
Marine ecology and conservation of the Galápagos penguin, *Spheniscus mendiculus*

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Kiel, Mai 2007

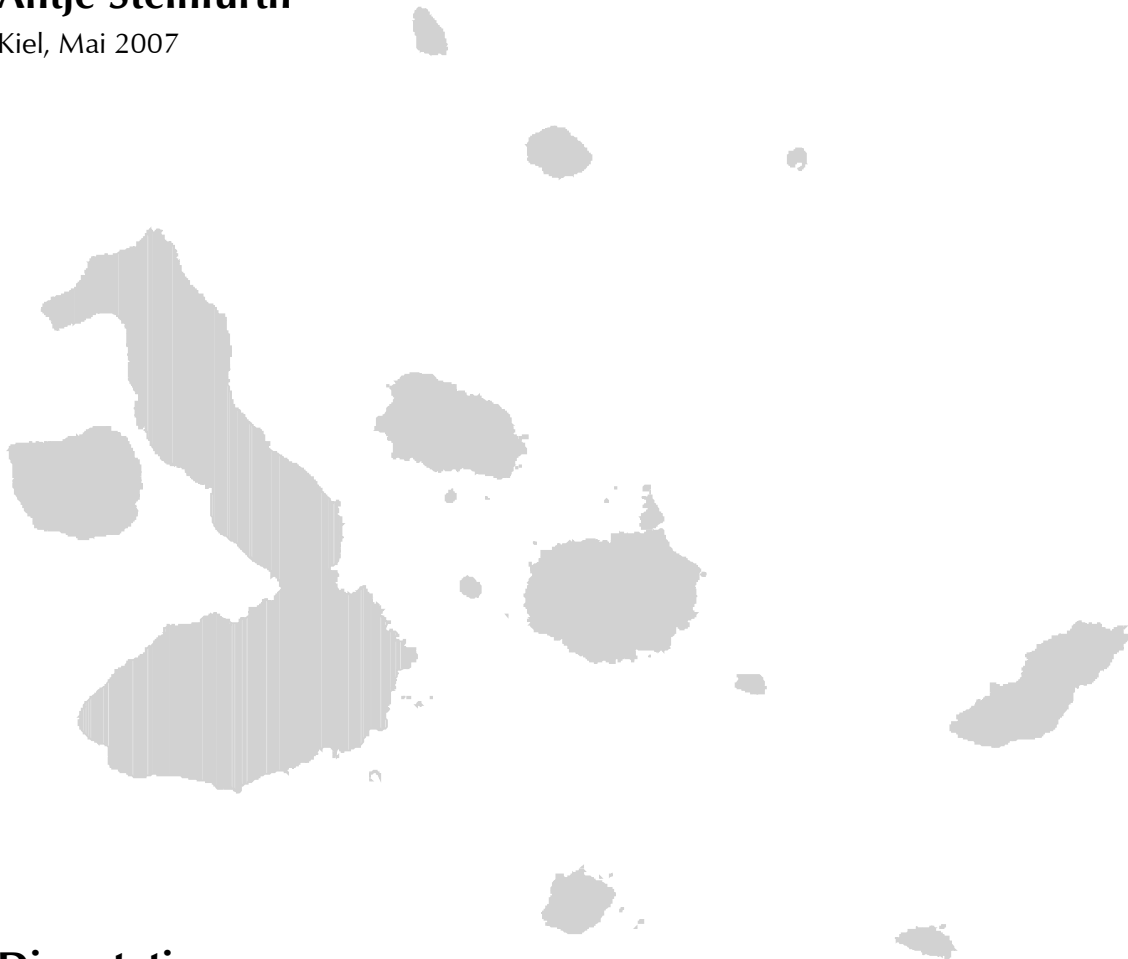
Dissertation

Zur Erlangung des Doktorgrades

der Mathematisch-Naturwissenschaftlichen Fakultät

der Christian-Albrechts-Universität

zu Kiel



But all natural history is much harder than it seems for even when the subjects are conspicuous it is hard to make sense in what you see, and penguins confuse in all conceivable ways.

C. Tudge in The plight of the penguins. 2001

to my parents

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vorgelegt von
Antje Steinfurth
Kiel 2007

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Summary

The presented thesis outlines several aspects of the marine ecology and conservation of the Galápagos penguin (*Spheniscus mendiculus*). This project was realised between July 2003 and September 2005 in the Galápagos islands as a collaborative project between the Charles Darwin Foundation, the Galápagos National Park Service and the University of Kiel in Germany.

In two concurrent years, 2004 and 2005, breeding activities of the Galápagos penguin were investigated. The majority of all the breeding sites was found on Isabela Island, the largest island in the archipelago, with the highest aggregations of active nests concentrated in the southwest of the island. The study showed that the distribution of the breeding sites is strongly related to nutrient-rich upwelling areas within the archipelago, caused by the Equatorial Undercurrent (EUC; also known as the Cromwell Current). Considering penguin breeding sites in light of the Galápagos Marine Reserve (GMR) zoning system however, raises interesting concerns. While only a few nests (25.2 %) are afforded the highest protection level, the large majority of nests (74.8 %) were found in areas designated for extractive uses (e.g., fisheries). The implications for penguin conservation may be significant. Even though nesting penguins may not feed in this adjacent coastal area, they need to pass through this zone on their way to their foraging sites. Although active nests could be discovered virtually throughout the year, the results showed generally two well-defined breeding peaks within the year: March to May, and from July to September. The region in the western part of the archipelago undergoes (except in El Niño years) a seasonal increase in phytoplankton biomass in the second part of the year (from June to December) which coincides well with the second period of egg-laying. The first egg-laying peak corresponds with the strengthening and shoaling of the EUC in April. An inter-annual and regional comparison in breeding patterns indicated that egg-laying was variable on both a temporal and spatial scale. Thus, the breeding biology of the Galápagos penguin seems to be well adapted to the highly variable oceanographic environment surrounding the Galápagos islands.

Between May 2004 and May 2005, the horizontal and vertical movements of foraging Galápagos penguins was studied during their breeding season to examine space use at sea and to compare the volume of water exploited by this penguin to those of other penguin species. Twenty-three adult penguins (11 males and 12 females) brooding chicks were equipped with Global Positioning System-temperature depth data logger at the three main nesting sites on south-western Isabela Island. Birds moved between 1.1 and 23.5 km (mean = 5.2 ± 4.9 km) from the nest, concentrating foraging in a strip of sea within 1.0 km of the shore. Foraging trips lasted a mean of 8.4 ± 2.0 hours. Although the deepest dive was 52.1 m, birds spent, on average, 90 % of their time underwater at depths less than 6 m.

Both foraging ranges and dive depths were below those predicted from allometric regressions derived from other penguin species. Applying the maximum values for movement to calculate space use, the Galápagos penguin exploits a maximum volume of water of $< 1.4 \text{ km}^3$, which is almost 90 times less than that predicted for its mass, and thus utilises only a small portion of the total potentially available upwelling area within the Galápagos archipelago.

This work was complemented by analysis of non-breeding penguin diet using the combined approach of stable-isotope analysis and conventional dietary sampling of stomach samples. The resulting data set revealed that diet was mainly composed of neritic, pelagic species typical of upwelling systems, dominated by Engraulidae (here represented by Pacific anchoveta (*Cetengraulis mysticetus*)). However, while other *Spheniscus* penguins are known to feed on adult schooling fish, this study provided strong evidence that Galápagos penguins' feeding preferences were young fish or even larvae ($\leq 30 \text{ mm}$). Since larvae and juvenile phases of these fish species inhabit the surface inshore waters, and migrate offshore when adult. The use of coastal habitat by device-equipped breeding Galápagos penguins corresponds well with the results obtained from the stomach samples of non-breeding penguins. The stable-isotope analysis provides estimates of diet changes on a temporal and spatial scale. There was no differences in diet composition detectable in our study animals.

These results provided critical information on the penguins' use of the GMR and will be applied to appropriately design the layout and protection levels of the zonation system. This data represents a strong argument for improved fisheries management to avoid undue competition between man and penguins.

Since the principal threat to seabirds breeding in the Galápagos islands past and present is that of introduced alien mammals, the predatory impact of cats (*Felis catus*) on the endangered Galápagos penguin population was studied at the penguins' main breeding site. Here, two methods were used to assess penguin mortality rate: 1) direct counts of penguin carcasses and 2) an energetic approach. The results of these two independent mortality assessments suggested that a single cat was responsible for an increase in adult mortality of 49 \% year^{-1} at this site. Although the annual penguin census shows a relative stable and even slightly increasing population trend over the last years, the vulnerability of this population to even small changes in mortality rates is well known and these results even reveal that the situation of the Galápagos penguin is more fragile than previously assumed. Greater attention should be paid to the impact of introduced species that are increasingly affecting this species.

Zusammenfassung

Die vorliegende Arbeit untersucht verschiedene Aspekte der marinen Ökologie und des Artenschutzes des Galápagos Pinguins (*Spheniscus mendiculus*). Dieses Projekt wurde zwischen Juli 2003 und September 2005 in Kollaboration mit der Charles Darwin Foundation, dem Galápagos Nationalparkamt und der Universität Kiel durchgeführt.

Die Brutaktivität des Galápagos Pinguins wurde in zwei aufeinanderfolgenden Jahren, 2004 und 2005, untersucht. Die Mehrheit der Nistplätze befand sich auf Isabela, der größten Insel des Archipels, wobei die höchste Dichte an aktiven Nestern im Südwesten der Insel beobachtet werden konnte. Die Untersuchung ließ einen deutlichen Zusammenhang zwischen der Verteilung der Brutgebiete und den nährstoffreichen Auftriebsgebieten innerhalb des Archipels, die durch den Äquatorialen Unterstrom (auch bekannt als Cromwellstrom) hervorgerufen werden, erkennen. Betrachtet man die Standorte der Brutplätze der Pinguine in Hinblick auf das Zonierungssystem der Galápagos Marine Reserve (GMR), so ist zu erkennen, dass nur wenigen Nestern (25.2%) der höchste Schutzstatus gewährt wird und die Mehrheit der Nester (74.8%) in Gebieten liegt, in denen Fischerei erlaubt ist. Dies kann unmittelbare Folgen für den Schutz der Pinguine haben. Selbst wenn die nistenden Pinguine nicht in den angrenzenden Küstengebieten auf Nahrungssuche gehen, so müssen sie diese auf dem Weg zu ihren Nahrungsgebiete durchqueren. Die Pinguine wiesen eine ganzjährige Brutaktivität auf, jedoch konnten zwei Hauptbrutperioden zwischen März und Mai und Juli und September beobachtet werden. Der Westen des Archipels unterliegt, zumindest in nicht El Niño Jahren, in der zweiten Jahreshälfte (Juni bis Dezember) einem saisonalen Anstieg an Phytoplanktonbiomasse, welcher zeitlich mit der zweiten Brutperiode übereinstimmt. Die erste Brutperiode wiederum steht in einem klaren zeitlichen Zusammenhang mit einem verstärkten Auftrieb der kalten nährstoffreichen Wassermassen des EUCs im April. Ein Vergleich der Brutaktivitäten zwischen den Jahren deutet darauf hin, dass die Eiablage sowohl zeitlich als auch räumlich variabel ist. Die Brutbiologie des Galápagos Pinguins ist demnach sehr gut an das marine Habitat mit sich schnell ändernden ozeanographischen Bedingungen angepasst.

Zwischen Mai 2004 und Mai 2005 wurden horizontale und vertikale Bewegungen nahrungssuchender Galápagos Pinguine während der Brutsaison aufgezeichnet, um die Habitatnutzung zu untersuchen und das genutzte Wasservolumen mit dem anderer Pinguinarten zu vergleichen. An den drei Hauptbrutplätzen im Südwesten der Insel Isabela wurden 23 adulte Pinguine (11 Männchen und 12 Weibchen) während der Kükenaufzucht mit GPS (Global Positioning System)-Temperatur-Tiefenrekordern ausgerüstet. Die Tiere entfernten sich zwischen 1.1 und 23.5 km (im Mittel 5.2 ± 4.9 km) von ihrem Nistplatz, wobei sie sich zur Nahrungssuche in einem parallel zur Küste verlaufenden, maximal 1.0 km breiten Streifen aufhielten. Die Beutezüge dauerten im Durchschnitt 8.4 ± 2.0 Stunden.

Obwohl die maximale Tauchtiefe bei 52.1 m lag, verbrachten die Vögel durchschnittlich 90% ihrer Zeit in Wassertiefen geringer als 6 m. Sowohl das zur Nahrungssuche genutzte Gebiet als auch die Tauchtiefe lagen unterhalb der durch allometrische Regressionen vorhergesagten Werte. Berechnet man den von den Galápagos Pinguinen genutzten marinen Raum mit Hilfe der maximalen Tauchtiefe und Distanzen zum Nest, ergibt sich ein maximales Wasservolumens von $< 1.4 \text{ km}^3$. Dieser Wert ist 90 mal geringer als angenommen, demnach wird nur ein kleiner Teil des potentiell verfügbaren Auftriebsgebietes innerhalb des Galápagos Archipels genutzt.

Desweiteren wurde mittels konventioneller Mageninhaltsuntersuchung und Stable-Isotope-Analyse die Nahrungszusammensetzung nicht-brütender Pinguine untersucht. Das Nahrungsspektrum bestand hauptsächlich aus für Auftriebsgebiete typischen pelagischen Arten, dominiert von Engraulidae (hier Pacific anchoveta (*Cetengraulis mysticetus*)). Während andere *Spheniscus* Pinguinarten sich vorwiegend von adulten Schwarmfischen ernähren, zeigt diese Studie, dass die Nahrung der hier untersuchten Galápagos Pinguine aus Jungfischen oder sogar Larven bestand. Die Larven und juvenilen Stadien dieser Fischarten halten sich im küstennahen Gewässer auf und wandern erst als Adulttiere in tiefere Gewässer ab. Die Nutzung küstennaher Gebiete brütender Pinguine stimmt daher mit den Ergebnisse der Mageninhalts-Analyse nicht-brütender Pinguine überein. Die Stable-Isotope Analyse ermöglicht unter anderem zeitliche und räumliche Veränderungen in der Nahrungszusammensetzung zu erkennen. Bei den von mir untersuchten Tieren konnten keine Unterschiede bezüglich der Nahrungswahl beobachtet werden.

