamonds) and without breeding hoods (open squares) between January and December 2004, 2005. Data from aged counts conducted monthly in Durban Bay (see Chapter 2).

Head moult of adults into non-breeding hoods occurred during the months November and December. Grey-headed Gulls acquired their breeding hoods between March and May, with the majority of birds having moulted into their breeding hoods by April.

Immatures

The chronology of the sample effort and the number of immature Grey-headed Gulls recorded in active primary moult during the study period are illustrated in Figure 5.7. Fourteen immatures (of the 44 sampled) were in active primary moult. Immatures in active primary moult were recorded in all months sampled, both in the breeding and non-breeding season. Two birds trapped in July and August, and which had not initiated primary moult yet, were moulting their retrices.

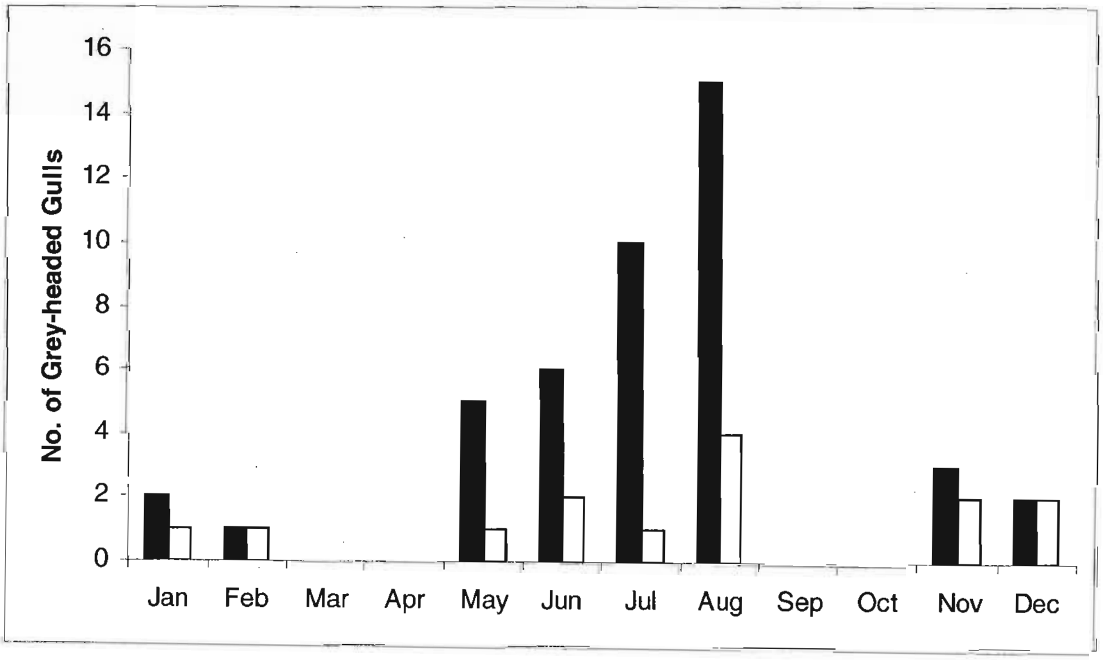


Figure 5.7. Total monthly numbers of immature Grey-headed Gulls sampled in Gauteng and Durban between April 2004 and July 2005 (black bars) and total number of immature Grey-headed Gulls recorded in active primary moult (white bars).

There was a greater variety in the timing of primary moult in immatures, when compared with adults. Exceptions included: two immatures sampled in November which were both actively moulting their inner primaries and were the only moulting first-winter birds sampled; and the two immatures sampled in January and February that were both in the latter stages of primary moult.

Moulting of the outer secondaries was recorded in four immature Grey-headed Gulls: one in June; two in August; and one first-winter bird in November. The bird trapped in June was actively moulting S5, S6, S7 (stages 2 and 3, Appendix 5.2) and S13 (stage 1), and was in the middle stages of primary moult, i.e. P5 and P6. The two birds in August were actively moulting their innermost secondaries (S1). In both birds, all secondaries from S2 – S14 were old feathers while the innermost secondaries (S15 – S20) were fully grown but of indeterminate age. These birds were in the middle stages of primary moult, i.e. P5 and P6.The first-winter bird, trapped in November, was moulting most of its secondaries (S1 – S14) simultaneously, except for S11 that was fully-grown. Of these feathers, S1 and S14 were at stage 3 (Appendix 5.2) while the remaining 11 were still contained within the feather sheath or just emerging (stages 1 and 2). The innermost secondaries in this bird were all new fully-grown feathers and the stage of primary moult was centrally situated, i.e. P4 – P6. In the remaining birds (n=6), secondary moult was limited to the innermost feathers (S15 – S20) and these birds were trapped in all sampled months other than June, August and November.

Eight of the 14 immature Grey-headed Gulls in active primary moult were recorded with tail moult. The three birds sampled in January, Febuary and May, respectively, had no active moult in the retrices. The limited sample indicates that tail moult is initiated within the early stages of primary moult.

Discussion

Ageing

Adults

The only discrepancies between our findings and those of Grant (1978) and Olsen & Larsson (2003) relate to the bare parts, notably the bill and leg colouration. Both these citations give bill and leg colour as red and do not mention any other variants. While most of the adults in this study had red colour variants, almost one third had orange or orange/brown bill and/or leg colours. Studies on moult in other areas of the integument, i.e. other than feathers, have been reviewed by King & Murphy (1990). Despite the paucity of information on the subject, these authors did find evidence to suggest some degree of episodic moulting in the integuments of both the beak (ramphotheca) and the legs and feet (podotheca). The variety of bill and leg colours recorded in this study may therefore have an important bearing on different stages of the Grey-headed Gull's life cycle. In this study, orange variants in bill and leg colours were more prevalent in immature birds, and adults with these features may be in the earlier stages of their adulthood. This may explain re-sightings of "ER" and "KL" (Table 5.6, Plate 5.6 a & b) both of which had orange/brown bills and were probably first year breeders.

Immatures

The re-sighting of "A3" and the re-capture of "EJ", both confirmed first-winter birds, have features similar to all but three immatures trapped during the non-breeding season, viz. white heads with dusky ear and eye patches, some extent of brown/dusky plumage in the upper-wing coverts, grey and white greater primary coverts with black terminal tips, dark contrasting dusky-grey secondaries with pale white/grey tips, no primary mirrors, dull-coloured (i.e. brown/horn, dark-brown and flesh/horn) bill and legs, dark-brown eyes and brown orbital rings; and dark terminal tail bars. Re-sightings of "A3" and "EJ" in their second non-breeding season would therefore constitute second-winter birds. These birds had similar features to the three birds trapped in the non-breeding season (mentioned above) and include: the absence of any brown/dusky plumage; the absence of a tail bar; grey secondaries; and light-brown to pale-greyish eyes.

Certain features can be used to classify the immatures trapped during the breeding season into two broad categories. These include the presence/absence of: brown/dusky plumage in the upper-wing coverts; dark contrasting dusky-grey secondaries with pale-white/grey tips; primary mirrors; and a dark terminal tail bar. The presence of brown/dusky plumage in the upper-wing coverts and/or a dark terminal tail bar is of particular significance in separating these birds out as first-summer birds as these plumages are unlikely to remain into the following non-breeding season. This is exemplified by the re-sightings of first-winter birds, "AL" and "B7" late in the non-breeding season and approaching their first subsequent breeding season, i.e. first-summer. Both these birds had replaced their brown/dusky plumage in their upper-wing coverts with grey plumage and the dark terminal tail bar in "AL" had disappeared. Further evidence is provided by the re-sightings of "A3" and "EJ" during their second non-breeding season; no brown/dusky plumage or dark terminal tail bars were observed in these birds. While the above-mentioned features are likely to be reliable in distinguishing first-year birds, it is difficult to separate those more advanced first-summer birds from second-summer birds. The presence of medium to large primary mirrors is probably a second-summer trait but one can not rule out the presence of small mirrors in first-summer birds, especially if they have completed their second wing moult during this season. The use of head and bare-part colouration to distinguish between these age groups is particularly unreliable. The re-sighting of "JK" (Plate 5.6c.) as a confirmed first-summer bird is a good case in point. This bird had no vestiges of brown/dusky plumage yet had attained a grey hood and pale-greyish eyes; on first inspection this bird resembled an adult.

Comparing these results with the descriptions of Grant (1978) and Olsen & Larsson (2003), there are two main discrepancies. Firstly, Olsen & Larsson (2003) describe the eye colour of first-summer birds as 'sometimes pale brown' and do not mention the possibility of these birds attaining pale-greyish eyes, as was the case for re-sighed bird "JK" (Plate 5.6c). Secondly, Grant (1978) and Olsen & Larsson (2003) describe the secondaries of second-winter birds as being dark-centred and contrasting with the upper-wing. The re-sighting of "A3" (Plate 5.5c) and the three birds trapped in Durban during this stage of their development showed little or no difference between these two areas of the plumage.

Age Classification

Based on the results of this study and comparison with the published literature, the following combination of features is proposed as a means to classify Grey-headed Gulls into various age categories:

1. Juvenile *(Plumage)* - head with extensive dark markings (invariably mixtures of brown, dusky and black); hindneck pale-grey or white with brown/dusky patches; mantle, scapulars, and upper-wing coverts with various amounts of brown/dusky and grey plumage; greater primary coverts grey and white with black tips; dark,

contrasting dusky-grey secondaries with white tips; no primary mirrors; and prominent dark terminal tail bar. (*Bare parts*) – bill and legs flesh to brown/horn; and eye and orbital ring dark-brown.