Die Ergebnisse dieser Arbeit über die Habitatwahl und der Ernährungsweise des Galápagos Pinguins liefern entscheidende Informationen über dessen Nutzung der GMR. Sie werden bei der Gestaltung und der Festlegung des Zonierungssystems zur Anwendung kommen und helfen, durch ein verbessertes Fischereimanagement eine potentielle Konkurrenz zwischen Mensch und Pinguin zu vermeiden.

Eine der Hauptbedrohungen für die auf den Galápagos Inseln brütenden Seevögel stellen eingeführte Säugetiere da. Aufgrund des gefährdeten Status des Galápagos Pinguins wurde daher der Einfluss von Katzen (*Felis catus*) auf dessen Population in seinem Hauptbrutgebiet untersucht. Hierzu wurden zwei Methoden zur Abschätzung der Mortalitätsrate der Pinguine angewandt 1) direkte Zählung von tot aufgefundenen Pinguinen und 2) energetische Berechnungen. Die Ergebnisse dieser beiden unabhängigen Mortalitätsabschätzungen führten zu der Erkenntnis, dass eine einzelne Katze einen Anstieg der Mortalität adulter Pinguine um 49% pro Jahr an diesem Brutplatz verursachen kann. Obwohl die jährlich stattfindenden Pinguinzählungen eine in den letzten Jahren relativ stabile und sogar leicht zunehmende Population anzeigt, kann bereits ein geringer Anstieg der Mortalitätsrate bedeutende Auswirkungen auf die Populationsentwicklung haben. Mit dieser Studie konnte gezeigt werden, dass eingeführte Arten eine ernstzunehmende Bedrohung für bereits gefährdete Tierarten darstellt.

Content

Summary.....	vii
Zusammenfassung.....	ix
Content	xi
1 General introduction.....	1
2 Background information	5
3 Breeding activities of the Galápagos penguin, <i>Spheniscus mendiculus</i>	13
4 Space use of foraging Galápagos penguins, <i>Spheniscus mendiculus</i> during chick-rearing.....	33
5 The diet of non-breeding Galápagos penguins, <i>Spheniscus mendiculus</i> , at Caleta Iguana, Isabela Island, Galápagos.....	47
6 The predatory impact of cats (<i>Felis catus</i>) on the Galápagos penguin (<i>Spheniscus mendiculus</i>) at Caleta Iguana, Isabela Island, Galápagos.....	59
7 General conclusions.....	71
8 References.....	79
9 Annex	101
Description of the individual scientific contribution to the multi-author paper	105
Acknowledgements.....	107
Curriculum vitae.....	109
Publications.....	111
Erklärung	113

1 General introduction

The four penguin species comprising the genus of *Spheniscus* - the African (*Spheniscus demersus*), Magellanic (*S. magellanicus*), Humboldt (*S. humboldti*) and the Galápagos penguin (*S. mendiculus*) - are morphologically very similar, being easily distinguished by the distinctive features of the breast band and area around the bill (Fig. 1-1).

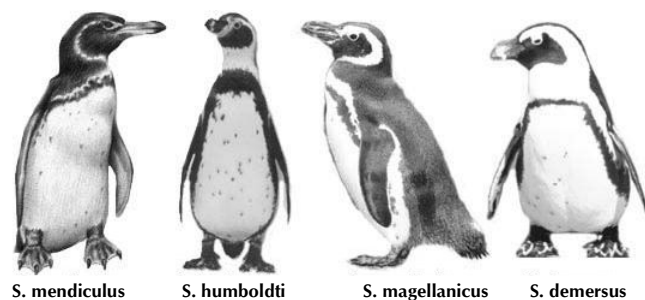


Fig. 1-1 The *Spheniscus* penguins.

Unlike Antarctic and sub-Antarctic penguin genera, all *Spheniscus* penguins are found at relatively low latitudes, and thus constitute the northern end of the penguin distribution (Williams 1995). Partially for this reason, all *Spheniscus* penguins are currently of conservation concern due to their interaction with man. The Galápagos penguin, in particular, is considered to be the most endangered of all penguin species.

Although *Spheniscus* penguins represent the most tropical of the penguin genera their breeding sites are nonetheless linked to cold and highly productive environments such as upwelling areas (Williams 1995) and continental shelves (Boersma et al. 2007), both conditions associated with particular oceanographic features that allows for a high density of prey (Boersma et al. 2007).

Compared to volant seabirds, flightlessness in penguins imposes limits on their foraging capabilities. This means that penguin foraging ranges and search capabilities are correspondingly reduced. If they are to breed successfully, penguins must have a predictable food supply within their limited foraging ranges (Lack 1968, Weimerskirch et al. 1994). For this reason it has been assumed that the Galápagos penguin's distribution may be strongly related to nutrient-rich upwelling areas within the archipelago (Jiménez-Uzcátegui et al. 2006).

Accordingly, approximately 98 % of the Galápagos penguin's population is found in the western part of the archipelago along the western coast of Isabela and around Fernandina Island which coincides with the primary areas of upwelling and the most productive waters of the archipelago caused by the Equatorial Undercurrent (EUC, also known as the Cromwell current) (Houvenaghel 1984, Coale et al. 1996).

This upwelling system, however, is regularly affected by frequent periods of the anomalous climatic conditions of the El Niño phenomenon (ENSO = El Niño-Southern Oscillation) (Palacios et al. 2006) which are known to reduce primary productivity and disrupt marine food webs (Arntz and Farbach 1991). How this marine perturbation affects Galápagos penguins was most evident after the two strong El Niño events in 1982-83 and 1997-98, when the penguin population underwent dramatic declines of 77 % and 65 %, respectively (Boersma 1977, 1998, Robinson 1987, Valle et al. 1987, Valle and Coulter 1987, Chavez et al. 1999, Vargas et al. 2006).

The declining numbers have been the impetus for annual surveys of the penguin population as part of the seabird monitoring programme of the Charles Darwin Foundation (CDF) (Valle 1986, Valle and Coulter 1987, Valle et al. 1987, Rosenberg and Harcourt 1987, Rosenberg et al. 1990, Trillmich 1991, Vargas et al. 2005b) and have greatly enhanced our understanding of the penguin population trends over the last few decades.

While the Galápagos penguin shares common threats such as introduced animals, oil pollution and by-catch with the other *Spheniscus* penguins (Boersma et al 1990, García-Borboroglu et al. 2006), the current small population size which represents only a small fraction of the one that was found in the seventies' (Boersma 1974, 1977, 1998, Harcourt 1980), places particular pressure on their population. For this reason the Galápagos penguin, with a total population of about 2000 individuals (Jiménez-Uzcátegui et al. 2006), was being classified as 'endangered' by the IUCN (International Union for the Conservation of Nature and Natural Resources) (BirdLife International 2000).

Recent conservation workshops including the *Conservation Assessment and Management Plan* workshop held in Argentina in September 2004 and the *Population and Habitat Viability Analysis* workshop held in the Galápagos islands in February 2005 have stressed the importance of studying the behaviour and movements of Galápagos penguins at sea as effective conservation plans can only be formulated when this is known.

These workshops identified following major areas of concern:

- fisheries (fishing brings penguins and fishing gear in close proximity and can harm penguins due to entanglement and drowning in nets),
- introduction of alien species (e.g. rats and cats),
- pollution (affecting marine and terrestrial habitat and/or species),
- habitat disturbance (loss/degradation – extraction) and
- tourism (human disturbance).

Ironically, however, virtually no research has been carried out on the marine ecology of this bird (Mills 1998, 1999) even though the Galápagos penguin, in common with other penguin species, spends extended periods at sea and is totally dependent on the marine environment for survival. Of immediate concern are gaps in our understanding of the penguin's foraging ecology, particularly issues pertaining on space and habitat use and how oceanographic conditions may affect the species' behaviour, restrict and/or influence its distribution, and relate to breeding strategies.

Although the scientific community has been aware of the importance of conducting studies on the marine ecology of the Galápagos penguin, appropriate methodology has only been available for the last few years. It should be noted here that although solid-state

devices, that can be attached to penguins to record foraging behaviour, have existed since the early 1990's (Weimerskirch and Robertson 1994, Sagar and Weimerskirch 1996, Culik and Luna-Jorquera 1997), the size of them has been prohibitive (the Galápagos penguin is the second smallest penguin species in the world, weighing about 2kg (Williams 1995)) and in any event, it is judicious to allow a reasonable body of data on the effects of such devices on penguin well-being to be built-up (cf. Wilson et al. 1986, Wilson and Culik 1992, Ropert-Coudert et al. 2007) before deploying them on the endangered Galápagos penguin. By the turn of the millennium, the effects of externally-attached devices were fairly well understood and the capacity of these devices had increased to the point where the information gained appeared to considerably outweigh the minimal potential detriment to the carriers (Ropert-Coudert et al. 2007). Thus, as part of an effort to address the gap in knowledge of the marine habits of the Galápagos penguin, I studied the marine ecology and conservation of this species in the Galápagos islands from August 2003 to July 2005. My research represents a collaborative project between the CDF, the Galápagos National Park Service (GNPS) and the University of Kiel in Germany. To do this, I attached GPS-temperature-depth loggers (GPS-TD) to numerous Galápagos penguins, which enabled me to derive information on the birds' horizontal movements at sea as well as dive depths and dive duration during foraging trips. Together, these data elucidate the three-dimensional habitat utilisation of the Galápagos penguin at sea during the chick-rearing periods. This work was complemented by analysis of penguin diet and examination of the breeding conditions of the penguins.

The specific goals of this study were to:

- determine whether Galápagos penguins forage in predictable oceanic habitats, characterised by specific oceanographic features,
- examine whether habitat use change regionally,
- characterise penguin's diet composition and relate them to both foraging patterns and oceanographic parameters,
- determine how oceanographic conditions influence breeding activity (breeding locations and patterns),
- identify current and / or potential threats faced by the penguin population in their marine and terrestrial environment.

I hypothesized, that the life-history of the Galápagos penguin will be strongly linked to upwelling areas within the archipelago and significantly adapted to temporal and spatial variation in oceanographic conditions and thus prey availability.

Furthermore, being the closest relative to the Humboldt penguin, I expected to find a similar pattern in both their marine ecology and life history.

Permission to conduct animal procedures

Permission for performing this study was required from the GNPS for both access to the study area and for handling of the birds. Sample collection followed the laws and regulations of Ecuador as well as the guidance of the GNPS. The specific site for the field work and for the base camp at Isabela Island was chosen for logistic reasons as well as in accordance with previous experience gleaned from scientists and authorities of the CDF and GNPS.

However, since most of the methodologies proposed in this project had not been previously used on the Galápagos penguin and in view of the precarious populational status of this penguin species special caution must be given to the well-being of the animals. Permission to carry out the work therefore, was granted on a restricted number of animals and sample collection, respectively or under the premise to conduct a pilot study to test the feasibility of the methodology with a minimum disturbance of the animal (in the case of the logger technology and stomach flushing).

Furthermore, studying a free-ranging and highly endangered species involves inevitably a small population that, in the case of the Galápagos penguin, is combined with a widely scattered distribution along the uninhabited and mostly inhospitable coast of the westernmost islands in the archipelago and thus makes the species additionally difficult to access (which partially explained the reason for the only few information existing on this species). Many times this resulted in a small sample size that in turn highly compromised statistical power. For this reason, in this study often a descriptive approach to the results had to be applied. However, nevertheless, I believe that these data will provide critical information on the penguins' habitat use and will help the GNPS, and the managers of the Galápagos Marine Reserve (GMR), to improve the layout and protection levels of the GMR zonation system, and formulate appropriate conservation strategies and management plans for the Galápagos penguin.

On behalf of the different aspects of this project each chapter represents an independent study and thus provides a separate introduction and the description of the methodologies before results are presented and discussed. In the end, a short general conclusion with an outlook and recommendations for further investigations are given.

In the following chapter background information are provided to relevant aspects of this project.

2 Background information

The Galápagos islands

The Galápagos islands are located approximately 1000 km west of the South American continent. They are the product of “hotspot activity”, having been formed from the emerging tips of submarine volcanoes that rise from the Galápagos platform, with the highest elevation rising up to 1,710 m above sea level (Volcano Wolf) (Houvenaghel 1984). Extending from 1°40′N to 1°36′S latitude and from 89°16′ to 92°01′W longitude, the Galápagos archipelago is composed of 13 larger islands (> 10 km²), six smaller islands, and over 100 islets and rocks (Snell et al. 1995) encompassing a total land area of 8006 km² (Black 1973). A map of the archipelago is shown in Fig. 2-1.

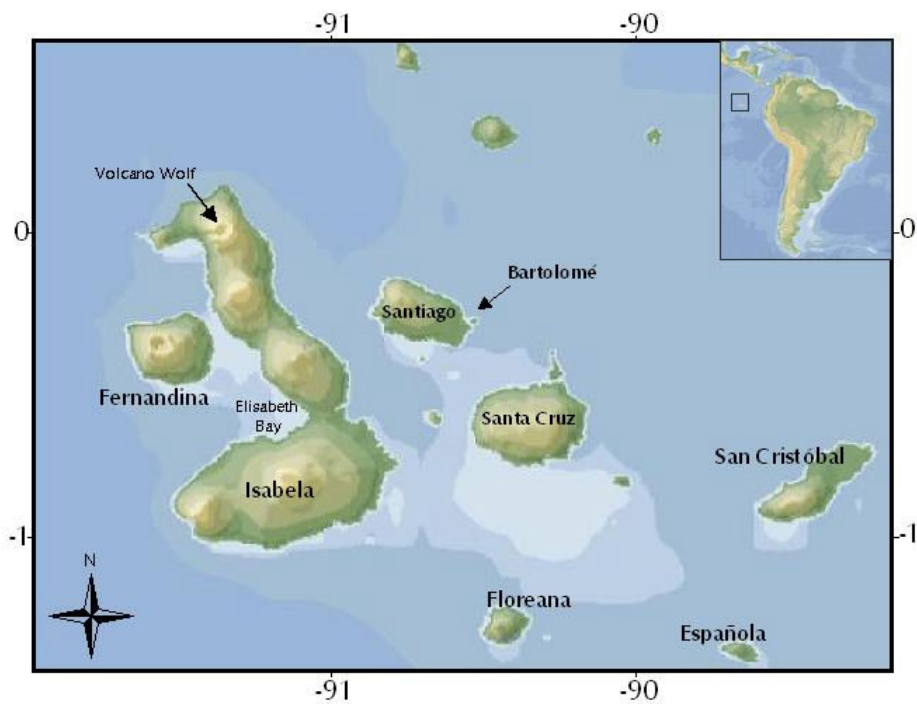


Fig. 2-1 Map of the Galápagos archipelago with the names of the main islands.

Oceanography and climate

Located in the eastern equatorial Pacific, the Galápagos islands lie at the confluence of several current systems, and as such within a hydrographically-complex region, being consequently subject to rapid changes in oceanographic conditions.

Currents

Two major trans-Pacific currents affect the region around the Galápagos, the South Equatorial Current (SEC) and the Equatorial Undercurrent (EUC) (Palacios 2003).

The SEC is a surface current that travels westward from about 10°S to 4°N, driven by the southeast trade winds (Fiedler 1992). It is fed by the Perú (or Humboldt) Current and by recirculating waters from the EUC and the Panamá Bight (see below). On encountering the region of the Galápagos islands the near-equatorial slow flow separates into a northern (SEC(N)) and a southern branch (SEC(S)) (Johnson et al. 2002). Due to its proximity to the Intertropical Convergence Zone (ITCZ) where winds are light and variable (the Doldrums) the waters of the SEC(N) are warmer (23.8°C) and fresher (34.1) than the waters of the SEC(S). The SEC(N) transports warmest temperatures and lowest salinities from January to June, when it shifts to the north. From July to December the current shifts southward carrying cool temperatures and high salinity. The SEC(S) carries cool and salty water at a mean temperature of 22.2°C and a mean salinity of 34.9 (Johnson et al. 2002). The seasonality of the SEC(S) roughly corresponds with that of the SEC(N), with cooler, saltier waters from June to January when it shoals and moves northward from February to May when it shifts southward.

The EUC originates in the western Pacific as the return flow that compensates the westward surface waters of the SEC. This subsurface current travels eastward in the thermocline as a narrow jet, generally found between 2°N and 2°S. It carries water at a mean temperature of 15.6°C and a salinity of 34.9. Seasonally, in March to July the EUC is shallow, fast, warm, and salty, while from August to February it is deep, slow, cold and fresh (Palacios 2003).

As the EUC hits the western edge of the Galápagos platform, which constitutes a steep topographic barrier within the deep oceanic environment, its cold, nutrient-rich water is forced to the surface and creates a localized upwelling habitat which sustains conditions for an elevated biological production year-round (Anderson 1977, Houvenaghel 1984, Lukas 1986, Coale et al. 1996). Once at the surface, part of the upwelled waters decelerate and split into two branches that pass the southern (most of the flow) and northern margins of the archipelago interacting with the complex sea-floor topography of the Galápagos archipelago (Anderson 1977, Lukas 1986), causing further small scale upwelling at several locations, including the central archipelago (Houvenaghel 1978). The other part is carried westward by the SEC, creating a productive habitat that sometimes extends offshore for several hundred kilometers (Arcos 1981, Feldman 1986).

However, while the western side of the archipelago has long been identified as the waters of lowest temperature and highest productivity (Harris 1969, Houvenaghel 1978, Feldman 1986), upwelling alone cannot explain the high phytoplankton biomass ($\text{chl} \geq 0.5 \text{ mgm}^{-3}$) generated in this area. The physical and ecological factors leading to this high chl values include a) the localized, year-round topographic upwelling of the Equatorial Undercurrent,

b) the seasonal wind-driven upwelling along the equatorial cold tongue, and c) the input of natural iron enrichment derived from the island platform (Gordon et al. 1997, 1998, Palacios 2002, 2004).

Generally speaking, the region in the western part of the archipelago undergoes a seasonal increase in phytoplankton biomass in the second part of the year (from June to December) compared to the first part (from February to May).

In addition to the SEC and the EUC, seasonal influx into the Galápagos region from the Panamá Bight and the North Equatorial Countercurrent can also have an impact on the islands ecosystem (Glynn et al. 1983, Houvenaghel 1984, Johnson et al. 2002).

Due to the closely-coupled complex ocean-atmosphere system of the eastern tropical Pacific the influence of all of these currents fluctuates in strength from season to season as well as from year to year. While seasonal variability actually only has a minor effect on the extent and biomass content of the extent of the primary production, the strongest impacts occur at intra-seasonal and inter-annual timescales i.e. caused by El Niño and La Niña events.

Fronts

Fronts separate waters with distinct physical and biogeochemical characteristics. Two large-scale fronts pass through the Galápagos region at different times of the year:

The Equatorial Front extends from the South American coast to near the international dateline (McPhaden et al. 1998), separating nutrient-rich equatorial upwelling waters to the south from the warm and low-salinity waters, resulting from rainfall in the ITCZ, to the north. From about May to January the Galápagos islands are mostly surrounded by this cold water (24.5°C isotherm) while the EF is just to the north of the islands. The cold tongue retreats toward the South American coast from February to April and the EF disappears.

Another front appears between the Gulf of Panamá and the Galápagos during January to April. This Panamá-Galápagos Front (26.5°C isotherm) delineates with the western boundary of a meridional plume of cool water extending from the Gulf of Panamá, as it is pushed offshore during upwelling events generated by northeast trade winds crossing the Isthmus of Panamá from the Caribbean Sea.

Small-scale fronts can also be found in the Galápagos, at the edges of upwelled water, where cold and warm water with different characteristics meet.

Climate

The climate of the Galápagos islands is determined by the closely coupled ocean-atmosphere system of the eastern tropical Pacific and changes in sea surface temperature due to different oceanic circulation patterns coinciding with meteorologic seasons in the region.

In general, this system is driven by the seasonal meridional migration of the northeast and southeast trade wind and the associated ITCZ. The ITCZ is most intense in August, when it reaches its northernmost position near 10°N, while it weakens and retreats to near 3°N in February. According to the timing of the north-south migration of the ITCZ, there are two main seasons at the Galápagos: from December to May there is a hot and wet period, and from June to November there is a cool and dry period.

The Galápagos National Park

Since 1959 about 97 % of the terrestrial area of the Galápagos islands has been managed as the Galápagos National Park, with the remaining 3 % zoned for urban, agricultural, military, and other uses (Emory 1988).

The primary planning document has been the “Management Plan for the Park” written in 1973, and revised in 1984. The Management Plan is considered a fundamental document for regional planning with the primary objective to protect the species unique to the Galápagos ecosystem. In 1985, the terrestrial portion of the Park was declared a Biosphere Reserve.

The archipelago is divided into five zones: *Intensive Visitor Zones* where a maximum of 90 people are allowed ashore at one time in smaller groups; *Extensive Visitor Zones* open to groups of no more than 12 people; *Special Use Zones* for the extraction of natural resources (e.g. stone and timber); *Urban and agricultural Zones* for colonization; and *Exclusive Zones* of no visitation or extractive pursuits, where scientific research may be carried out with the appropriate access permits from the Galápagos National Park Service and the Ecuadorian government (Cepeda and Cruz 1994).

These zones have been carefully selected to satisfy all parties with different interests in the islands while minimizing possible effects on wildlife.

However, both economic and political interests in the islands are accelerating, putting considerable pressure on the managers of the National Park, leading to increasingly intense conflicts (Boersma et al. 2007).

Still, little is known about how some of these developing activities are affecting the Galápagos ecosystem and it is the marine environment where information is most scarce.

The Galápagos Marine Reserve

The oceanographically-complex region surrounding the Galápagos has led to a fascinating marine ecosystem with an exceptional diversity of species.

Designed to protect these waters and the resources they contain, the Galápagos Marine Reserve (GMR) was created in 1998 and encompasses the waters within the archipelago and a 40 nautical mile buffer zone around it (totalling 70,000 km²). A year later, with the acceptance of the Galápagos Marine Reserve Management Plan, the Participatory Management Board (PMB) was formed and agreed (in 2000) on the zonation of the GMR into areas that allow various levels of extractive uses (Zone 2.3, e.g. fisheries), non-extractive uses (Zone 2.2, e.g. tourism) and protection and conservation of its marine life (Zone 2.1, e.g. research and management activities) (Fig. 2-2). The protection afforded to the marine biota contributed to the designation of the GMR as a natural World Heritage Site in December 2001.

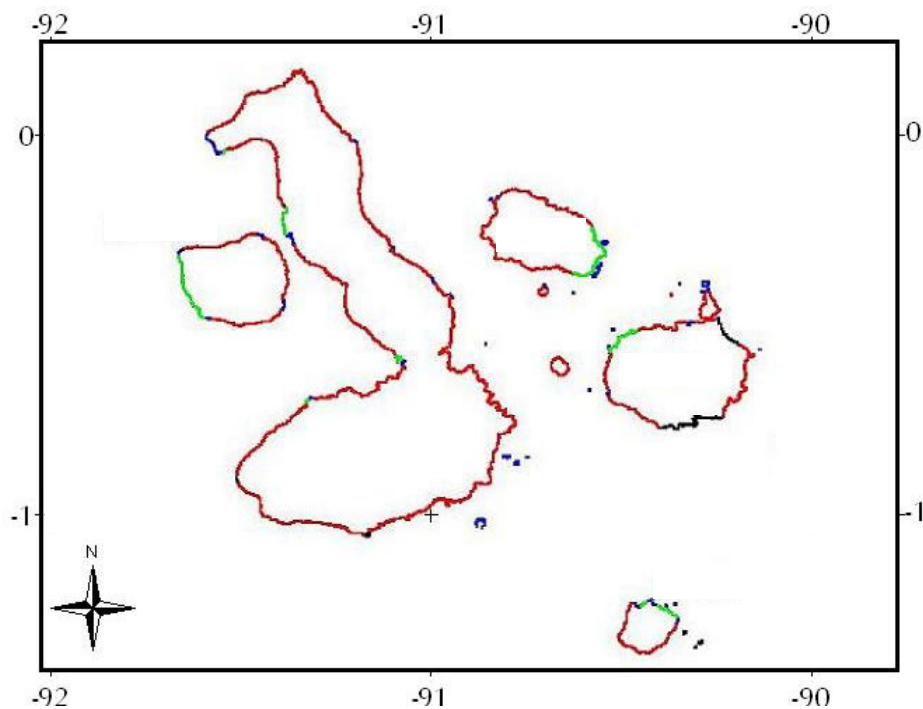


Fig. 2-2 Map of the Galápagos Marine Reserve zonation system. The zones are in blue: 2.1 fully-protected 'no-take' area [6.3 %], in green: 2.2 non-extractive use areas [10.8 %], in red: 2.3 regulated extractive uses [78.2 %], in black: 2.4 special zones nearby the inhabited port areas [4.7 %].

However, planning of this system, and indeed successful management, is critically dependent on the quality of available information.

This was most evident after the 16 January 2001 when the fuel tanker "Jessica" grounded off the western point of San Cristobal Island. Approximately 180,000 gallons of diesel and bunker fuel oil escaped from the ship over the following two weeks, moving primarily northwest, west and southwest of the grounding site. Fortunately, this event happened at a site where penguins are not believed to occur although it had a severe negative impact on the marine iguana (*Amblyrhynchus cristatus*) population in that area (Wikelski et al. 2002).

The fact that a significant amount of national and international shipping passes through the Galápagos means that there is always the possibility of future contamination which may affect critical habitat for Galápagos penguins.

Events of this type highlight the importance of identifying regions that encompass biological critical or sensitive areas to prioritize accurately both species and their habitats, so that appropriate management strategies can be adopted and, if necessary, higher protection levels implemented.

Conservation aspects

The geographic isolation of the Galápagos islands combined with its young age (3 and 5 million years (McBirney and Williams 1969)) and the island's late human colonisation resulted in the evolution of a small, but unique, flora and fauna with a high degree of speciation and endemism (Grant 1999).

The Galápagos penguin is one of the endemic seabirds in the Galápagos islands and is ranked as a species of high conservation concern (BirdLife International 2005). The reason for this concern is the penguin's small population, restricted distribution and its vulnerability to ever-increasing human threats in form of introduced alien species (Steinfurth and Merlen 2005), fisheries (Boersma et al. 2005), and national and international shipping (Cepeda and Cruz 1994, Boersma et al. 2005). These issues, combined with severe population fluctuations due to natural marine perturbations such as the El Niño Southern Oscillation, have led to its classification as 'endangered' by BirdLife International in 2000 and to its inclusion in the IUCN Red List of Threatened Species (BirdLife International 2005).

Human-induced threats

Many of the problems currently faced by seabirds in the Galápagos were initiated in the 1600 – 1800s when pirates, whalers and fur sealers introduced black rats (*Rattus rattus*) and mice (*Mus musculus*) into the insular ecosystem (Hoeck 1984).

After the islands were officially claimed by Ecuador in 1832, human colonisation started shortly thereafter which changed the Galapagos ecosystems due to the introduction of numerous plants and further alien animals including pigs (*Sus scofra*) and goats (*Capra hircus*) (MacFarland and Cifuentes 1996, Brockie et al. 1988, Snell et al. 2002).

Dogs (*Canis ssp.*) and cats (*Felis ssp.*) were introduced for hunting, protection and as pets. Many of these species became a threat to the endemic ecosystem as they contributed to the decline in reproduction in several species of pelagic, coastal or terrestrial birds mainly due to destruction of nests and habitat and the loss of eggs, chicks, fledgelings, and adults due to predation (Hoeck 1984, Valle 1986, Cruz and Cruz 1987, Loope et al. 1988).

In addition, mosquitoes (*Culex quinquefasciatus*) arrived on the Galápagos in the 1980s as a result of human actions. Since they are vectors for avian malaria (Fonseca et al. 1998), and penguins in the genus *Spheniscus* are highly susceptible to this disease (Fix et al. 1988, Graczyk et al. 1995) these insects represent a potential new threat for the penguins (Miller et al. 2001, Wikelski et al. 2004, Travis et al. 2006).

Due to economic growth benefiting local residents, and encouraged increased immigration from continental Ecuador, the number of colonists in the archipelago has more than doubled between 1988 and 1990, currently being around 27,000 humans (Emory 1988, Boersma et al. 2005). With the additional impact of increasing numbers of tourists visiting the archipelago since 1969, about 100,000 tourists visit annually (Boersma et al. 2005), the threat of an increasing abuse of the islands' natural resources is likely (e.g. increasing infrastructure, waste disposal etc.).