2. First-winter (*Plumage*) – head sometimes faded version of juvenile but usually white with dark-dusky ear and eye patches; hindneck usually pale-grey; mantle and scapulars mostly grey but sometimes with small remnants of brown/dusky plumage; upper-wing coverts grey with varying amounts of brown/dusky plumage invariably fading to grey towards the end of the season; greater primary coverts grey and white with black tips; contrasting dusky-grey secondaries with white tips; no primary mirrors; reduced and faded white primary tips; and tail with dark terminal tail bar which is usually lost toward the end of the season. (*Bare parts*) – bill mostly flesh/horn with dark, contrasting tip; legs brown to flesh/horn; and eye and orbital ring dark-brown.
3. First-summer (*Plumage*) - usually with grey hood; hindneck usually pale-grey, sometimes white; mantle, scapulars, and lesser, median and greater secondary coverts usually grey, sometimes with small remnants of brown/dusky plumage; greater primary coverts usually grey and white with black tips; contrasting dusky-grey secondaries with white tips; usually no primary mirrors; reduced and faded white primary tips; and usually no tail bar. (*Bare parts*) – bill and legs variable from flesh, brown/horn to red/orange/brown; eye various shades intermediate between juvenile and pale greyish; and orbital ring brown to orange.
4. Second-winter (*Plumage*) – head usually white with dusky ear and eye patches, remnants of grey hood may still be evident early in the season; hindneck white or pale-grey; mantle, scapulars, and upper-wing coverts grey; greater primary coverts grey and white; secondaries either grey or contrasting slightly with rest of wing; primary mirrors reduced, small or absent; reduced and faded white primary tips; and tail bar absent. (*Bare parts*) – bill flesh/horn to orange and orange/brown; legs orange to orange/brown; and eye light-brown to pale-greyish.
5. Second-summer (*Plumage*) – grey hood; hindneck white; mantle, scapulars, and upper-wing coverts grey; greater primary coverts grey and white; secondaries usually grey; primary mirrors small to medium or reduced on outermost one or two primaries; reduced and faded white primary tips; and tail bar absent. (*Bare parts*) – bill and legs variable orange/brown to red/orange/brown; eye light-brown to pale-greyish; and orbital ring orange.

6. Adult *(Plumage)* – head rich-grey with dark, contrasting border (breeding), white with dusky ear and eye patches (non-breeding); hindneck white (breeding), pale-grey (non-breeding); mantle, scapulars, and upper-wing coverts grey; greater primary coverts grey and white; secondaries grey; primary mirrors present usually medium to large on primaries P10, P9 and sometimes on P8; reduced and faded white primary tips; and tail bar absent. *(Bare parts)* – bill and legs variable from bright red/orange and red/orange/brown to orange and orange/brown; eye pale white/yellow; and orbital ring red/orange.

Morphometrics

Table 5.12 gives a comparison of measurements taken in this study with those published in other sources. Kok & van Zyl 's (1996) weights for both males and females were substantially higher than those measured in this study. These may be related to a number of factors which include dietary differences (Murphy 1996), seasonal variations in energy demands (Ricklefs 1996), weighing methods or a combination of these.

The majority of Grey-headed Gulls caught during this study were birds that were actively feeding on landfill sites. It is therefore possible that a large percentage of these birds' diet consisted of food items coming from these landfill sites. All birds sampled in Kok & van Zyl's (1996) study were obtained from non-landfill sites, with ca.85% coming from airports at Bloemfontein, Kimberley and Johannesburg. Grey-headed Gulls frequently feed on natural food items, especially insects (see Chapter 4) and have been recorded feeding on insects and termite alates at Johannesburg International Airport (Underhill 1987; Kok & Hewitt 1990). The discrepancy in weights may therefore be influenced by differences in the nutritional value of food, with insects having higher nutritional value than food items coming from landfill sites; this reasoning has been previously suggested for gulls (Pierotti & Annett 1987).

An alternative and a potentially compounding explanation could be the influence that the breeding season has on the energy demands of adults and the subsequent influence

Table. 5.12. Comparative morphometrics of Grey-headed Gulls from this study and other sources.

	Mass				Wing				Culmen				Tarsus				Tail				
Sex	**min**	**max**	**mean**	***n***	**min**	**max**	**mean**	**n**	**min**	**max**	**mean**	***n***	**min**	**max**	**mean**	**n**	**min**	**max**	**mean**	**n**	**Reference**
male	278	373	313.7	29	303	336	318.9	34	35.3	42.3	38.6	34	45.5	53.5	49.6	34	114	132	123.7	34	this study
female	245	323	285	13	290	317	306.9	14	31.1	37.2	34.2	14	39.9	51.7	46.8	14	115	126	119.4	14	
unsexed	225	385	299.6	275	280	341	312.8	277	30.1	42.7	36.6	277	40.9	55.4	48.7	277	109	135	121.8	277	
male	-	-	-	-	308	343	328	52	34.4	42.5	38	57	46.3	55.5	51	57	-	-	-	-	Olsen & Larsson 2003
female	-	-	-	-	290	328	309.9	53	31.2	41.3	35.2	49	43.7	53.9	48.6	53	-	-	-	-	
male	-	-	-	-	283	330	313	18	46.5	57.5	52.1	18	44	51	47	18	102	124	117	18	Johnstone 1982
female	-	-	-	-	290	317	302	13	45	51	47.4	13	40	48	44	13	111	120	114	13	
male	190	414	336.1	287	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	Kok & van Zyl 1996
female	232	380	303.5	236	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
male	-	-	-	-	290	333	318	32	39	41	40.4	10	50	54	52.1	10	117	132	125	10	Crawford & Hockey 2005
female	-	-	-	-	285	334	309	23	35	37	36.1	8	45	52	47.5	8	114	123	118	8	
unsexed	211	377	280	50	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
male	-	-	-	-	309	343	324	21	34.4	41.8	37.7	26	46.5	55.5	51.6	26	116	138	124	25	Cramp & Simmons 1983
female	255	335	303.3	3	290	323	306	21	31.2	37.1	35.2	20	45	51.9	48.7	23	112	134	118	21	

that this has on body condition, a phenomenon that has been well documented (e.g. Ricklefs 1996; Deeming 2002). Although Kok & van Zyl's (1996) sample showed no significant differences between winter and summer Grey-headed Gull weights, these authors do not give details of sample size and localities and it is not possible to determine what proportion of birds were in a breeding/non-breeding state. Indeed, the discrepancy in weights between these authors' sample and the results coming from this study suggests that most of these birds weren't breeding.

The results of Johnstone (1982) for culmen and tail differed markedly from those of this study, being larger and smaller for culmen and tail, respectively. This author's results were similarly different to all other published accounts and it is therefore likely that this was due to the method of measurement employed.

Age variations

Published comparisons of adult/juvenile weights for masked gulls are scarce, with most sample sizes being inadequate to draw firm conclusions. The limited data, however, show a tendency for adults of western Palearctic species, e.g. Black-headed Gull *Larus ridibundus*, to be heavier than juveniles (Cramp & Simmons 1983). The only study on masked gulls with good sample sizes appears to be on Silver Gulls *Larus novaehollandiae* in Australia, with juveniles averaging significantly heavier than adults (Higgins & Davies 1996). A possible explanation for this difference between these southern (Grey-headed and Silver gulls) and northern (Black-headed Gull) hemisphere gulls may relate to diet during the breeding season, with the southern hemisphere gulls utilizing land fill sites during this period (this study; Higgins & Davies 1996), while their northern hemisphere counterpart forages mostly on natural food items during this season (Cramp & Simmons 1983). Comparative feeding studies have shown that juvenile gulls are more successful at landfill sites than at natural feeding situations (e.g. Searcy 1978; Burger & Gochfeld 1983). Adults, on the other hand, at landfill sites are likely to be in a poorer condition than those that utilise more natural food sources (see discussion above). Therefore, adults and juveniles that utilise landfill sites, as has been documented in this study, are expected to be relatively lighter and heavier respectively than their counterparts away from these sites.

Sex variations

Sexual differences in gull measurements have been well documented, with most studies showing significant differences for all measurements, e.g. Coulson *et al.* (1983) for Herring *Larus argentatus* and Lesser Black-backed *Larus fuscus fuscus* gulls and Black-legged Kittiwakes *Rissa tridactyla* ; Bosch (1996) for Yellow-legged Gulls *Larus michahellis*; and Rodriguez & Pugesek (1996) for California Gulls *Larus californicus*. These studies have also identified head as the most important variable in determining sex and suggest that the use of this variable alone can discriminate sexes with a high level of accuracy. Results from this study have confirmed that sex variations in the Grey-headed Gull are very similar to other studied gull species.

Moult

The comparative proportionate masses of all primary feathers for Hartlaub's Gull *Larus hartlaubii*, taken from Crawford & Underhill (2003), and Grey-headed Gull are illustrated in Figure 5.8. The proportions are almost identical, except the innermost and outermost primaries, viz. P1 and P10. These are smaller and larger for Grey-headed Gull, respectively, and may relate to the differences in seasonal movements

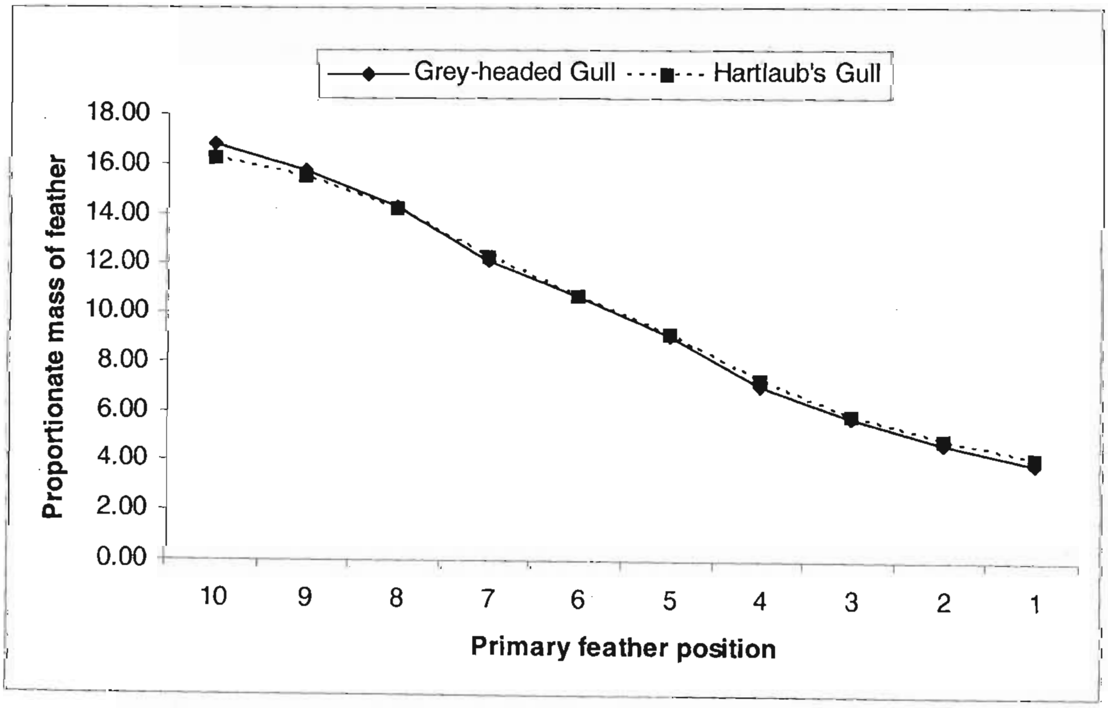


Figure 5.8. Comparison of proportionate masses (%) of each primary feather to total mass of all primaries for Hartlaub's and Grey-headed gulls.

between these species. Hartlaub's Gull is resident to the south-western coast of Africa (Williams *et al.* 1990) where movements are mostly restricted to this area. Grey-headed Gulls are partly migratory/dispersive with juveniles having been regularly recorded substantial distances from their natal colonies (Underhill *et al.* 1999) and adult birds are known to migrate between Gauteng and Kimberley and between St Lucia and Durban (see Chapter 2). Grey-headed Gulls probably travel longer distances than what has been documented here. The disproportionately larger outer primary in Grey-headed Gulls could, therefore, be an adaptation for longer migratory/dispersal movements in and out of the breeding season (Berthold 1993). The mean total mass of all primaries feathers for Grey-headed Gulls: 2.6 g, was higher than that recorded for Hartlaub's Gull: 2 g (Crawford & Underhill 2003); the Grey-headed Gull is on average larger than Hartlaub's Gull (Hockey & Crawford 2005) and this difference is therefore expected.

The estimated mean primary moult duration for Grey-headed Gulls of 136 days is intermediate between Hartlaub's Gull (115 days, Crawford & Underhill 2003) and Kelp Gull (172 days, Ward *et al.* in prep). These are the only gull species for which primary moult duration has been calculated using the PFMG method (L. Underhill pers. comm.). This is probably related to the greater feather mass that needs to be generated by Grey-headed Gulls compared to Hartlaub's Gulls. This difference could also possibly be influenced by birds arresting moult during migration, as was recorded for the two birds trapped in Durban during December and January.

The discrepancy between the primary moult starting dates for the six adult Grey-headed Gulls trapped in August (in Gauteng) and the expected starting dates as calculated from birds mostly trapped in Durban, may be related to the occurrence of two separate breeding populations. Re-sightings of colour-ringed adult Grey-headed Gulls in South Africa indicate a tendency for Durban's Grey-headed Gulls to constitute, at least in part, birds that return to St Lucia during the breeding season (see Chapter 2). The breeding season for Grey-headed Gulls at St Lucia has historically been more restricted (June-September) than the range of months when they have been recorded breeding in Gauteng (January-November) (Brooke *et al.* 1999). The onset of primary moult towards the end of the breeding season is a common occurrence in gulls. The great variation in the timing of moult, as is related to different breeding populations, has been documented in five other masked gull species (Slender-billed *Larus genei* and Black-headed gulls, Cramp & Simmons 1983, Olsen & Larsson 2003; Silver and Black-billed *Larus bulleri* gulls, Higgins & Davies 1996; and Hartlaub's Gull, Crawford & Underhill 2003). The predicted time of primary moult initiation, which was based mostly on a sample of birds trapped during their non-breeding season in Durban, would coincide with the termination of breeding activities for Grey-headed Gulls at St Lucia.

The variation in timing of primary moult in immature Grey-headed Gulls is probably related to the non-reproductive state of these birds during the breeding season and the variety of different immature stages present in the sample (i.e. first- and second-year birds). There is a tendency for the immatures of other masked gull species to initiate primary moult earlier than adults, e.g. Slender-billed and Black-headed gulls (Higgins & Davies 1996; Olsen & Larsson 2003). This phenomenon has also been documented for larger gulls: Herring, Great Black-backed *Larus marinus* and Lesser Black-backed gulls (Harris 1971) and could explain the advanced stage of moult for Grey-headed Gull immatures sampled between May and August, in Gauteng.

Despite the small sample size, there is evidence that, in both adults and immatures, the onset of secondary moult coincides with the moulting of the central primary feathers. The same situation has been recorded for Black-headed, Silver and Black-billed gulls (Cramp & Simmons 1983, Olsen & Larsson 2003, Higgins & Davies 1996), and Dwight (1925) and Harris (1971) describe this phenomenon as the norm for gulls in general. There appear to be two waves of secondary moult in the Grey-headed Gull, starting with the outer secondaries (S1-S10) and then followed by a second wave between S11 and S14. The absence of any observable secondary moult in adult Grey-headed Gulls, despite birds having been sampled in successive months during this period, is probably indicative of rapid moult in this region, with the possibility of simultaneous moult as shown by the first-winter bird. Both the Silver and Black-billed gulls moult their outer secondaries (S1-S14) sequentially inward, followed by a second wave between S15 and S19, which also moult inwardly (Higgins & Davies 1996). In contrast to these species, results coming from this study indicate that Grey-headed Gulls are more similar to the large gulls studied by (Harris 1971) who noted these birds having large gaps in each wing during secondary moult. This may have something to do with the relative wing-aspect ratios and wing-loading values of these species when compared to those species that employ the sequential moult strategy; higher aspect ratios being beneficial in gliding and lower wing loading values being beneficial in take-off (Maclean 1990). If Grey-headed Gulls have higher aspect ratios and/or lower wing loading values compared to these other species, then they could afford to sacrifice this part of the integument temporarily. Alternativelly, this strategy may have evolved in conditions that favour soaring and take-off flight movements where the temporary absence of large tracts of secondaries may be compensated for by consistent and amplified wind velocities, e.g. windy conditions such as those that persist as on-shore north-easterly winds during Durban's summer.

Conclusion

This chapter highlights the great variability in the plumage and bare parts of Grey-headed Gulls according to different age groups. Clearly, there is more to be learnt, especially with regard to adult bill- and leg-colour variation. A more detailed study might unravel important associations with this variability and the ages of adult birds, as well as their dominance within territorial systems. By using photographs of individually recognisable birds, the age classification produced here is the first to use information of known-age birds and is therefore considered more robust than other classifications that have been published to date. Similarly, the discriminant function for sexing Grey-headed Gulls provides a valuable tool for future studies that involve the trapping of live individuals. Unfortunately, the sample size used to produce this discriminant function was only just adequate and refinement in this area would be beneficial. The discrepancy between the weights of adults and juveniles poses a number of interesting questions. One of the possible reasons that I have given for this occurrence, as has previously been suggested by other authors, is the relative benefit of landfill sites to juvenile birds. This hypothesis can be tested by comparing the weights of Gauteng Grey-headed Gulls with those of a more naturally occurring population, e.g. at Lake St Lucia, where juveniles would be expected to be less reliant on landfill sites for feeding. The information on moult coming from this chapter is the first attempt to describe this part of the Grey-headed Gull's life cycle. The species is widely distributed in South Africa warranting a more thorough investigation into the timing of moult between different regions. This may be complicated by a lack of knowledge of movements between these areas and a project of this nature would benefit by simultaneously incorporating a study on movements.

Appendix 5.1. Description of method used for trapping Grey-headed Gulls during this study (source: AFRING News).

A speargun-driven net for catching gulls

McInnes, A.M, Allan, D.G., Bryan, M.C. & Merson-Davies, M.