For example, along with increasing numbers of both visitors and colonists, transportation to the islands has become more frequent and led to an increased number of boats, flights and supply ships. Contamination from oil spills poses a severe potential threat to the

sensitive and vulnerable marine life while no oil spill contingency plans (i.e. clean-up crews or equipment) exist in the islands.

This potentially alarming development will require attention if the status of the National Park is to be maintained.

Commercial fisheries

The commercial fisheries operating in the Galápagos waters are potentially capable of harming piscivorous seabird populations due to entanglement and incidental drowning in nets (Cepeda and Cruz 1994, Simeone et al. 1999).

Occasionally, fishing boats operate in inshore waters, especially in the western part of the archipelago, and have been reported to have accidentally caught Flightless cormorants and Galápagos penguins (Cepeda and Cruz 1994). The low number of these species are particularly susceptible to the effects of increased mortality. However, there is no systematic monitoring of the fishing boats, and this, coupled with poor data on area use by the two species at sea makes an assessment of the extent of the problem difficult.

El Niño

Aside from the human threats, the Galápagos penguin undergoes severe population fluctuations, primarily as a result of marine perturbations caused by the El Niño Southern Oscillation (ENSO) phenomenon in the eastern tropical Pacific.

The El Niño phenomenon plays an important role in the Galápagos ecosystem, with the frequent occurrence of the oceanwide ENSO greatly affecting the local marine biota through dramatic changes to the environmental conditions of the islands (Boersma 1998). During ENSO, the EUC is known to weaken or even disappear (Johnson et al. 2002), leading to warmer sea surface temperatures (SST) and lower salinities than average. Consequently, the primary production is dramatically reduced (Chavez et al. 1999) and the marine food web disrupted (Jácome and Ospina 1999, Nicolaidis and Murillo 2001). On the other hand, a stronger and shallower EUC during La Niña may lead to cooler SST and an increase in phytoplankton biomass (McPhaden et al. 1998).

Several ENSOs have occurred in the past 40 years, however, the effects of the El Niño events in 1982-83 and 1997-98 were extremely strong and caused severe biological disruption (Robinson 1987, Valle et al. 1987, Chavez et al. 1999). The Galápagos penguin population underwent population declines by 77 % and 65 %, respectively (Boersma 1977, 1998, Valle and Coulter 1987, Trillmich 1991, Vargas et al. 2006). After this, the population entered a slow recovery phase (Boersma 1998, Mills and Vargas 1997, Ellis et al. 1998, Vargas et al. 2005a), however it is still 75 % below the pre-El Niño population (BirdLife International 2005, Jiménez-Uzcátegui et al. 2006) (Fig. 2-3).

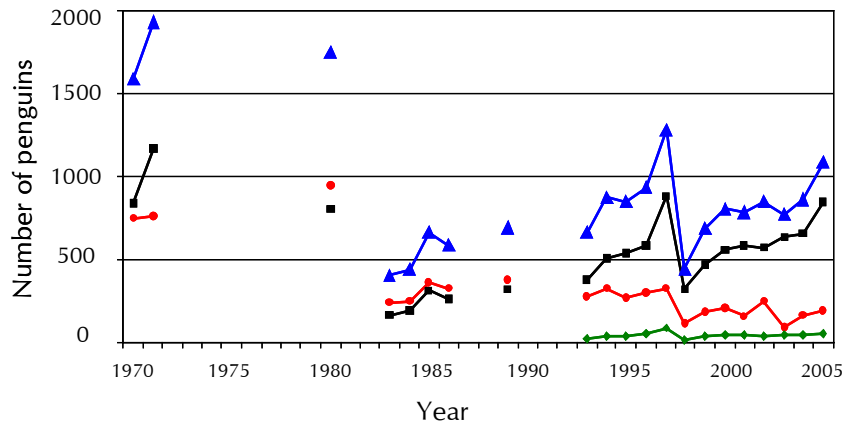


Fig. 2-3 Number of penguins counted between 1970-2005 in the Galápagos archipelago (blue) on Isabela (black), on Fernandina (red) and on the smaller islands (Floreaana, Bartolomé, Santiago, Sombrero Chino and Rábida surveyed since 1993; green) (Vargas et al. 2005b).

In a population viability analysis (PVA) workshop held in the Galápagos islands in February 2005, researchers estimated that under the current El Niño scenario, the Galápagos penguin has a 30 % probability of extinction within the next century (CBSG 2005, Vargas et al. 2007). They further suggest that the likelihood of extinction increases when other catastrophic factors such as disease outbreaks, oil spills, or predation by introduced predators are added into simulations (Boersma 1998, CBSG 2005, Travis et al. 2006, Vargas et al. 2007).

As the ENSO shifts likely towards more warming events with higher frequency and severity (Trenberth and Hoar 1996, 1997, Houghton et al. 2001, Karl and Trenberth 2003, Mendelsohn et al. 2005, Vargas et al. 2007), the Galápagos penguin is predicted to be at higher risk in the 21st century.

In general, endemic island populations with small population sizes are more vulnerable to extinctions (Frankham 1998) but the threats outlined here, alone or in combination, make it clear that the endangered Galápagos penguin survives under very particular conditions.

3 Breeding activities of the Galápagos penguin, *Spheniscus mendiculus*

3.1 Introduction

Birds are expected to adjust the timing of breeding to when environmental conditions are favourable and food is abundant so that their reproductive success is maximized (Lack 1954). Thus, the breeding frequency and time of year at which it occurs are important aspects of their reproductive strategy (Perrins and Birkhead 1983, Löfgren 1984, Paredes et al. 2002).

Generally, the length of the breeding season correlates negatively with latitude (Sharp 1996). The higher the latitude, when increasing daylength in spring and summer is associated with a period of maximum food availability, the greater is the seasonal variation in food supply and the shorter the time window for breeding (Croxall and Gaston 1988). Thus, birds breeding in the tropics are exposed to low amplitude or no seasonal changes in daylength. Here, birds show autonomous rhythms of reproductive activity which is typically synchronized to the pattern of optimal availability of food to ensure that breeding occurs at the appropriate time of year (Lack 1954, 1967, Furness and Monaghan 1987, Sharp 1996).

In addition to temporal restrictions, for flightless birds, the proximity of the food supply is crucial, particularly during breeding when birds are central place foragers (*sensu* Orians and Pearson 1979). While albatross and petrels can cover hundreds of kilometers on their foraging trips (Weimerskirch et al. 1993, Waugh et al. 2002) and thus may exploit food sources distant from their breeding sites (Davis and Cuthbert 2001), penguins are much more restricted in their foraging range (cf. Wilson 1985b). Since the cost of swimming is more expensive and slower than flying (Pinshaw et al. 1977, Schmidt-Nielsen 1999), flightlessness in penguins imposes limits on their foraging capabilities compared to volant seabirds and thus foraging ranges are correspondingly reduced (Wilson 1985b). To compensate for the high costs of getting the food, as well as to allow them to catch enough food to raise their chicks successfully (Croxall and Davis 1999), penguins must have a predictable food supply within their limited foraging ranges (Lack 1968, Weimerskirch et al. 1994).

Although *Spheniscus* penguins, the most tropical of the penguin genera (Williams 1995), occur at low latitudes their breeding sites are linked to cold and highly productive environments such as upwelling areas (Williams 1995) and continental shelves (Wilson et al. 1995b), both conditions that provide a high density of prey (Boersma et al. 2007). For this reason it has been assumed that the Galápagos penguin's (*Spheniscus mendiculus*) distribution may be strongly related to nutrient-rich upwelling areas within the archipelago (Boersma 1974).

Accordingly, approximately 98 % of the Galápagos penguin's population is found in the western part of the archipelago along the western coast of Isabela and around Fernandina Island, which coincides with the primary areas of upwelling and the most productive waters of the archipelago caused by the Equatorial Undercurrent (EUC, also known as Cromwell Current) (Palacios 2004, Jiménez-Uzcátegui et al. 2006). The remaining 2 % of the population inhabits the central-south islands of Floreana, Santiago, and Bartolomé.

While access to food near to the nest site during chick rearing must be a primary determinant regarding suitability of potential breeding sites (Bost and Jouventin 1990, Olsson 1996, Olsson and Brodin 1997), a number of other factors also play a role in influencing whether such sites are suitable for successful breeding. Factors found to modulate breeding success in penguin species others than food supply, include outcome of the previous reproduction (Bost and Jouventin 1990, Van Heezik et al. 1994), sea surface temperature (Warham 1975, Reilly and Cullen 1981), breeding experience or parental quality (Ainley et al. 1983), predation on land (Berruti 1981, 1986, Massaro and Blair 2003) and habitat characteristics (Stokes and Boersma 1998, García-Borboroglu et al. 2002). Nest sites in the tropical penguin species are variable in their characteristics (Paredes and Zavalaga 2001, García-Borboroglu et al. 2002) and therefore may differ in their effectiveness at fulfilling one or more of these functions. Consequently, it can be assumed that penguins select their breeding sites according to most ideal conditions and the distribution of penguin's breeding sites should thus reflect availability of habitat that provides maximum breeding success.

Boersma (1974) first described breeding activities of Galápagos penguins on Fernandina Island where she noted that Galápagos penguins may lay one to two similar-sized eggs per clutch over a three to four day interval. The incubation period is 38 to 42 days, and chicks hatch asynchronously, 2-4 days apart. Chick rearing lasts 60 days on average.

However, as yet no comprehensive survey of nesting sites and breeding activities of the Galápagos penguins in the archipelago has been undertaken. Given the precarious position of this species (BirdLife International 2000, 2005) and the huge difference that nest characteristics can make with regard to breeding success (Stokes and Boersma 1998) it would seem judicious to examine the nesting habits of this species. The objectives of this study were to examine the distribution and size of breeding colonies of the Galápagos penguin in the Galápagos archipelago and to give detailed information on breeding activity (nest description, locations, mate and nest site fidelity, breeding frequency, egg-laying pattern, clutch size and breeding success) at the main breeding sites over two years. In addition to general descriptive information, I hypothesized that time of breeding would vary between years and locations in response to seasonal and regional variation in oceanographic factors, including marine productivity.

This work also considers the nest sites in light of the various protection levels provided by the Galápagos Marine Reserve (GMR) zoning system. Designed to protect the waters surrounding the Galapagos islands and the resources they contain, in 1998 the GMR was created, which encompasses the waters within the archipelago and a 40 nautical mile buffer zone around it (totalling 70,000 km²). In March 2000 the Participatory Management Board agreed on the zonation of the GMR into areas that allow various levels of extractive uses (Zone 2.3, e.g., fisheries), non-extractive uses (Zone 2.2, e.g., tourism) and protection and

conservation of its marine life (Zone 2.1, e.g., research and management activities) (Fig. 3-1).

3.2 Material and Methods

Survey of breeding sites, August 2003 to September 2006

As part of the annual Galápagos penguin survey carried out by the Charles Darwin Foundation and the Galápagos National Park Service over four subsequent years (2003 - 2006), a 10-day census was conducted in late August and early September across the distributional range of the Galápagos penguin. According to Boersma (1974) this period of the year coincides with penguins incubating their eggs or guarding their young (detailed information about the annual survey is provided in Mills and Vargas (1997)).

The survey took place along the western coast of Isabela, around the three Las Marielas*, Fernandina, along Floreana, Santiago, Lougie, Bartolomé, Sombrero Chino and Rábida Islands (approximately 462 km coastline) (Fig. 3-1) from an inflatable rubber boat (Zodiac) which allowed close access to the shore (15 – 50 m). The remaining islands were not searched as penguins have never been sighted there and time was constrained.

All shores that could be closely accessed were searched for signs that Galápagos penguins were coming ashore. When signs of penguins (such as faeces and birds ashore) were found, a comprehensive search for nests was undertaken. Using visual and olfactory clues as well as vocal signals by adults and/or chicks, penguin tracks from landing sites were followed and the surrounding areas were searched for penguin breeding signs. In areas where anecdotal and historical records reported penguins and breeding sites, extensive nest searches were also undertaken even if no recent signs of penguins could be found. The location was defined as a breeding site if one of the following scenarios were found: nests with penguins in courtship, incubating adults, nests with chicks, abandoned nests with eggs, and nests with at least one adult and evidence of nesting material such as branches and (mangrove) leaves.

The location of each nest was recorded with a hand-held Garmin 12 CX Global Positioning System (GPS) receiver and mapped using ArcView3.2. Nests were permanently marked with a white painted number on the lava close to the nest at the beginning of the study to avoid recounting. During all subsequent visits, new active nest sites were additionally marked and checked.

When present, adult birds and chicks were caught and morphometric data were taken. Due to the precarious population status of this species, no incubating birds were captured to avoid nest desertion (Yorio and Boersma 1994c, Wilson et al. 1989a, Fowler et al. 2000, Taylor et al. 2001). Birds were then weighted to the nearest 100 g with a 5 kg spring balance (Pesola®, Baar, Switzerland). Measurements of bill length, depth, and width, as well as flipper length were taken with callipers to the nearest 0.1 mm to sex the individual (Boersma 1977). Additionally, to identify breeding pairs and nest site fidelity, but also to detect possible movements of (nesting) birds within the archipelago, all birds were

* Unless otherwise stated, the three islets, Las Marielas, are referred to as part of Isabela Island.

individually marked with a PIT- (Passive Integrated Transponder) tag in their left leg as part of a separate study (Vargas unpublished data). The wound was closed with surgical glue (Vetbond, 3M).

Nest type was recorded and breeding substrate was classified as (1) large basaltic rocks, (2) AA Lava (a very rough lava formed when there was very little gas which often lies in a clinker-like manner), (3) Cinder (often found on the flanks of the main volcano as the result of very explosive eruptions, where there was a lot of gas in the magma, which expands rapidly as the magma comes to the surface), (4) Pahoehoe (smooth or ropy lava, often forming intricate patterns. It is a result of the magma containing a large amount of gas), or (5) Tuff (form of compacted volcanic ash) (Fitter et al. 2000).

Breeding frequency, egg-laying pattern, breeding success, mate and nest site fidelity at the three main breeding sites

To obtain detailed information on the reproductive strategy, between May 2004 and September 2005 breeding events were monitored almost monthly for *Spheniscus mendiculus* at the main breeding sites. At each visit active nests were individually checked to determine nest attendance, nest contents and fledging success. Nests were defined as active when they contained adults with eggs and/or chicks while nests attended by only one (or more) adults were not considered active. A nest was recorded as abandoned when, although active on the previous visit, it was found deserted i.e. there was absence of adults, eggs, or dead chicks were present in the following visit.

All birds were weighted, and PIT-tags were injected into adults and chicks > 7 days. Additionally, adult birds were sexed by bill measurements (Boersma 1974) and individuals found marked with a PIT-tag were used to examine whether a change in partner or nest site had occurred.

We defined pairs to be birds that were observed together at a nest site, whether or not they had laid eggs. Females/males were considered to have changed mate when they bred with a different partner between successive reproduction attempts, while a change in breeding site was considered when the same pair was breeding at a different site than for their previous reproduction attempt.

We defined mate fidelity to be the proportion of birds observed in a given year that paired again with the immediately previous partner. Similarly, nest fidelity was defined as the proportion of pairs that returned to their previous nest site.

To reveal egg-laying patterns in the numbers of nests with eggs we plotted the numbers of active nests observed against time of the year (months).

Breeding pairs were categorised according to the number of clutches laid per year. Pairs that laid one clutch we refer to as single brooders, while pairs that laid two clutches were defined as double brooders.

Both groups of nests were used to determine the phenology of laying, which was estimated from direct observations of eggs laid between nest checks or, if the actual time of laying was unknown, by subtracting 40 days from hatching dates. A chick was considered to have fledged successfully if it was seen moulting into adult plumage and those pairs which raised at least one chick to fledging stage were defined as successful.

3.3 Results

Breedings sites within the archipelago, August 2003 to September 2006

A total of 115 nests at 17 different locations in the archipelago was found on Isabela, Las Marielas, Fernandina, as well as on Bartolomé, Lougie and Floreana Islands. Breeding sites ranged in size from one to 43 nests. Three islands did not have breeding penguins (Fig. 3-1) (Tab. 3-1).

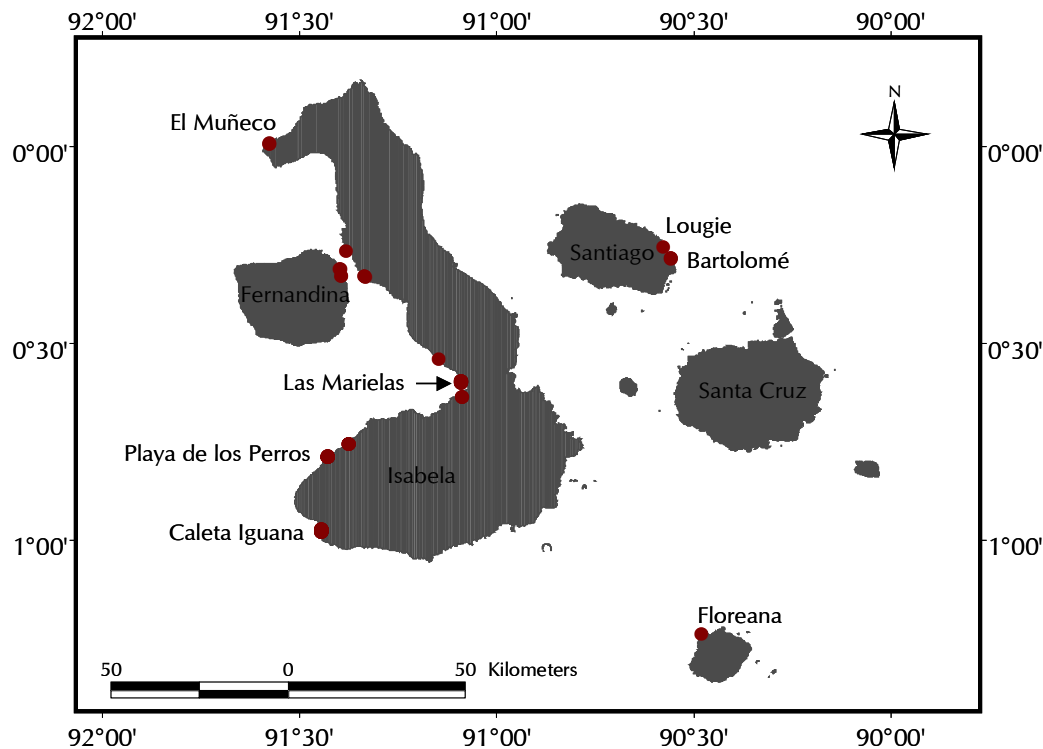


Fig. 3-1 Map of the Galápagos archipelago. Breeding sites of the Galápagos penguin, *Spheniscus mendiculus* found in the Galápagos archipelago between 2003 and 2006 are indicated by red dots.

Seventy-one percent of all the breeding sites were found on Isabela Island, the largest island in the archipelago, which also had the highest aggregations of active nests (85.2 %, $n = 98$) concentrated in the island's southwest. Here, the main breeding sites were found at Caleta Iguana (43 nests) (S 0.98/W 91.45), Playa de los Perros (19 nests) (S 0.79/W 91.43) and Las Marielas (23 nests) (S 0.60/W 91.09) (Fig. 3-1). The main breeding range (including 87 % of all nests) was thus limited to less than 402 kilometres along the coastline of the two westernmost islands in the Galápagos archipelago.

The size of islands containing penguin breeding sites ranged between $< 0.05 \text{ km}^2$ and 4588 km^2 , and size of islands without breeding penguins varied between $< 0.22 \text{ km}^2$ and 585 km^2 (Tab. 3-1).

All breeding pairs found in this study nested exclusively in lava holes, caves and crevices formed by fallen basaltic boulders, cracks in the lava, tunnels or eroded material in cliffs. No dug out burrows (as in other *Spheniscus* penguins – cf. Williams 1995) were observed.

However, type of lava varied notably among the breeding sites. Pahoehoe lava was the most common habitat type at all breeding sites (29.4 %, n = 5), while the majority of all penguin nests (38.3 %, n = 44) were found in a habitat formed by basaltic boulders (Tab. 3-2).

Tab. 3-1 Breeding sites and locations of the Galápagos penguin, number of active nests and nest type found in the Galápagos archipelago between 2003 and 2006.

Breeding location		Coordinates		No. of located nests	Habitat type*	GMR Protection level
Island (km ²)	Site	Latitude	Longitude			
Floreana (173 km ²)	Piedra Dura	-1.236	-90.480	1	Large basaltic boulders	2.3
Isabela (4588 km ²)	Caleta Iguana	-0.978	-91.446	43	Large basaltic boulders	2.3
	Playa de los Perros	-0.788	-91.429	19	AA lava	2.3
	Puerto Pajas	-0.756	-91.376	7	Pahoehoe lava	2.3
	Caleta Derek	-0.635	-91.087	4	AA lava	2.3
	Bahía Elisabeth	-0.596	-91.069	1	AA lava	2.2
	Encanada	-0.541	-91.148	1	AA lava	2.3
	Canones	-0.333	-91.335	3	Pahoehoe lava	2.3
	Caleta Tagus	-0.265	-91.383	1	Tuff	2.1
	Muneco	0.007	-91.578	3	Pahoehoe lava	2.3
Las Marielas (< 0.05 km ²)	Mariela Grande	-0.599	-91.090	12	Cinder	2.1
	Mariela Mediana	-0.595	-91.091	9	Cinder	2.1
	Mariela Pequena	-0.595	-91.090	2	Cinder	2.1
Fernandina (643 km ²)	Pargus Sur	-0.312	-91.398	2	Pahoehoe lava	2.3
	Colonia Pargus	-0.329	-91.395	3	Pahoehoe lava	2.3
Lougie (< 0.05 km ²)	Lougie	-0.255	-90.578	1	Cinder	2.1
Bartolomé (1.2 km ²)	Torre	-0.285	-90.558	3	Tuff	2.2

*Habitat predominating at the breeding site

Tab. 3-2 Habitat types related to numbers of nests and breeding sites.

Lava type	No. of nests	Nests [%]	No. of breeding sites	Breeding sites [%]
Basaltic boulders	44	38.3	2	11.8
AA lava	25	21.7	4	23.5
Cinder	24	20.9	4	23.5
Pahoehoe lava	18	15.6	5	29.4
Tuff	4	3.5	2	11.8

Interestingly, the three main breeding sites all represented different habitat types with large basaltic rocks predominating at Caleta Iguana, AA lava at Playa de los Perros and Cinder at Las Marielas. Although most common in the archipelago, non of these sites represented the Pahoehoe habitat type (Tab. 3-1).

Conservation implications

All nest sites found in the archipelago occurred within the 97 % of the Galápagos National Park land mass that is managed and regulated to varying degrees for the protection by the Galápagos National Park Service.

However, in light of the Galápagos Marine Reserve Zoning system, 41.2 % (n = 7) of the breeding sites are afforded the highest protection level of the zones 2.1 and 2.2 (indicated in blue and green in Fig. 3-2) and only few nests (25.2 %, n = 29) were located within that area. The large majority of nests (74.8 %, n = 86) was found in areas designated for extractive uses e.g. fisheries (indicated in red in Fig. 3-2), (Tab. 3-3).

Tab. 3-3 Numbers (percentages) of breeding sites and active nests as related to the zoning system of the Galápagos Marine Reserve.

	No. of sites	Sites [%]	No. of nests	Nests [%]
Protection and Conservation (Zone 2.1, 6.3 %)	5	29.4	25	21.7
Conservation and non-extractive use (Zone 2.2, 10.8 %, e.g.)	2	11.8	4	3.5
Conservation, non-extractive use and extractive use (Zone 2.3, 78.2 %)	10	58.8	86	74.8

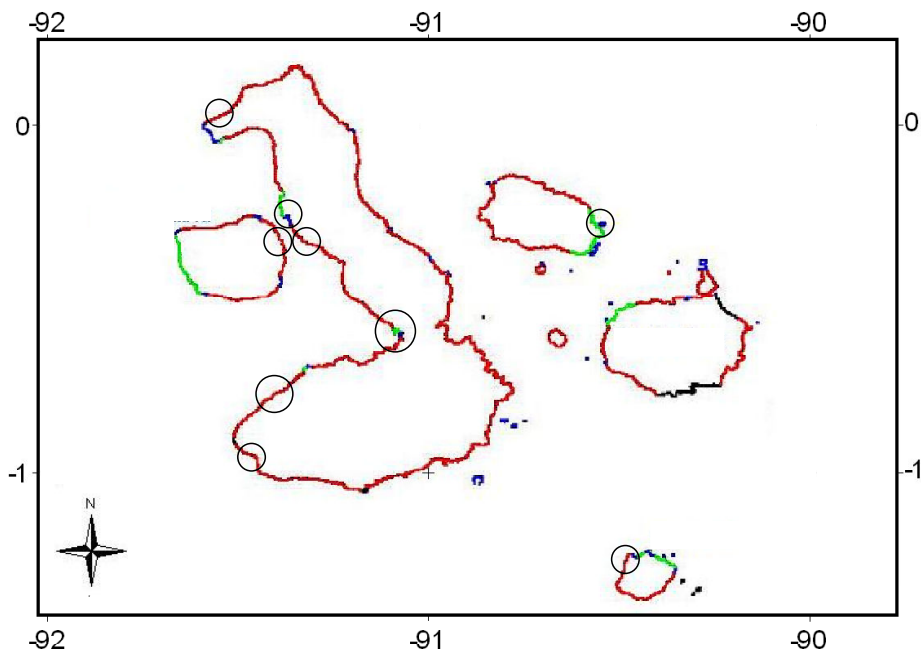


Fig. 3-2 Location of nesting sites (indicated by black circles) related to the zoning system of the Galápagos Marine Reserve. The zones are in blue: 2.1 fully-protected 'no-take' area [6.3 %], in green: 2.2 non-extractive use areas [10.8 %], in red: 2.3 regulated extractive uses [78.2 %], in black: 2.4 special zones nearby the inhabited port areas [4.7 %].

Breeding pattern, clutch size, breeding success

Among the main breeding sites, a total of 37 active nests was monitored at Caleta Iguana, 17 at Playa de los Perros and 20 at Las Marielas.

However, logistic and financial reasons constrained my ability to visit the colonies at Las Marielas and Playa de los Perros as frequently as desired. Thus, the monitoring could not be completed monthly, resulting in an incomplete data set for the purpose of our study. For this reason, the following results on egg-laying patterns and breeding success are mainly based on the data from Caleta Iguana but will be discussed and compared with available data from the two other breeding sites whenever possible. Furthermore, the severe difficulties in accessing some of the nests at Caleta Iguana, it was sometimes impossible to accomplish a reliable survey on the presence of adults, eggs and chicks at all nest sites. This reduced the sample sizes accordingly. Thus, the 37 monitored nests at Caleta Iguana in 2004 only 28 nests, in 2005 17 nests provided appropriate information that was required to delineate the breeding activity. At Las Marielas, in 2004, 9 nests provided enough information.

This forced reduction in sample size for data that could only be collected over two subsequent years resulted in a loss of statistical power. The statistical analysis was carried out using linear mixed effect model (Software R 2.4.1 lme4) (Pinheiro and Bates 2000) whenever appropriate to do so, however often a descriptive approach had to be applied. In 2004, the monitored nests at Caleta Iguana showed that 53.6 % ($n = 15$) of the adults bred once, while 42.8 % ($n = 12$) of the adults bred twice and one pair laid three clutches. Although active nests could be discovered virtually throughout the year, the study indicates evidence of two well-defined breeding peaks of egg-laying by double brooders. The first event occurred mainly in March (41.7 %, $n = 10$) while the second egg-laying peak could be observed in August and September (37.4 %, $n = 9$) (Fig. 3-3a). Little egg-laying occurred between April and May, in July and December while no egg-laying was observed in February, October and November. Single brooders had a rather extended period of egg-laying, starting in March and ending in August, although the majority laid eggs in March and May (33.3 % and 40.0 %, respectively) (Fig. 3-3a).