The speargun-driven net method (SNM) is a substitute for the cannon-net method (CNM) (e.g. Mundy & Choate 1973), the basic concept being the same, except in the mechanism that propels the net. A similar device has been used successfully to catch vultures in the Kruger National Park (P.C. Benson pers. comm.). While the CNM is undoubtfully more efficient in propelling heavier nets a further distance, the advantages of the SNM lie in its ability to do a similar job without the use of explosives. Both systems have been used effectively to catch large numbers of ground-feeding birds, especially larger gregarious non-passerines. The Grey-headed Gull *Larus cirrocephalus* (GHG) occurs in large numbers on landfill sites in Gauteng and other areas where human activities provide scavenging opportunities. These sites provided us with an excellent opportunity to catch and individually mark these gulls as part of a project looking into their movements and population dynamics. Owing to the nature of these areas and the lack of expertise with regards to explosives, it was decided that the CNM would be too dangerous and would probably not be permitted by the relevant authorities. With the help of a few enthusiastic craftsmen, as well as advice from designers of similar methods for other species, we decided to use speargun instead of canons. Particulars of our design are detailed below. This design forms a framework for interested ringers to build on, adapt and improve for their particular target species.

Construction

The device consists of two spearguns mounted on aluminium frames (Figure 1). These mount-bases were placed approximately 10 m apart allowing for a concertinaed net to be laid between them. The leading edge of the net was attached to 1.5 m leaders connected to the distal end of the spears. The trailing edge of the net was secured to anywhere on the mount frame by leaders of similar length. Each speargun was loaded while positioned in its base, usually requiring two people to achieve this task. The

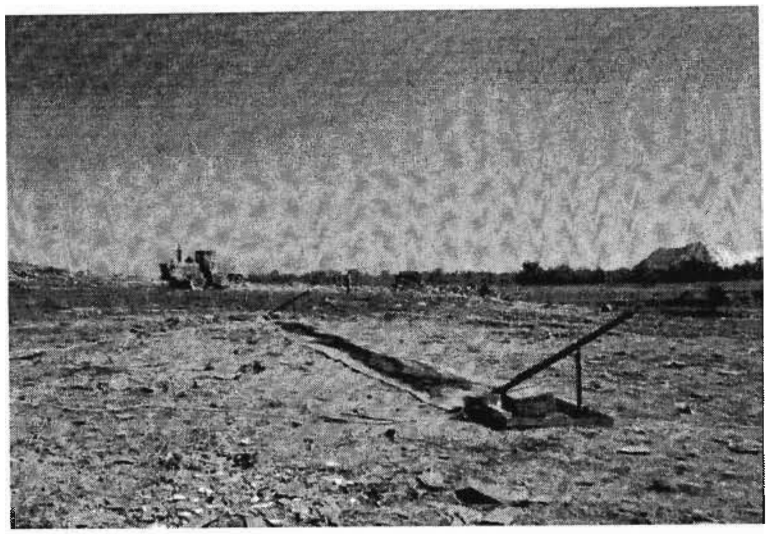


Figure 1. The speargun-driven net device set up in Weltevreden Landfill, Gauteng

triggering devices of both guns were set off simultaneously by solenoids mounted to the back of the frames. The solenoids were connected to a common cable attached to a regular 12v car battery. Details of each component are listed below:

The mount base (Figure 2) – constructed of scrap aluminium metal angles bolted together in a square frame. A footrest bar A (made of ordinary water piping with welded metal angles) was secured to the frame – this ensured better leverage when loading. A flat piece of plywood was firmly attached to half the surface area of the square frame – this enabled the user to anchor the device firmly by placing heavy objects (e.g. rocks) on this platform. The trigger casing B was held in place by two wooden blocks C screwed to the base of the plywood and the aluminium frame respectively. The gun-support arm D was made up of two sizes of aluminium piping forming a telescopic device that provided some variability in the angle at which the user wished to fire the device. This variability was made possible by drilling a number of holes (we used three) through the narrower inner pipe E and one set of holes through the outer pipe D, making sure they lined up so that a peg could secure them in place. The arm was attached to the base via two angles connected by a freestanding bolt that enabled the arm to swivel into the correct position to support the gun (at the specified angle). The hollow end of the inner pipe E was securely plugged with wooden dial to allow for a U-shaped clamp to be attached. Two holes were drilled into this clamp to provide space for a metal peg that fastened the barrel of the gun to the support arm.

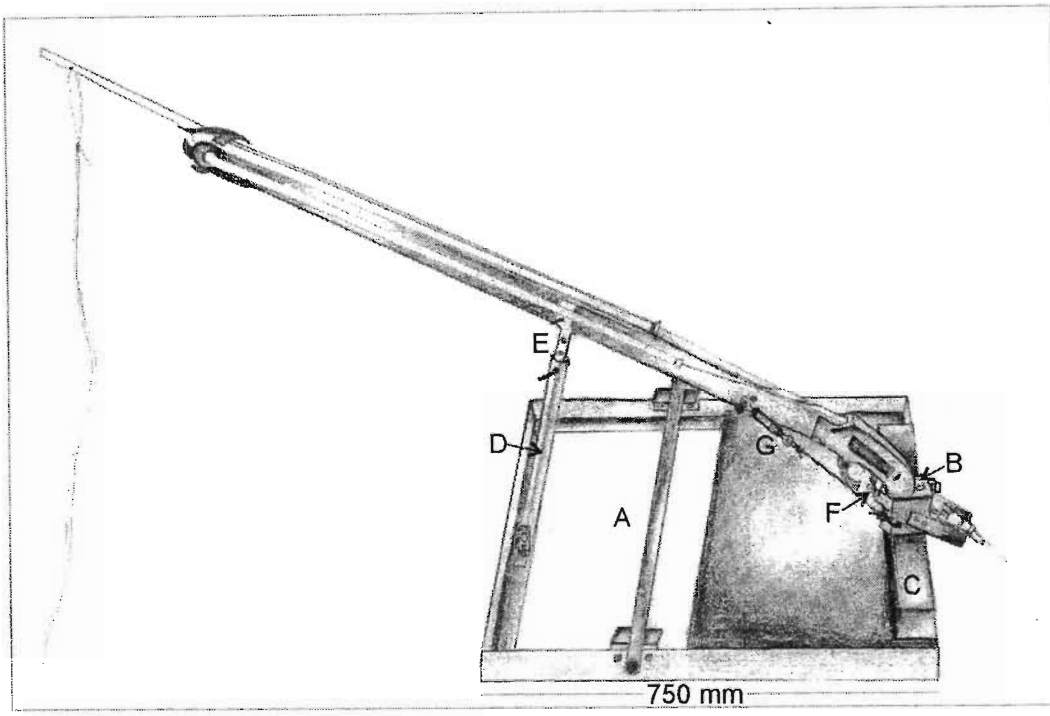


Figure 2. Mount base with modified speargun attached.

The speargunsBEGINNING (Figure 2) – a few adjustments to the speargruns were neccessary. A narrow notch in the trigger was cut (we used a small hacksaw) to allow for the attachment of the saddle F. Further up the barrel E two holes were drilled through the speargun barrel to accommodate the pin that attached the speargun to the moveable arm. The spear was drilled, approximately 7cm from the tip, for attachment of the leader rope connecting the net. In order to prevent the speargun from shifting forward while loading, a turn-buckle G was secured through the base-end of the speargun barrel with a bolt and nut. A piece of cable was then threaded through this buckle and fastened to the trigger casing (Figure 3, C).

The triggering device (Figure 3) – consisted of the solenoid A (we used Toyota solenoids, the type used to open door locks) with mounting plate Aa, suspended on the back of the speargun mounting frame by two flat steel mounting arms B. Flat steel brackets Ba were welded to the arms B and drilled to allow for the attachment of the solenoid mounting plate Aa. Before the solenoid was attached, we made sure that the mounting arms B were suitably lined up to allow for the moving arm Ad to pass freely through the drilled opening I in the back of the casing C. This casing consisted of two right angle pieces of aluminium that formed an open box. The inside of the casing was lined with two blocks of foam rubber F that served to hold the butt-end of the speargun firmly in place. The flat end of the moving arm was connected to the trigger