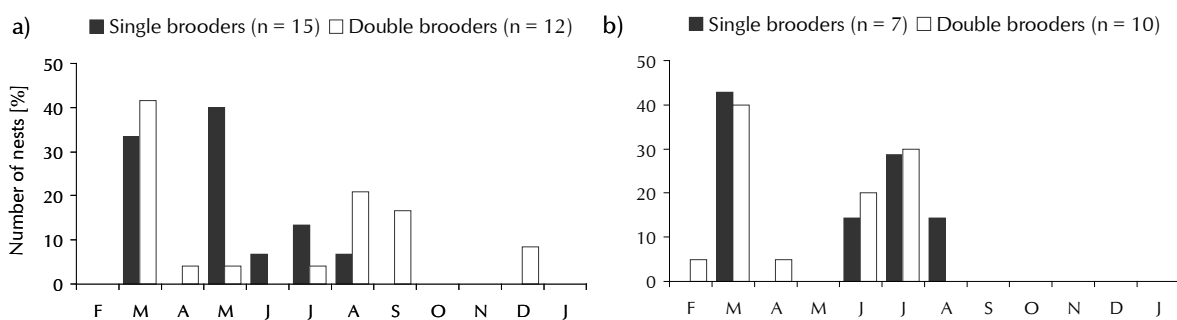


Fig. 3-3 Phenology of egg-laying by Galápagos penguins at the main breeding site Caleta Iguana for two different breeding categories (single brooders and double brooders) in a) 2004 and b) 2005.

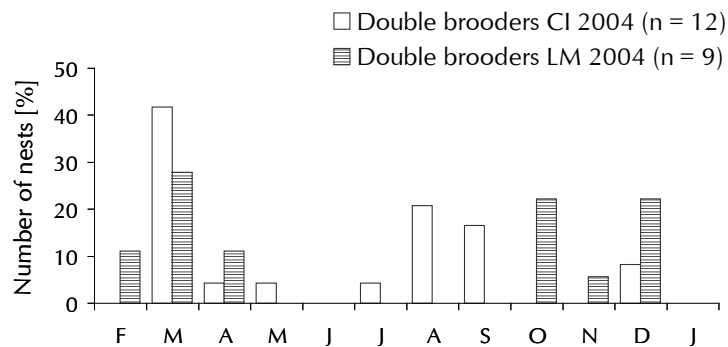


Fig. 3-4 Comparison of time of egg-laying (month) by Galápagos penguins for double brooders at the breeding sites Caleta Iguana (CI) and Las Marielas (LM) in 2004.

Data from double brooders at Las Marielas indicate that egg-laying of first clutches occurred roughly in phase with the birds at Caleta Iguana, though the latter started a month later. The egg-laying of the second clutch at Las Marielas, however, occurred between October and December and thus started three months later than at the southernmost colony (Fig. 3-4).

In the subsequent year (2005), at Caleta Iguana, 41.2 % (n = 7) birds bred once and 58.8 % (n = 10) bred twice. In both, single and double brooders, two well-defined breeding peaks of egg-laying could be observed, showing a clear bimodal distribution of clutches. In single brooders, egg-laying occurred in March and from June to August (Fig. 3-3b). In double brooders, egg-laying occurred mainly in phase with the egg-laying pattern of the single brooders, with a peak for the first clutch in March and for the second clutches between June and July (Fig. 3-3b). An inter-annual comparison indicates that egg-laying for first clutches of double brooders started earlier in 2005 than in the previous year, whereas the shift towards an earlier egg-laying date in the second peak was much more pronounced (Fig. 3-5a). The differences in laying dates of single brooders between these two years occurred mainly due to the additional egg-laying peak in May 2004, and with less breeding activity from June to August (26.7 % versus 57.2 % in 2005) (Fig. 3-5b).

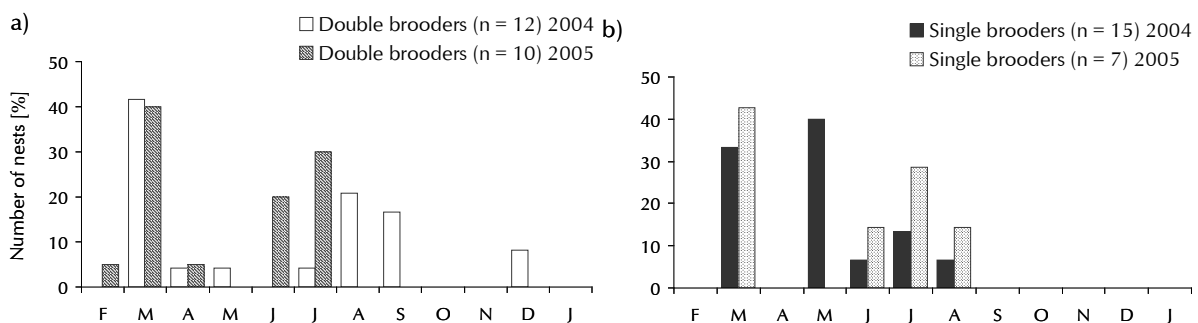


Fig. 3-5 Inter-annual comparison (2004 - 2005) of time of egg-laying (month) by Galápagos penguins at Caleta Iguana in two different breeding categories (single and double brooders).

As shown in Fig. 3-6, the second breeding peak was mainly the result of double brooding Galápagos penguins having a second clutch in both years.

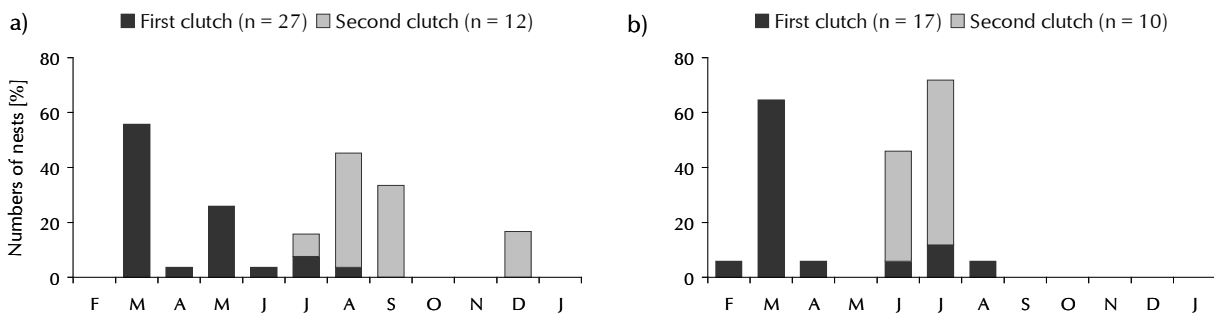


Fig. 3-6 Distribution of Galápagos penguin egg-laying for first and second laid clutches in a) 2004 and b) 2005.

Breeding success

Tab. 3-4 Breeding success (BS) in [%] in the different breeding categories (single brooders and double brooders) at Caleta Iguana over two years (2004 and 2005). NA = value not available.

Month	Single brooders			Double brooders		
	No. of nests	[%] nests	[%] BS	No. of nests	[%] nests	[%] BS
2004						
February	0	0	0	0	0	0
March	5	33,3	100	10	41,7	100
April	0	0	0	1	4,2	0
May	6	40	66,7	1	4,2	100
June	1	6,7	0	0	0	0
July	2	13,3	50	1	4,2	0
August	1	6,7	100	5	20,8	100
September	0	0	0	4	16,6	50
October	0	0	0	0	0	0
November	0	0	0	0	0	0
December	0	0	0	2	8,3	50
January	0	0	0	0	0	0
2005						
February	0	0	0	1	5	0
March	3	42,8	66,7	8	40	25
April	0	0	0	1	5	0
May	0	0	0	0	0	0
June	1	14,3	0	4	20	NA
July	2	28,6	NA	6	30	NA
August	1	14,3	0	0	0	0
September	0	0	0	0	0	0
October	0	0	0	0	0	0
November	0	0	0	0	0	0
December	0	0	0	0	0	0
January	0	0	0	0	0	0

PIT-tag resightings

Based on PIT tag resightings in adults ($n = 17$) at their nest sites during the two year survey at Caleta Iguana, mate-switching was observed on three occasions with a change in the female partner once, while the male partner was changed twice, resulting in a mate fidelity of 82.4 %. However, it was not possible to determine if the partner changes occurred due to 'divorce' or mortality. From nine marked breeding pairs at Las Marielas no change in partner could be detected.

Ninety-four point one percent of the monitored adult Galápagos penguins at Caleta Iguana returned to the same breeding location and thus showed a high level of nest site fidelity. Of the pairs that switched nest sites one known pair (double brooders) was found breeding at their neighbour's (single brooders) nest site during their absence.

In another case a new pair was found at a known nest site. The particular history of this nest site suggested different explanations for this. The first pair found at that nest site had failed in their breeding attempt after which, on a subsequent visit, the female was found to have changed partners. The new pair also failed to breed. It was in the check following this that the nest was found to have been occupied by a new pair.

At Playa de los Perros we found one case of a known nest that was occupied by another pair during one of our subsequent visits however since in general, at that site breeding pairs either could not be individually marked or adults within the nests could not be checked appropriately no confidential information on mate or nest fidelity can be given for this colony.

Since the PIT-tag marking programme was initiated in 2001 (Jiménez-Uzcátegui et al. 2006), the life history of some birds was well known so that, in some cases, movements of nesting birds could be detected within the archipelago.

Results obtained from the PIT-tag marked and resighted birds in this study show that non-breeding Galápagos penguins (adults and juveniles) migrated up to 63.5 km away from their colony. Four birds nesting at Caleta Iguana in 2004 (three males and one female) were originally marked at Punta Moreno in April 2001 (42.5 km further north) (the female being juvenile at that time). Additionally, one chick marked at Caleta Iguana in May 2004 was found as a juvenile bird at Puerto Pajas nine months later in February 2005 (36.3 km further north) while another chick (marked in August 2003) was found as a juvenile bird in Puerto Villamil in May and again in August 2004 (63.5 km further east).

One female and one male breeding at Playa de los Perros in May 2004 and August 2004 had been marked at Punta Moreno in 2003 (13.4 km farther north) and at Las Marielas in April 2004 (50.8 km farther north), respectively. Furthermore, two chicks that hatched at Playa de los Perros in August 2004 were resighted at Puerto Pajas (7.2 km farther north) as juveniles in January and February, respectively, the following year.

A nesting female bird at the colony Pargos on Fernandina Island in September 2005 was originally marked in August 2003 at Punta Espinoza (Fernandina Island) (15 km farther north).

All of our nesting and monitored birds that got resighted at other places were found there without nests which emphasises the importance of high nest site fidelity in this species.

3.4 Discussion

This work was the first attempt to study on the breeding activities of the Galápagos penguin comprehensively, with the general aim being to give detailed information on breeding locations and strategies.

Errors, biases and short-comings in the study

Data collection was subject to a variety of difficulties. Due to the widely dispersed breeding locations of this penguin species along the often inaccessible coastlines of the archipelago it is likely that some nests or nesting sites may have been missed during the survey. The difference in numbers of nests between Isabela and the other islands, however, suggests that there is a real variation on penguin breeding sites and that this is not due to differences generated by incomplete surveys. Furthermore, the difficulties in accessing the nests resulting from the inhospitable habitat at most of the sites made reliable nest checking sometimes impossible. Additionally, for both financial and logistic reasons we were unable to conduct regular monthly surveys at the colonies Playa de los Perros and Las Marielas. The considerable reduction in the final sample size therefore, led to the approach of the penguin's breeding strategies being necessarily somewhat descriptive. Nevertheless, this study provides important and interesting new insights into the Galápagos penguins' breeding activities.

Animals are known to change behaviour following disturbance and handling (Wilson et al. 1989a, Taylor et al. 2001). The physical disturbance and handling in this study was inevitable and theoretically could have negatively affected factors such as breeding success (Fowler et al. 1994, Yorio and Boersma 1994b, Giese 1996, Hull and Wilson 1996, Fowler et al. 2000, Walker et al. 2000). For this reason, special care was taken during bird handling and during nest checks to ensure that animals were as little affected as possible.

Unlike Antarctic and sub-Antarctic penguin species, all *Spheniscus* penguins are temperate in distribution and breed in much warmer climates than other penguins (Williams 1995). The Galápagos penguin in particular constitutes the northern end of the penguin distribution, representing the most northerly breeding penguin species. While well adapted to life in cold water, they seem to be overinsulated for life on land (Stonehouse 1970, Boersma 1974, cf. Frost et al. 1976a). However, in adaption to this warm climate this species has evolved a variety of anatomical, physiological, and behavioural adaptations (Stonehouse 1970). Their nesting habits are one of these adaptations for survival under these conditions (Stokes and Boersma 1998).

Distribution of breeding sites past and present

Within this study we could show that the Galápagos penguins' breeding habitat is strongly associated with cold and nutrient-rich waters within the archipelago.

Since for flightless birds, the proximity of the food supply is crucial, particularly during breeding when birds are central place foragers (*sensu* Orians and Pearson 1979), this distributional pattern had been expected. To compensate for the high costs of getting the

food, as well as to allow them to catch enough food to raise their chicks successfully (Croxall and Davis 1999), penguins must have a predictable food supply within their limited foraging ranges (Lack 1968, Wilson 1985a, Weimerskirch et al. 1994).

However, over the penguin's distributional area of breeding sites the species faces considerable variation in oceanographic factors, including marine productivity and sea surface temperature. For this reason it seems likely that such oceanographic variation reflects local differences in food supply which in turn influence the distribution pattern of the Galápagos penguin's population.

Within this study we found 82.4 % of the nesting sites and 95.7 % of all active nests in the western part of the archipelago which have been shown to be linked with the frequent and strong process of ocean upwelling caused by the EUC that supports a high biomass of phyto- and zooplankton, making the main prey of the Galápagos penguin (the Pacific sardine *Sardinops sagax* and the anchovy *Engraulis ringens*) available throughout the year (Palacios 2003). Gordon et al. (1998) showed that upwelled waters become significantly enriched with iron by contact with the islands platform, particularly at the Canal de Bolívar (Martin et al. 1994) while Palacios (2004) identified Elizabeth Bay, where the second largest breeding colony is situated, as the area where the phytoplankton response is most dramatic and persistent in the whole archipelago (Fig. 3-1).

Furthermore, relatively high numbers of penguins and nests were annually found at El Muñeco on the north side of Isabela Island (Fig. 3-1), representing the only penguin colony in the northern hemisphere (Jiménez-Uzcátegui et al. 2006). Although not located in the region directly influenced by the upwelling caused by the EUC, the surrounding waters provide high productivity. Since this area lies in the lee of the highest elevation in the Galápagos at 1,710 m, Volcano Wolf (Mouginis-Mark et al. 1996), it has been suggested that the regional high productivity could be generated by local Ekman pumping, due to the prevailing southeast trade winds, and iron upwelling from beneath the pycnocline driven by orographically modified wind stress for most of the year (Palacios 2002).

17.6 % of the breeding sites and only 4.3 % of the nests were found on the central and south islands of the archipelago, Bartolomé, Loughie and Floreana that are generally surrounded by warmer, shallower and less productive water compared to western Isabela (Palacios 2003). However, part of the western upwelled waters pass the southern and northern margin of the archipelago causing small scale upwelling at several locations also in the central archipelago and thus could well explain the occurrence of penguins at these sites.

But the distribution pattern of breeding Galápagos penguins in this study interestingly indicates that there is a clear southward trend of breeding sites detectable on the islands over the past 30 years. Although previous information on the Galápagos penguin breeding sites relied heavily on anecdotal reports and partial surveys, these investigations showed a more northerly distribution of breeding sites than has been found in our study (Boersma pers. comm.). While Las Marielas at Elisabeth Bay have been confirmed to be traditional breeding sites since the first penguin surveys in the 1970s, there have been no records that identified Playa de los Perros and Caleta Iguana as breeding sites (Boersma pers. comm.).

On the contrary, Boersma (1974) indicated Punta Espinoza, the north-eastern tip on Fernandina Island (Fig. 3-1), as one major breeding site. Although we did observe penguins around that area, no active nests could be detected between 2003 and 2006. Furthermore, the results of our study suggest that Galápagos penguins nesting numbers on Fernandina in general have significantly declined.

Thus, over the last decades traditional breeding sites have shifted into non-traditional nesting regions and vice versa. This shift may be linked to various factors such as oceanographic features (see above) and changes in terrestrial habitat (whether by natural or human-induced causes) making certain habitats either unavailable or unsuitable.

The occurrence of predators at breeding sites could also have been contributing to a shift in breeding site's distribution as an important aspect. While the only natural predator of seabirds known on the islands is the Galápagos hawk (*Buteo galapagoensis*) with a rare impact on the Galápagos penguin (Harris 1970, 1974), mortality in penguins across all age classes (eggs, chicks and breeding adults) is greatly augmented by predatory introduced mammals such as rats (*Rattus rattus*), cats (*Felis catus*) and dogs (*Canis familiaris*) (Berruti 1986, Yorio and Boersma 1994a). (The relationship between introduced cats and mortality rate in penguins was being investigated in detail as another part of this thesis (see chapter 6)). But, since Fernandina is free of introduced mammals, the low number of breeding pairs occurring on this island is unlikely to be explained by an increased predatory impact of Galápagos hawks. The situation on Isabela Island however, concerning the impact of introduced animals, differs considerably and might be indeed a potential reason for changes in suitable breeding sites on this island. For example, before the eradication programme of feral dogs in the island's southwest was carried out in the late seventies', dog predation must have played a major role in the reduction of the penguins' population, particularly at Playa de los Perros (Kruuk 1979, Boersma pers comm.). Trips performed to the southwest of Isabela Island at that time confirmed a high number of dogs, less numbers of penguins and no penguin breeding activity. Thus, it is likely that dogs may have caused penguins to move and breed further north. However, reasons for the shift in breeding sites still need to be carefully discussed for evidence indicating which cause may represent the best explanation.

Nesting habitat characteristics

Although the location of the nest site and the importance of its proximity to available food is one of the most important aspect in penguin's breeding strategy (Paredes and Zavalaga 2001, García-Borboroglu et al. 2002), the impact of nest characteristics (e.g. nest cover) on reproductive outcome has shown to influence lifetime reproductive success substantially (Stokes and Boersma 1998).

Several studies on *Spheniscus* penguins have shown that the degree of nest cover is an important aspect for the reproductive success with well-covered nests being significantly more successful (Frere et al. 1992, Stokes and Boersma 1998).

To avoid heat stress, imposed by high ambient temperatures, *Spheniscus* penguins generally use covered nest sites that provide protection against direct solar radiation and thus create a more stable microclimate for both adults and chicks (Stonehouse 1970, Boersma 1974, Frost et al. 1976, La Cock 1988). In the Galápagos islands on a hot, sunny

day, daily maximum temperatures can easily exceed 30 °C. Here, nest characteristics should be an important determinant of adult survivorship and breeding success in Galápagos penguins (Nettleship 1972, Montevecchi 1978, Potts et al. 1980, Saliva and Burger 1989, Stokes and Boersma 1998).

In this study all nests represented sheltered sites such as lava holes, caves and crevices, however with different degrees of cover. Although it would have been possible, at least in some types of lava as tuff or cinder, no dug out burrows were observed. This suggests that there seems to be no need to dig burrows to create additional nest sites.

Sheltered sites may also better protect breeding birds against predators than do open nests as it reduces the likelihood of detection (Frere et al. 1992, Stokes and Boersma 1998). However, once a predator detects a nest it must be able to reach the nest cup. Consequently, the size of the largest opening will determine whether the predator is able to enter. Thus nest entrance must be the most critical characteristic of a nest. For this reason, protection of nest contents from predation can provide sometimes another benefit of nest cover (for more details see chapter 6).

Furthermore, habitat dynamics can considerably affect suitability and availability of breeding habitat for penguins as lava erode and transform, and thus some nests deteriorate over time as it has been very apparent at Las Marielas (pers. observations). Over the course of our surveys, substantial parts of the substrate at Las Marielas eroded, and destroyed and collapsed nests were frequently observed. In general, due to their characteristics, both lava types, Tuff and Cinder, are considered to be highly susceptible to severe weather conditions, thus to erosion and nest stability is likely much more unpredictable than nests formed by basaltic boulders.

Probably at Las Marielas, both, the small area of the islets and the particular loose type of lava make these breeding site in general very susceptible to storm and rain denudation (pers. observations) and raises concern for the future of this breeding site.

Large-scale coastal habitat modification due to e.g volcanic eruption however, has not occurred neither on Isabela nor on Fernandina Island in the last decades, and thus it is unlikely that changes in terrestrial habitat explain the large variation in penguin breeding numbers between these two islands nor the southward trend in general.

Since availability of breeding habitat is one factor that determines breeding distribution and abundance patterns, two obvious reasons could likely deliver an explanation: 1) The larger size and the extensive coastline of Isabela Island offers potentially more areas of breeding habitat to penguins than does Fernandina and 2) Flightlessness in penguins imposes that they have to walk from the sea to their nests, and thus being limited in their access to their colonies compared to volant birds. Consequently, the slope of the coast at access points to the colonie is, among others, an important factor that determines the probability of occupation of suitable sites (García-Borboroglu et al. 2002, Frere et al. 1992). For example the western part of Fernandina Island consists of steep cliffs that are not suitable landing sites for penguins. And thus, they are inaccessible for penguin to the shore and therefore unlikely to suit as breeding sites (Frere et al. 1992) while in contrast on Isabela the existence of gentle slopes along wide distances of the coastline facilitate penguin access and thus increase the availability of potential habitat.

Since Santiago, Sombrero Chino and Rabida Islands all provide suitable nesting habitats, this factor cannot explain the observed lack of breeding activities at these sites.

Breeding patterns and breeding success related to oceanographic conditions

While seasonal breeding at latitudes greater than about 30°S or 30°N coincides with spring and summer when increasing daylength is associated with a period of maximum food availability, birds breeding in the tropics are exposed to low amplitude or no seasonal changes in daylength. Thus, as expected for a subtropical species, timing of breeding should be flexible for *Spheniscus* penguins as they often have to respond rapidly to favourable oceanographic conditions to ensure that breeding occurs at the appropriate time of year (Lack 1954, 1967, Stonehouse 1967, Furness and Monaghan 1987, Sharp 1996).

Additionally, in the eastern Pacific, El Niño events had a particularly strong effect along the coast of Ecuador and Perú causing extremely variable and unpredictable oceanographic conditions (Barber and Chávez 1983, Tovar and Guillén 1987, Valle et al. 1987, Duffy 1990) that probably had an important effect on the Galápagos ecosystems, exerting strong selection pressures on breeding and survival strategies of island species. A marked seasonal absence of breeding patterns including its ability to breed rapidly and opportunistically when conditions are favourable seems to be therefore a characteristic feature in Humboldt penguins' population (Paredes et al. 2002) and are equally expected for the Galápagos penguin.

In our study we found Galápagos penguins at Caleta Iguana virtually breeding throughout the year, however with two marked peaks of egg laying periods from March to May and from July to September. Although the EUC creates an nutrient-rich upwelling habitat in the western part of the archipelago year-round, this region shows slight seasonal variation with an increase in phytoplankton biomass in the second part of the year (June to December) which coincides well with the second period of egg-laying. The first egg-laying peak corresponds significantly with the strengthening and shoaling of the EUC in April. However, while seasonal variability is rather small, much stronger effects would be expected on an interannual and intraseasonal timescale (Palacios et al. 2006).

In the two concurrent years of our study the pattern was roughly in phase for both single and double brooders though the well-defined peaks were clearer in 2005 than in 2004. The annual second breeding peak was mainly the result of Galápagos penguins having a second clutch (Fig. 3-6). A potential explanation for the earlier laying date for the second clutch in 2005 could be the particular low breeding success for the first clutch (Tab. 3-4) that could have led to a replacement clutch as known for other penguin species (Gentoo penguins (*Pygoscelis papua*) (Bost and Jouventin 1990), little blue penguins (*Eudyptula minor*; Reilly and Balmford 1975, Woodell et al. 1984), African penguins (*Spheniscus demersus*; La Cock and Cooper 1988, Randall and Randall 1981) and Humboldt penguin (*Spheniscus humboldti*; Zavalaga and Paredes 1997)).

However, since a) due to the small sample size of nests and only few information obtained on fledgling success and b) we could not distinguish between double brooders and replacement brooders, this can only be rated as a speculation.

As birds are expected to adjust the timing of breeding when conditions are most favourable the shift in breeding pattern could also suggest that the penguin's behaviour was dictated by local oceanographic features and thus due to a flexible response to available food supply.

Also the obvious 'delayed' second egg-laying peak at Las Marielas in 2004 compared to Caleta Iguana (Fig. 3-4), could be an indication for local variability and thus, small scale differences in oceanographic conditions within the western archipelago.

In summary, the breeding biology of the Galápagos penguin seems to be well adapted to this unpredictable environment (Boersma 1977) and seems to have not diverged from those observed in Humboldt penguins in Perú (Paredes et al. 2002).

Interannual variance

Changes in breeding patterns and behaviour likely occur during El Niño events, when depletion in food interrupts breeding attempts and forces birds to abandon their nests in search of more productive areas at sea, that often results in an increase of bird mortality (Hays 1986, Paredes and Zavalaga 1998, Culik et al. 2000).

Furthermore, Kelvin waves (eastward propagating waves caused by fluctuations in wind speed at the ocean surface at the Equator) in a strong El Niño year create higher than normal sea levels around the Galápagos and are expected to increase risks of flooding (Vargas et al. 2006) which can likely cause breeding failure (pers. observation) as has been reported for other penguin species (Stokes and Boersma 1998).

Mate and site fidelity

In this study, Galápagos penguins are shown to be highly site faithful. A nest that proved to have the appropriate conditions for a maximised breeding outcome will be likely to be occupied again while unsuccessful nests will be more likely abandoned.

Furthermore, as the Galápagos penguin is an endemic species to the Galápagos islands and described as in-shore feeders (Davis and Renner 2003) (for further details see also chapter 4), this species is expected to stay close to its breeding sites even outside the breeding period, thus being essentially resident and having a low 'divorce' rate of < 20% (Croxall and Davis 1999). Our results confirm the 'divorce' rate for Galápagos penguins given by Croxall and Davis (1999). The only times mate-switching occurred was when they had previously failed to raise their brood.

Implication for conservation

All nest sites found in the archipelago occurred within the 97 % of the Galápagos National Park that is managed and regulated to varying degrees for the protection by the Galápagos National Park Service. Access to these coastal sites is strictly regulated and research is only possible with special permission.

However, penguins at Las Marielas and Bartolomé Islands are part of a major tourist attraction where the penguins be viewed by passing Zodiaks. Although tourists cannot touch them or walk around the colony there is frequent human presence at this breeding location and chronic human disturbance has been shown to be a potential threat to the conservation of penguins (Yorio and Boersma 1994b, Walker et al. 2000). But these sites

are known as traditional breeding sites over the last three decades, and thus a human-induced negative effect does not seem to be the case up to present.

Nevertheless, as the Ecuadorian Government encourages the expansion of the lucrative tourist trade in the Galápagos islands, an increasing number of tourists should be expected and a sensible monitoring of the breeding site would be highly recommended to detect a potential alteration of the impact.

Considering penguin breeding sites in light of the Galápagos Marine Reserve zoning system raises interesting concerns. Although the penguin breeding sites are located on the terrestrial portion of the coastline, our study found 73 % of the breeding sites within zone 2.3. (designated for conservation, extractive use and non-extractive activities) although this would be expected as that area covers 78.2% of the archipelago's coast (Fig. 3-2, Tab. 3-1). And thus only few breeding Galápagos penguins are afforded the highest protection levels of the GMR. Most penguins are recorded in the areas set aside for fisheries, and extractive uses.

The implications for penguin conservation may be significant: Even the penguins that are not feeding in that immediate area have to at least pass through the zone on their way to their foraging sites and while returning to their nest site.

Around the colony thus, two scenarios are likely: a) penguins that are breeding within zone 2.1 or 2.2 (designated for comparison and protection or conservation and non-extractive use, extractive use, and non-extractive use) for foraging (Fig. 3-2) and b) penguins that are breeding within zone 2.3, no matter if they are feeding in this area or not, have to pass this zone on their way to their foraging sites and while returning to their nest site. Fishery is potentially capable of harming penguin populations due to entanglement and drowning in nets (Simeone et al. 1999, CDF unpubl. data).

Areas for penguins which are afforded higher protection include the parts of the Canal de Bolívar and Las Marielas in the western archipelago and almost all penguin locations on Santiago and Bartolomé Island.