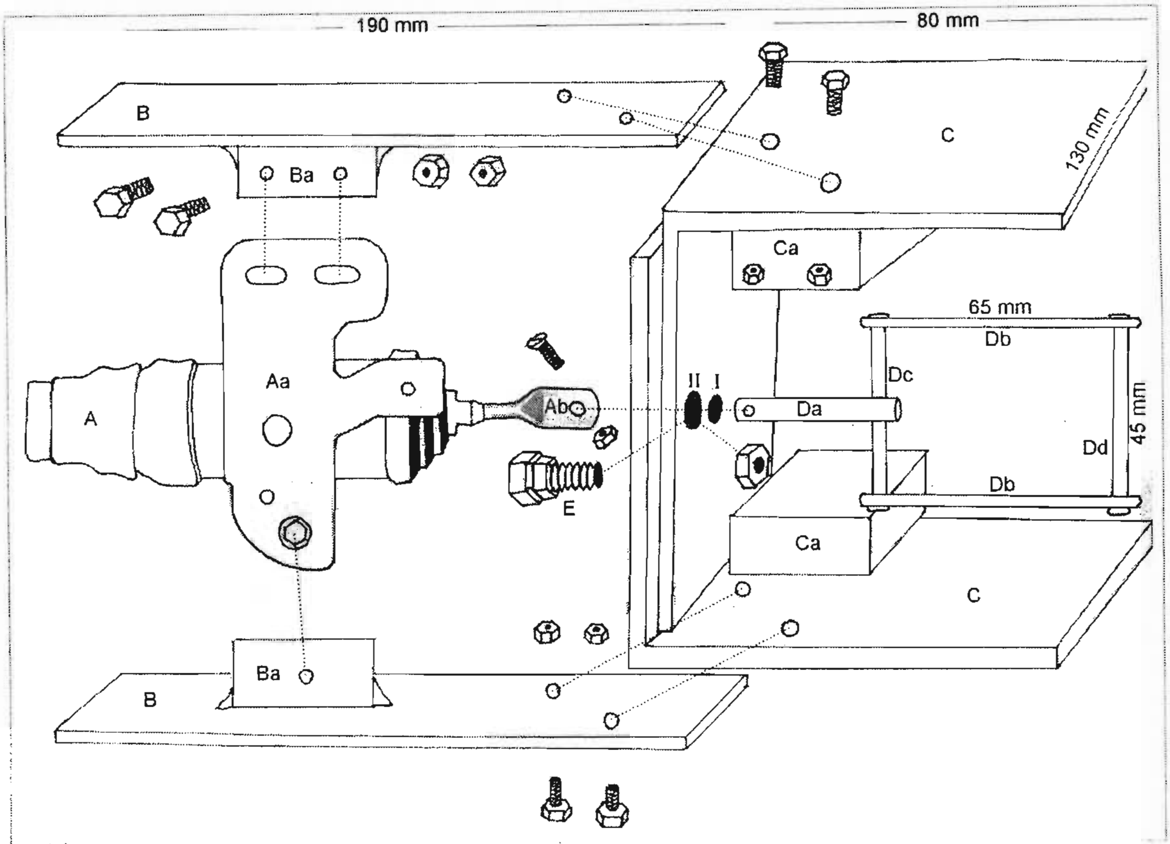


Figure 3. Triggering device.

saddle D. This consisted of a cylindrical steel bar Da welded to a rectangular frame made up of two steel plates Db welded to two steel nails Dc and Dd (Dd attached to the trigger). The proximal end of Da was drilled and hacksawed to allow for the attachment of the flat end of the moving arm Ab with a counter-sunk machine screw and nut. Above the drilled hole I, another hole II was drilled to allow for an adjusting bolt with lock nut to be inserted. This served as an adjustable backrest for the speargun butt so that the trigger could be lined up with the trigger saddle.

<u>Nets</u> – two nets were used, each for a different trapping situation. We used a nylon pilchard net (net size – 10 m X 4 m; mesh size - 12 X 57mm) for catching gulls at landfill sites and a mono-filament gill net (net size – 10 m X 8 m; mesh size - 8mm extended diameter) for gulls caught on the beach. The size of the mesh will depend on the species in question (for a summary of what sizes to use for different species see Underhill & Underhill 1987). A 5 mm ski rope was woven into the periphery of the net and secured with fishing gut at 30 cm intervals. This maintained the structure of the net while the ski rope also ensured that propulsion pressure was distributed evenly. Four metal washers were secured to each corner for the attachment of the leader ropes.

Setting up

Both mount bases were placed approximately 30 cm on either end of the extended net. Before the net was secured to the spears and mount bases, we removed all debris lying within the net run, thereby preventing it from becoming entangled after firing. The net was then carefully concertinaed and laid in a narrow stretch between the bases, making sure that the leading edge lay on top and forward of the folded net. For each speargun-base, we attached both leaders to the spear and mount base respectively. The guns were then loaded with both rubber elastics, to ensure maximum propulsion. Special care must be taken to prevent anyone from being present in front of the spears during loading, in case of misfire (it is also reccomended that spears should be blunted and even padded to prevent potential injury). The cable was then connected to the solenoids and car battery making sure the switch was turned off. Bait (we used restaurant waste for landfill sites and pilchards for the beach) was laid out not further than 1 m from the net (the closer the better, but this will depend on the sensitivity of the target species).

Results and advice of using the SNM with gulls

All results presented in Table 1 relate to gulls caught on landfill sites in Gauteng's East Rand and on Durban's Blue Lagoon beach. The great variability in both numbers caught per catch-effort as well as the numbers caught per day can be explained by a number of related reasons.

<u>Landfill sites</u>

Firstly, the best chance of catching large numbers of GHG's was when the birds were unfamiliar with the device and fed confidently within close proximity to the net. These opportunities came typically during first catch attempts (i.e. in the morning) or when new groups of birds entered the system (later on in the day when there was a large time delay between catches). Smaller catches (Table 1) were usually associated with subsequent catch efforts (on the same day) when birds had become trap-shy. It is important therefore to choose the timing of your initial catches carefully so as to maximise these opportunities. Another important aspect related to proximity to the feeding areas of the birds (e.g. on landfill sites - the actual site where garbage is dumped). On one particular day at Linbro Park, Gauteng we were only able to catch one bird. This was because the site failed to provide us with any suitable catching

Table 1.

	Landfills	Beach
no. of catch efforts	38	40
mean catch	8	1
min catch	1	1
max catch	40	2
no. of catching days	15	17
mean daily catch	29	2.5
min daily catch	1	1
max daily catch	54	6
total birds caught	385	46

areas (i.e. fairly level ground, out of the way of traffic) in close enough proximity to the gulls' feeding area. Although we managed to chase approximately 30 birds to within metres of the net, they were not interested in our restaurant treats and preferred, rather, to roost nearby. The point here is that the trap should be set up as close as possible to the feeding birds.

Beach

Catching gulls on Durban's beachfront proved far less fruitful than on landfill sites in Gauteng. The birds were present every day but in far fewer numbers and this is reflected both in our mean catch effort and in the total number of gulls caught per day (Table 1). The trap was set up adjacent to fisherman at Blue Lagoon, a well-known fishing spot, and the gulls were lured to the site with pilchards – a dietary item these birds are very familiar with. Our maximum catch for this site (six gulls, Table 1) came from our first day of catching. Subsequent catch days proved to be progressively poorer in overall numbers caught per day and this is likely to be as a result of the familiarity of the local GHGs with the trap (re-sightings of previously ringed individuals were noted returning to the same catch area and showing signs of trap-shyness). Those gulls that did approach the bait tended to keep a safe distance from the net. This prompted us to make a larger and more lightweight net that could be propelled a further distance at an increased velocity. Our monofilament net (described above) proved to be successful in catching these outlying birds. However, by the time the new net was employed, overall numbers of GHGs in Durban were dwindling (due to seasonal emmigration) and we were only able to catch one or, at most, two gulls a day. Here again the advice is to make the most of early catches even if it means familiarising the gulls to the baiting site, first, without deploying the net, and then, firing off the trap as soon as large numbers are within range.

Acknowledgements

We would like to thank Rob Allen Spearguns for supplying us with the modified spearguns, especially Jeremy Williams and Rob Allen who gave valuable advice on the construction of the trap. We are also very grateful to Greg Turco who helped with the electrical component of the trap and kindly donated the cable and switch.

All catches would have been impossible were it not for the help of various individuals who generously volunteered their time to help. Thanks go to Terry Walls, Lynne Bingham, Richard, Job, Pat Cochran, Joel Avni, Greg & Fiona Brown and Fran de Jager.

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Appendix 5.2. Codes and abbreviations for different topographically defined plumage and bare part characteristics and moult scores of Grey-headed Gulls trapped in Gauteng and Durban.

Plumage

Head

1 head with extensive dark markings
2 head white with dark-dusky ear and eye patches
3 head white with faint-dusky ear and eye patches
4 complete pale-grey hood usually without contrasting border
5 complete rich-grey hood usually with dark dusky contrasting border Hind-neck
1 white
2 pale-grey
3 white or pale-grey with brown/dusky patches

Mantle, lesser coverts & greater secondary coverts

1 grey and brown/dusky in almost equal proportions
2 mostly grey, little brown/dusky
3 grey

Scapulars & median coverts

1 mostly brown/dusky, little grey
2 grey and brown/dusky in almost equal proportions
3 mostly grey, little brown/dusky
4 all grey

Greater primary coverts

1 grey and white
2 grey and white with black terminal tips

Secondaries

1 grey
2 dark contrasting dusky-grey with pale white/grey tips

Appendix 5.2 continued.

Primary mirrors

0	mirrors absent
1r	mirror reduced to shaft on one primary: usually P10, less frequently P9
1s	mirror small on one primary, usually P10, less frequently P9
2r	mirrors reduced or very small on two primaries, P10 and P9
2s	mirrors small on primaries P10 and P9
2m	mirrors medium on primaries P10 and P9
2l	mirrors large on primaries P10 and P9
3l	mirrors on three primaries, large on P10 and P9, and usually small on P8

Primary tips

1	prominent white primary tips (larger on inner primaries)
2	reduced or faded primary tips mostly on primaries (P4 – P6)
0	primary tips absent

Tail bar

1	prominent dark terminal tail bar
2	reduced or faded terminal tail bar
0	tail bar absent

Bare parts

Bill & leg colour

bro	bright red/orange
bh	brown/horn
db	dark-brown/black
dr	dark-red
fh	flesh/horn
o	orange
ob	orange/brown
rob	red/orange/brown

Appendix 5.2 continued.

Bill tip

0 dark contrasting bill tip absent

1 dark contrasting bill tip present

Eye colour

1 pale-white/yellow

2 pale greyish

3 light-brown

4 dark-brown

Orbital ring

1 red/orange

2 brown

Moult scores

0 – old feather

1 – missing or new feather completely in pin

2 – new feather just emerging from sheath or up to 1/3 grown

3 – new feather 1/3 – 2/3 grown

4 – new feather 2/3 to fully grown but with some sheath remaining

5 – new feather but no trace of sheath

8 – fully grown feather age uncertain

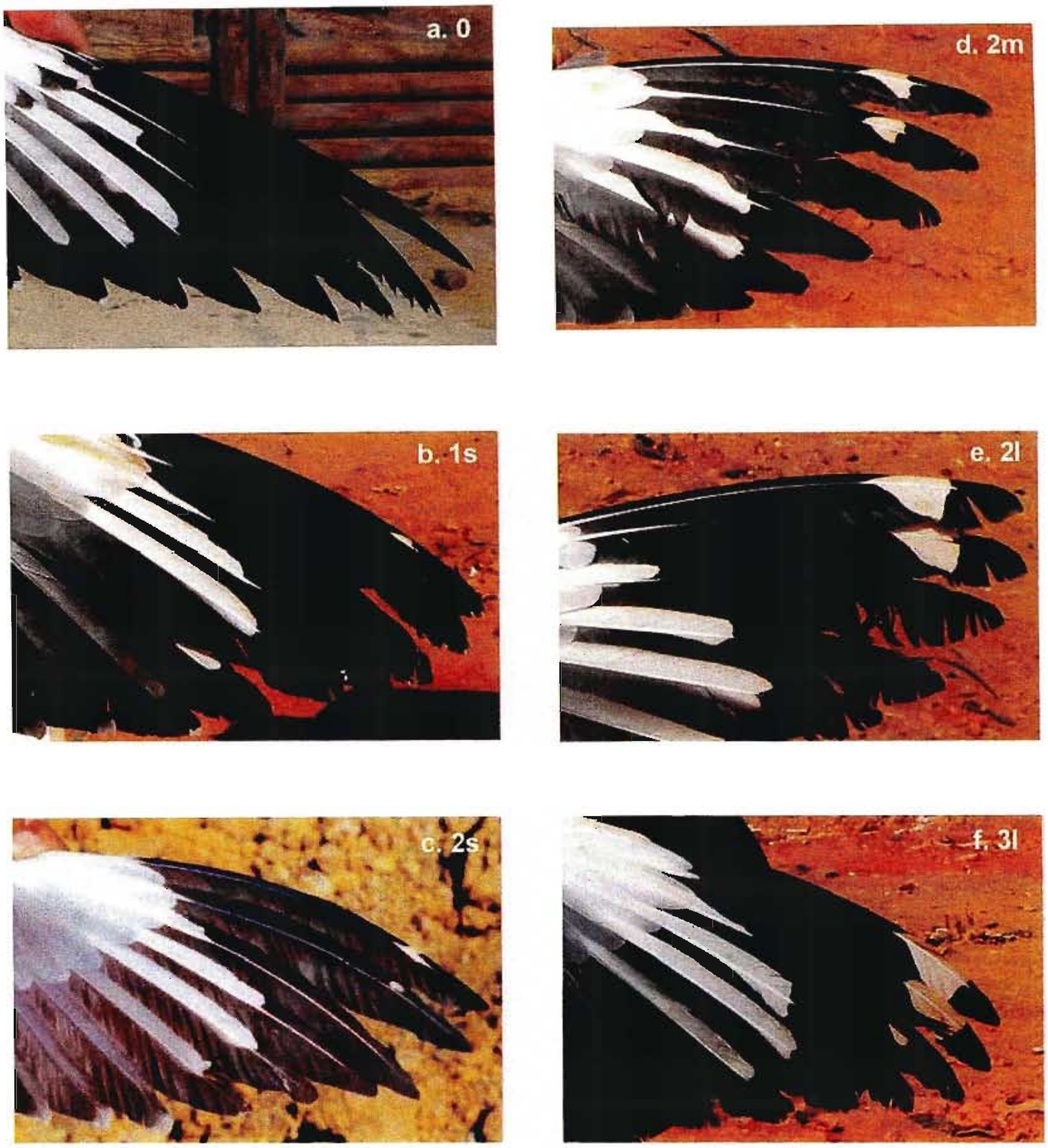

Plate 5.1. Photographs of different primary mirror categories allocated to Grey-headed Gulls trapped in Gauteng and Durban: a. 0 - mirrors absent; b. 1s - mirror small on P10; c. 2s - mirrors small on P10 and P9; d. 2m - mirrors medium on P10 and P9; e. 2l - mirrors large on P10 and P9; f. 3l - mirrors large on P10 and P9, mirror small to medium on P8.

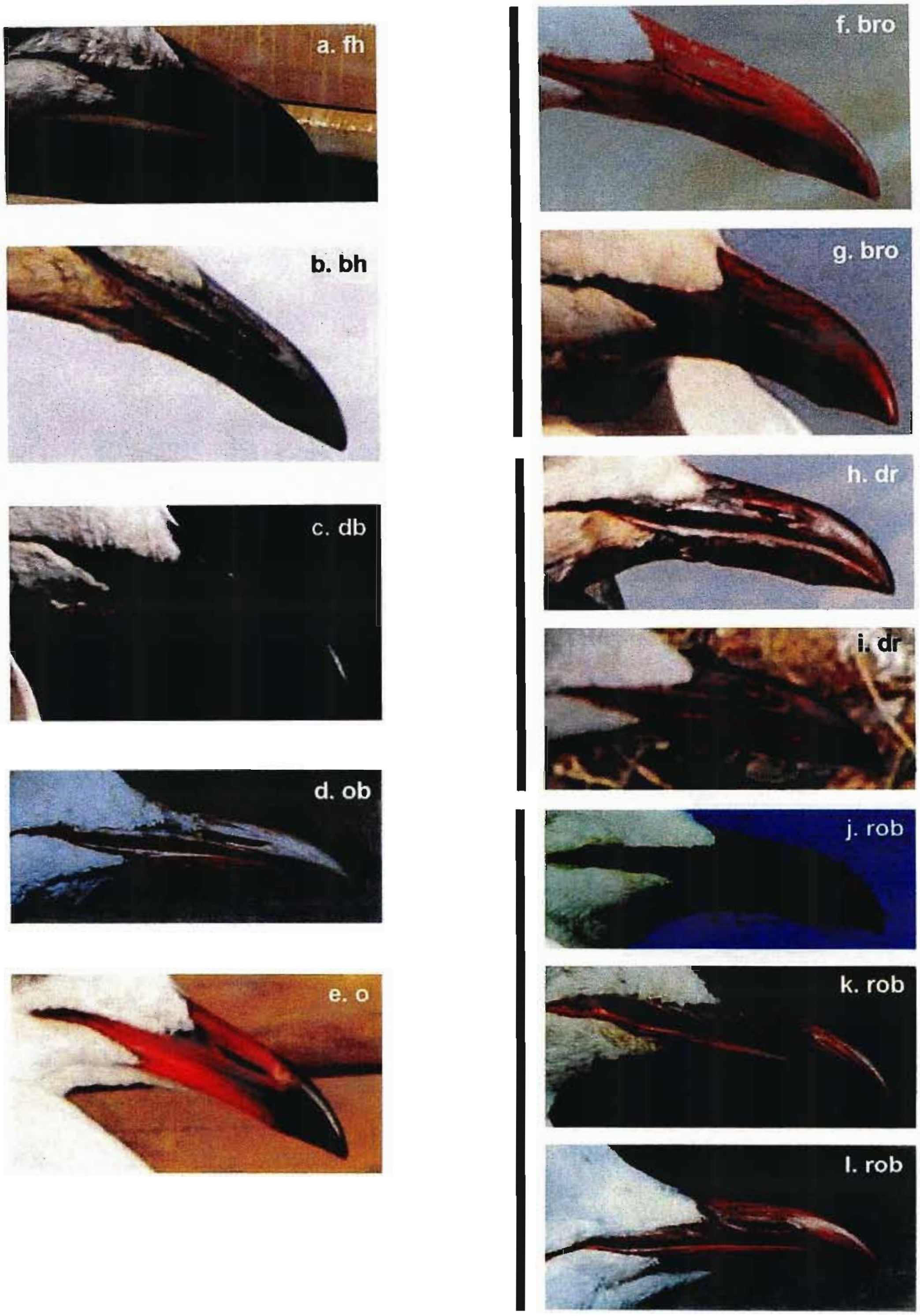

Plate 5.2. Photographs of different bill colours of Grey-headed Gulls trapped in Gauteng and Durban: a. fh - flesh/horn; b. bh - brown/horn; c. db - dark-brown; d. ob - orange/brown; e. o - orange; f., g. bro - bright-red/orange; h., i. dr - dark-red; j., k., l. rob - red/orange/brown.

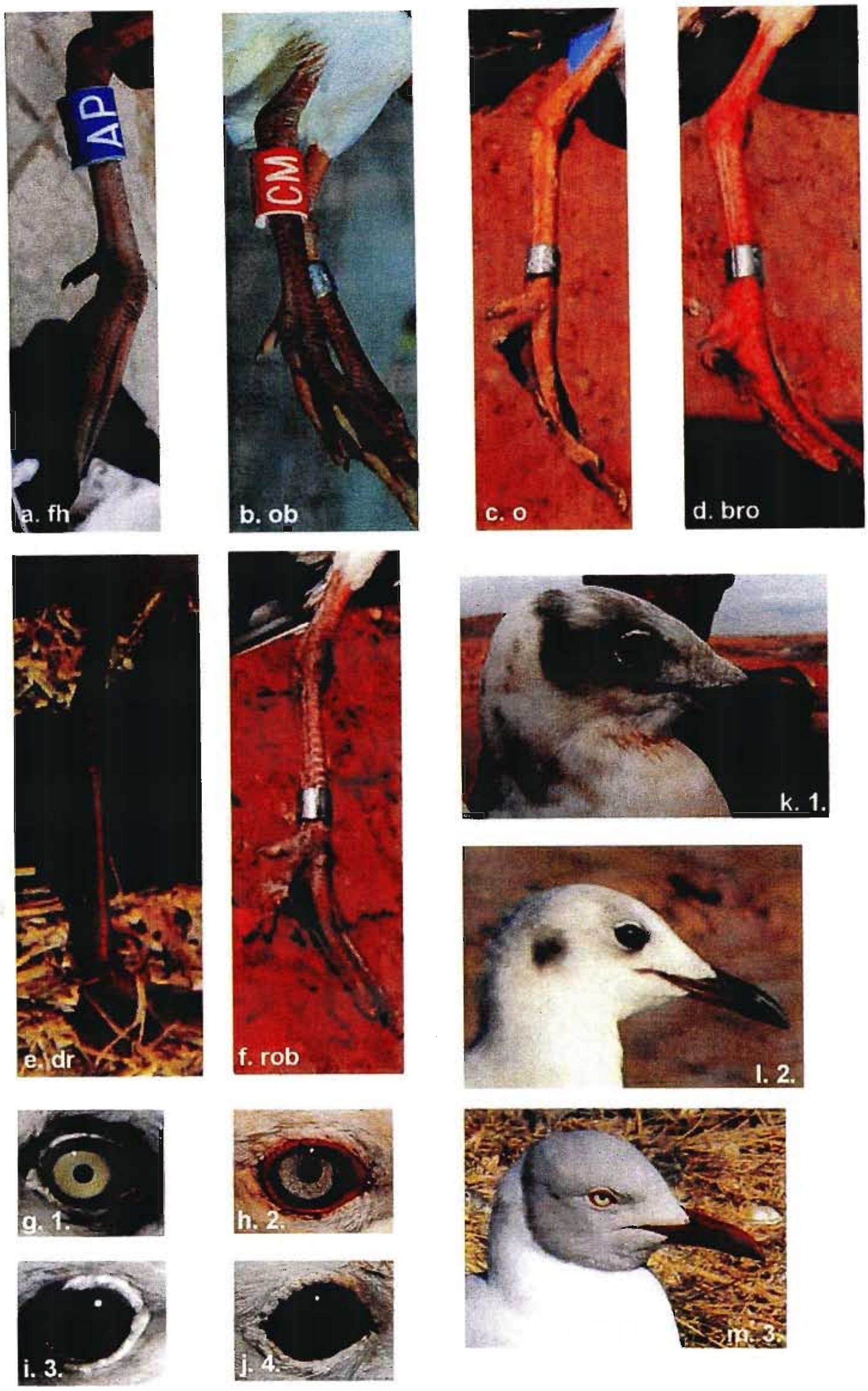

Plate 5.3. Photographs of leg colours, eye colours, and different head categories of Grey-headed Gulls trapped in Gauteng and Durban: **leg** a. fh - flesh/horn; b. ob - orange/brown, c. o - orange, d. bro - bright-red/orange, e. dr - dark-red, f. rob - red/orange/brown (leg colours' bh and db not illustrated) ; **eye** g. 1 - pale-white/yellow, h. 2 - pale-greyish, i. 3 - light-brown, j. 4 - dark-brown; **orbital ring** g., h. 1 - red/orange, i.,j. 2 - brown; **head** k. 1 - with extensive dark markings, l. 2 - white with dusky ear and eye patches, m. 3 - grey hood.

a. juvenile: hindneck - 3, mantle - 2, scapulars - 2, lesser coverts - 2, median coverts - 1, greater secondary coverts - 2, greater primary coverts - 2, secondaries - 2, tail bar - 1.

b. immature: hindneck - 2, mantle - 3, scapulars - 2, lesser coverts - 2, median coverts - 2, greater secondary coverts - 2, greater primary coverts - 2, secondaries - 2, tail bar - 2.

c. immature: hindneck - 1, mantle - 3, scapulars - 4, lesser coverts - 2, median coverts - 3, greater secondary coverts - 3, greater primary coverts - 2,

d. immature: hindneck - 1, mantle - 3, scapulars - 4, lesser coverts - 3, median coverts - 4, greater secondary coverts - 3, greater primary coverts - 2, secondaries - 2, tail bar - 0.

e. immature: hindneck - 1, mantle - 3, scapulars - 4, lesser coverts - 3, median coverts - 4, greater secondary coverts - 3, greater primary coverts - 1, secondaries - 1, tail bar - 0.

f. adult: hindneck - 1, mantle - 3, scapulars - 4, lesser coverts - 3, median coverts - 4, greater secondary coverts - 3, greater primary coverts - 1, secondaries - 1, tail bar - 0.

Plate 5.4. Photographs of Grey-headed Gull plumage from birds trapped in Gauteng and Durban: **hindneck** 1 - white, 2 - pale-grey, 3 - white or pale-grey with brown/dusky patches; **mantle, lesser coverts, greater secondary coverts** 1 - grey and brown/dusky in almost equal proportions, 2 - mostly grey, little brown/dusky, 3 - grey; **scapulars, median coverts** 1 - mostly brown/dusky, little grey, 2 - grey and brown/dusky in almost equal proportions, 3 - mostly grey, little brown/dusky, 4 - grey; **greater primary coverts** 1 - grey and white, 2 - grey and white with black terminal tips; **secondaries** 1 - grey, 2 - dark contrasting dusky-grey with pale-white/grey tips; **tail bar** 1 - prominent dark, 2 - reduced or faded, 0 - absent.

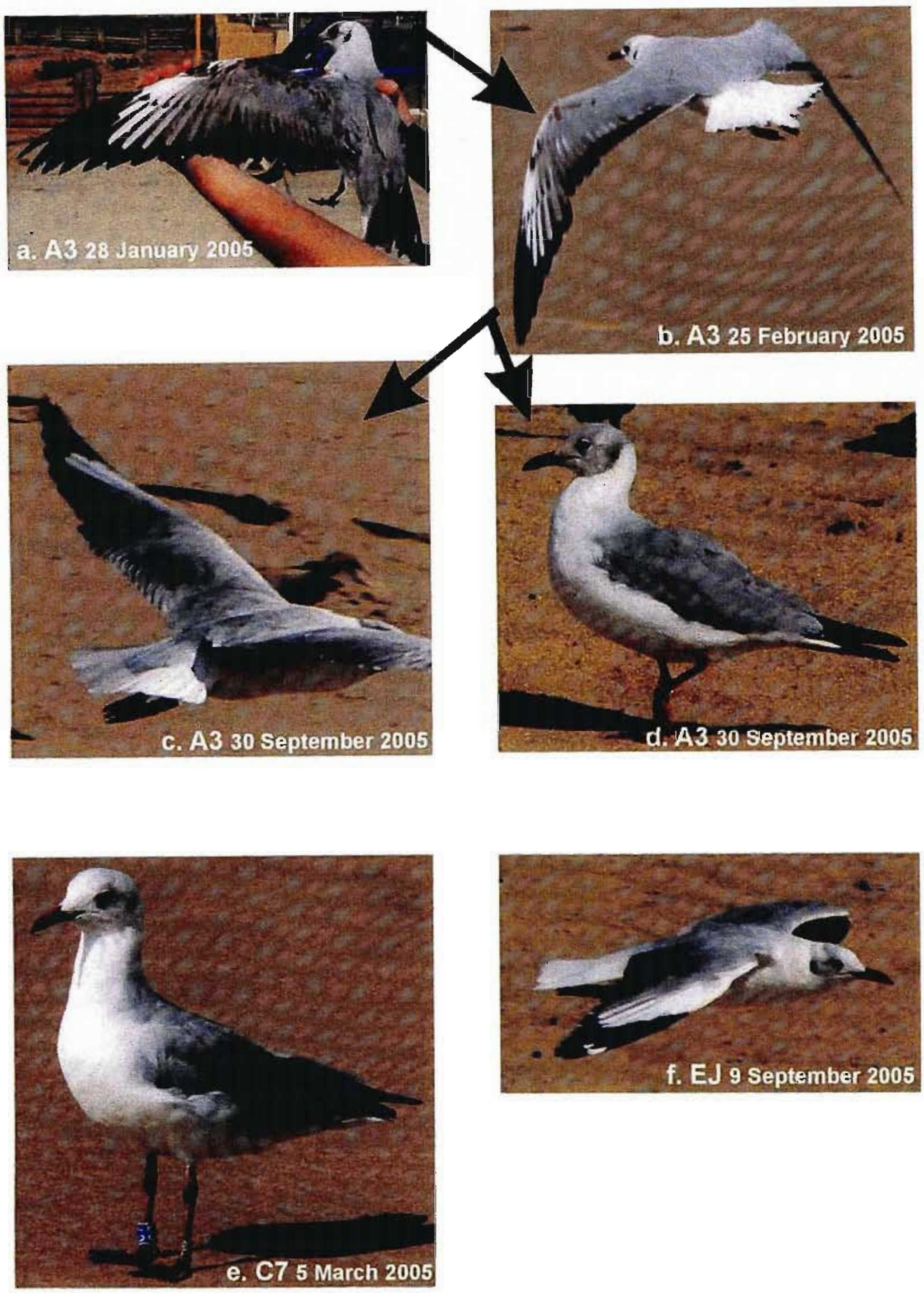

Plate 5.5. Photographs illustrating re-sightings of Grey-headed Gulls ringed at Blue Lagoon, Durban. Photograph captions: bird identification (two engraved characters), date of re-sight. Photographs b. - f. were taken on Durban's beachfront between one and 12 months after capture. Capture dates of birds: a., b., c., d. 28 January 2005; e. 1 December 2004; f. 29 December 2004.

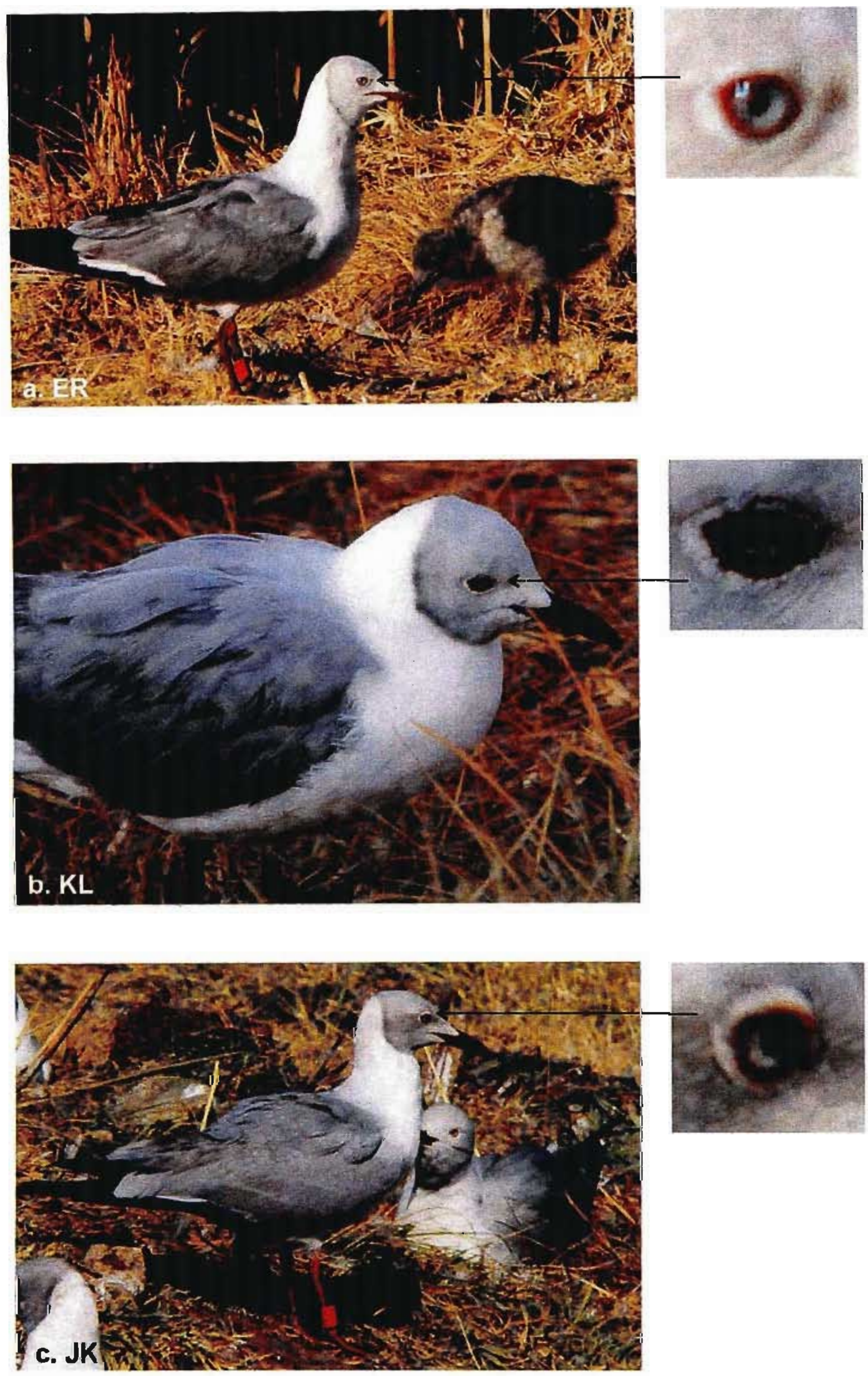

Plate 5.6. The three Grey-headed Gulls re-sighted at Lakefield Pan, Gauteng, June and July 2005: a. ER with young ½; b. KL; c. JK (left) with partner (right) on empty nest. Eyes have been enlarged to illustrate their colour.

Chapter 6

Conclusion

The preceding chapters have provided an overview of the biology of the Grey-headed Gull in commonly studied areas of gull biology that, hitherto, have not been investigated for this species. These include an account of the distribution and relative abundance of this species in South Africa and changes in seasonal abundance at different localities and provinces, during the breeding and non-breeding seasons. It gives the first account of adult movements within South Africa, calling into question the hypothesis that adult birds have large-scale, regular movements between Gauteng and KwaZulu-Natal. The recorded movements and the seasonality data indicate that, rather, there is a strong likelihood of regular movements of adult birds between Durban and Lake St Lucia. This information is significant as it highlights the importance of Durban, and especially Durban Bay, to the continued health of Lake St Lucia's breeding population. With increasing pressure to expand Durban's harbour facilities, and the potential for further displacement of intertidal feeding habitats, the population status of this bird in KwaZulu-Natal may see some major alterations in the future.

The sections on the breeding biology of the Grey-headed Gull provide the first documented accounts of important life-history traits: the incubation period; differential parental investment during incubation; and relative growth rates of different morphological features. These chapters go beyond just a description of these traits, by comparing intraspecific differences between breeding parameters. The differences in laying synchronicity between Lake St Lucia and Gauteng birds were a notable finding. Unfortunately, studies at Lane Island were terminated at the egg stage (due to high levels of natural predation) and comparisons of chick growth rates and survival probabilities between Gauteng and Lake St Lucia were not possible. These two sites clearly provide for an interesting comparative study on the breeding ecology of the Grey-headed Gull and further research into this area could produce interesting results. Future research should include a comparison between the diets and provisioning rates of parental birds and attendance rates at the nest. This could be expected to differ under different levels of predation. It would also be interesting to compare the breeding parameters of Grey-headed Gulls between different years at Lake St Lucia, especially between dry and wet periods when the ecological dynamics of this system show great variability.

Results of both the egg and chick stages of the Grey-headed Gulls' breeding biology in Gauteng have revealed some interesting intraspecific differences. The inclusion of the Modderfontein Pan breeding colony shed some interesting light on the comparative breeding ecology of this species at a local scale. This site is on the periphery of the Grey-headed Gulls' core breeding range, yet was clearly advantageous to breeding birds during 2005. This suggests that density-dependent factors may be limiting certain breeding parameters within their core distribution in the East Rand. Clearly, more information is necessary to validate this hypothesis, including comparative differences in levels of territoriality and competition both at the breeding colonies and at feeding sites, such as landfills. Results of the dietary analysis from this study, while useful in being the first quantitative account of chick diet for this species, are limited in that they do not determine the relative nutritional quality of each dietary item and the sample sizes are mostly inadequate to draw any firm conclusions between different age categories, especially at Lakefield Pan. Despite these shortcomings, the results of the dietary analysis have elucidated the relative importance of invertebrates in the diet of young chicks. It is not known exactly how important these food items are but it would be interesting to establish the relative importance of invertebrate supplies to the breeding success of this species. Perhaps the abundance of artificially enhanced aquatic invertebrate populations in Gauteng was one of the key reasons for the rapid colonization of this system.

The formulation of an updated age-classification and a discriminant function to sex adult gulls in Chapter 4 provide useful tools for further research into population dynamics of this species. The information on moult, while based on a relatively small sample size, has provided the first detailed account of this aspect of the Grey-headed Gull's biology.

What has astounded me while working through the many scientific papers on gull biology and after realizing just how accessible and productive breeding gull colonies can be for investigation, is the lack of any scientific research on this species in

Gauteng. When compared to other well-studied species, such as the Black-headed Gull *Larus ridibundus*, I have only scratched the surface of the Grey-headed Gull's breeding biology. There are many interesting questions that can be formulated and the information discovered can be compared to the wealth of knowledge already generated on other masked gull species. The breeding localities in Gauteng present themselves as the ideal opportunity for further studies on Grey-headed Gull breeding biology and more detailed research on this species should be encouraged by the many tertiary education institutes in the area.

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