Since main breeding sites are important areas for penguins regarding a successful reproduction and population stability (Vargas et al. 2007) potential threats in their marine environment are serious and thus, these areas would afford higher protection levels within the Galápagos Marine Reserve.

However, based on PIT-tag marked and resighted birds in our study there is evidence that out of the breeding season adult Galápagos penguins do perform foraging trips of longer duration and extension. Although up to present there is almost no information on at sea movements of non-breeding adult and juvenile Galápagos penguins (see chapter 4).

Doubtless, the annual populational surveys carried out by the Charles Darwin Foundation and Galápagos National Park Service provide an important and valuable tool to estimate the overall population and show population trends into the future but they will not necessarily identify breeding numbers and important nesting sites where losses or gains may be occurring during the breeding season.

However, knowledge of detailed habitat requirements and breeding locations may be helpful in designing effective conservation plans (Martínez et al. 2003), since the

availability of suitable nest sites is often an important factor determining population size (Newton 1998).

Furthermore, the evidence that birds were found at other sites during their non-breeding period could lead to the hypothesis that those sites might have an importance e.g. for moulting. At Puerto Pajas for example, during each visit an unproportional high number of moulting birds could be observed (Vargas unpubl. data).

Still, there exist many gaps in our understanding about the penguin's breeding ecology e.g. which factors trigger the birds to become single or double brooders and how this varies between years and is linked to reproductive success or how moulting patterns are linked to oceanographic features.

In summary, in this study the southwestern part of Isabela Island could be identified as an important area for Galápagos penguins' breeding in the archipelago. This coastal sector seems to provide adequate nesting sites and those ideal conditions that allows maximum breeding success. Furthermore, it has shown that Caleta Iguana, a non-traditional breeding site, currently supports the largest number of breeding penguins, though, factors that explain why this part of Isabela Island became a major breeding site over the last decades still remains unclear.

The Galápagos penguin is unique in many aspects of their biology. The results obtained in our study are based on only two breeding seasons but they highlight for further work.

For this reason continuous long-term monitoring programmes should be considered in the design of future surveys by the CDF and GNPS so that benchmark breeding numbers can be identified, and potential habitat dynamics consistently monitored on a temporal and spatial scale for the overall stability and protection of suitable nesting habitat. Only detailed knowledge of the bird's breeding ecology would help to define, if necessary, appropriate conservation strategies e.g. restrictions on fishing and other human activities in sensitive areas to protect this charismatic species.

4 Space use by foraging Galápagos penguins, *Spheniscus mendiculus* during chick-rearing

4.1 Introduction

The Galápagos Penguin, *Spheniscus mendiculus*, the most northerly breeding penguin species and endemic to the Galápagos archipelago, is classified as ‘endangered’ by the IUCN (BirdLife International 2000) with a total population of around 2000 individuals (Jiménez-Uzcátegui et al. 2006).

Total populations of the three congeners (African penguin *Spheniscus demersus*, Magellanic penguin *S. magellanicus* and Humboldt penguin *S. humboldti*) have historically numbered millions of individuals (Williams 1995), whereas studies since 1970 (Vargas et al. 2005a,b) indicate that the Galápagos penguin population has always been consistently low. All *Spheniscus* penguins are specialized to feed on pelagic school fish such as anchovies (*Engraulis* spp.) and sardines (*Sardinops* spp.) (for review see Williams 1995, Wilson and Wilson 1995) and, due to their limited foraging range as a consequence of their flightlessness (Wilson 1985b), exploit primarily highly productive environments such as upwellings (Williams 1995) and continental shelves (Boersma et al. 2007).

Accordingly, the Galápagos penguin distribution coincides with the main upwelling areas of the archipelago (Boersma 1978). Although this upwelling is not as extensive as either the Benguela or Humboldt systems which feed African and Humboldt penguins, respectively, or the Patagonian Shelf, over which Magellanic penguins forage (Boersma et al. 2007), approximately 98% of the penguin’s population is found along the western coast of Isabela and around Fernandina Islands, which are the primary areas of upwelling caused by the Equatorial Undercurrent (also known as the Cromwell Current) (Palacios 2004, Jiménez-Uzcátegui et al. 2006) (Fig. 4-1). However, distributional records (Mills 1998, 2000, Jiménez-Uzcátegui et al. 2006) suggest that this species may not use the whole extent of the upwelling habitat potentially available to it.

We examined the foraging range used by Galápagos penguins, by equipping birds with Global Positioning System and depth (GPS-depth) loggers during their breeding period in 2004 and 2005. We measured the penguin’s horizontal and vertical movement at sea to assess whether Galápagos penguin’s foraging ranges and volumes of sea exploited differ from other species.

(Travis et al. 2006). All birds were individually marked with a PIT- (Passive Integrated Transponder) tag in their left leg as part of a separate study (Vargas unpublished data). After capture, birds were equipped with the GPS loggers placed on the lower back, mid-line following Bannasch et al. (1994) using overlapping layers of black waterproof tape (10 mm-wide strip Tesa-Tape Nr. 4651, Beiersdorf AG, Germany) which matched the birds' plumage in colour and did not compromise feather structure (Wilson and Wilson 1989, Wilson et al. 1990). The complete procedure, from capture to release, took less than 20 minutes. The GPS-depth loggers (Earth and Ocean Technologies, Germany) (Ryan et al. 2004, Petersen et al. 2006) consisted of electronics in a streamlined aramide fibre/epoxy-composite housing with polyoxymethylene cap, and had maximum dimensions of 100 mm x 48 mm x 24 mm (75 g). Geographical position (referred to the World Geodetic System (WGS) standard) and pressure (0-10 bar with 12 bit resolution – absolute measurement uncertainty ± 0.03 bar) were nominally recorded once per second although positional estimates were only actually recorded when the birds were long enough at the surface for a fix to be obtained from the satellite data. Using this set-up, data could be collected over a period of up to 12 hours. In most cases, device deployment took place in the late afternoon, when both parents were attending the chick/s. The GPS-depth units were programmed to switch on automatically at 5:00 h the following morning, before birds headed out to sea. Equipped birds were recaptured after one to three days; removal of the equipment took about five minutes. The recorded data were downloaded onto a field computer for subsequent analysis.

Data analysis and Statistics

Pressure data were analysed using MT-Dive software (Jensen Software System) to derive the total time spent per unit depth for each individual bird histogram with time summed over 0.5 m intervals. The time elapsed between leaving the nest and returning to it was used to define foraging trip length.

GPS data were analysed in ArcView3.2. Distances between positional fixes and shoreline and for distances moved from the nest were calculated with ArcView 3.2, extension Geoprocessing. Distances were measured in a straight line (and not following the coastline), and therefore represent minimum values. A base map of the Galápagos islands (1996, Datum WGS 84, scale 1:100.000) was used to examine foraging ranges and distances from shore. Due to errors of the base map of the Galápagos islands (of about 50 m) and the GPS-depth units (between ± 3 and ± 19 m, see GPS-depth manual, Earth and Ocean Technologies, Germany; see also Ryan et al. 2004), the map of Isabela Island was manipulated in ArcView and shifted approximately 200 m eastward. This manipulation was validated by our foraging movement GPS data (indicating that birds were diving at sea), by GPS tracks taken by an author walking along the high tide level, and by fixes taken with a hand-held Garmin 12CX GPS receiver to locate nest sites. The statistical analysis was carried out using linear mixed effect model (Software R 2.4.1 lme4) (Pinheiro and Bates 2000).

4.3 Results

Logger deployment

Twenty-three birds (11 males and 12 females) were successfully fitted with GPS-depth loggers while brooding one (12 birds) or two (11 birds) small- to medium-sized chicks. Of these, 16 individuals were studied at Caleta Iguana, six at Playa de los Perros and one at Las Marielas. All the devices were recovered, no nest was deserted and no other adverse effects were apparent from individual birds. Of all the device-equipped birds, mean \pm SD body mass was significantly higher in males (2.1 ± 0.2 kg) than females (1.8 ± 0.3 kg) ($p = 0.0083$).

Of the 23 equipped birds, 21 yielded useful GPS data and are included in the present analysis. Reasons for unsuccessful deployments involved birds not leaving their nesting site (one bird) and no data recording due to errors in programming (one bird). Only twelve data sets provided information on the full foraging trip length and were thus used in the dive parameter analysis. In the remaining 8 cases the battery had run out before the foraging trip was completed.

Movements at sea

The mean maximum distance travelled away from the nest during foraging irrespective of the direction was 5.2 ± 4.9 km (range 1.1 - 23.5 km, $n = 21$), there being no difference between males (mean 6.4 ± 6.5 , range 1.1 - 23.5 km, $n = 11$) and females (mean 3.9 ± 1.7 , range 1.6 - 6.6 km, $n = 10$) ($p > 0.05$). One particular bird (PP-19) moved at least 23.5 km from the nest in one day, nearly 5 times the mean maximum distance. If this outlier is removed, the mean maximum distance away from the nest was 4.3 ± 2.7 km; with location-specific mean distances of 4.8 ± 2.7 km (Caleta Iguana, range = 1.8 - 11.5), 2.5 ± 1.9 km (Playa de los Perros, range 1.0 - 5.2) and 3.1 km (Las Marielas; only one bird sampled) (Fig. 4-2a).

Fig. 4-2a)

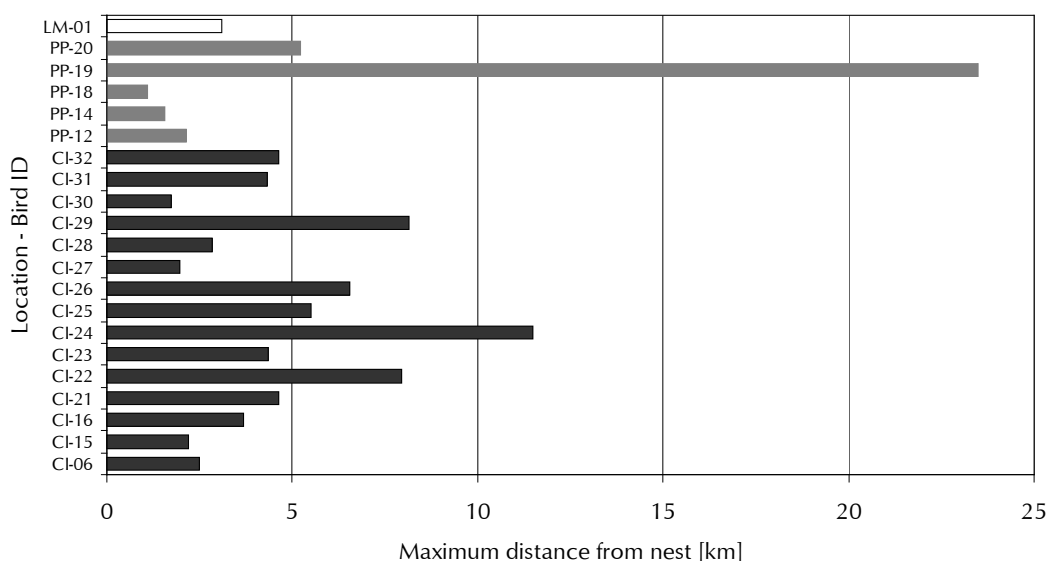


Fig. 4-2b)

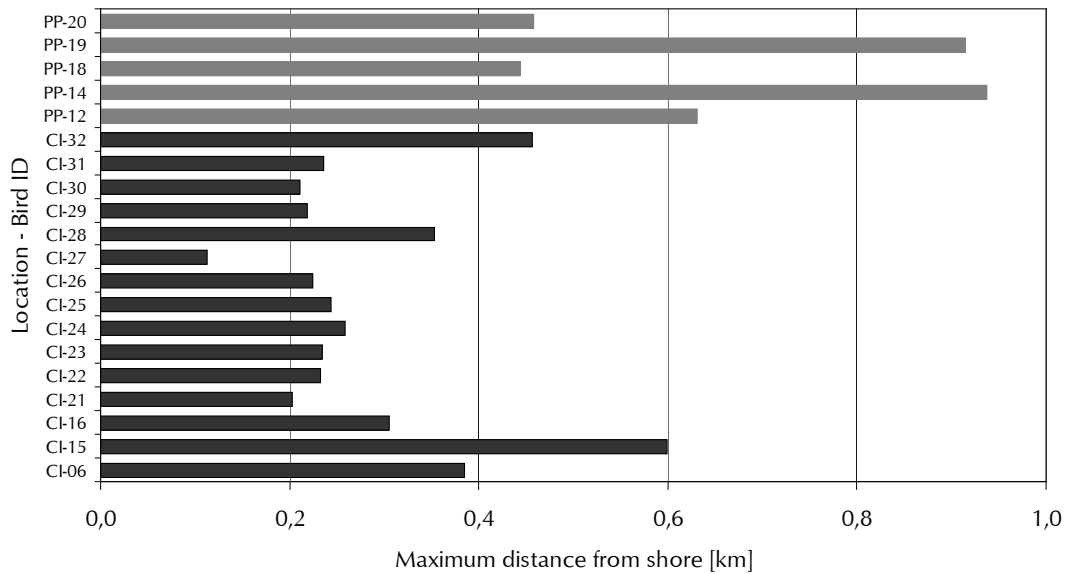


Fig. 4-2 (a) Maximum distances moved by penguins (measured in straight line) from the nest at Caleta Iguana (CI), Playa de los Perros (PP) and Las Marielas (LM). Note that bird PP-19 travelled nearly five times farther than the overall mean. (b) Maximum distance moved from shore by 20 penguins at Caleta Iguana (CI) and Playa de los Perros (PP).

Furthermore, penguin movement at Caleta Iguana and Playa de los Perros was highly biased towards travelling parallel with the coast. The single device-equipped bird at Las Marielas actually travelled away from this small islet but then travelled close inshore to Isabela Island (Fig. 4-3a). Due to the small sample size this single bird was excluded for all statistical analysis. The maximum recorded distance from the coast was 0.9 km ($n = 20$ birds) (Fig. 4-2b) indicating that foraging occurred within the 50 m depth zone off the coast. Although there were no inter-sex differences, site-specific differences were apparent ($p < 0.0001$) with birds at Playa de los Perros foraging further offshore than at Caleta Iguana (Fig. 4-3b-c). Also, no differences in movement behaviour occurred for adults raising one chick compared to two chicks ($p > 0.05$).

Fig. 4-3a)

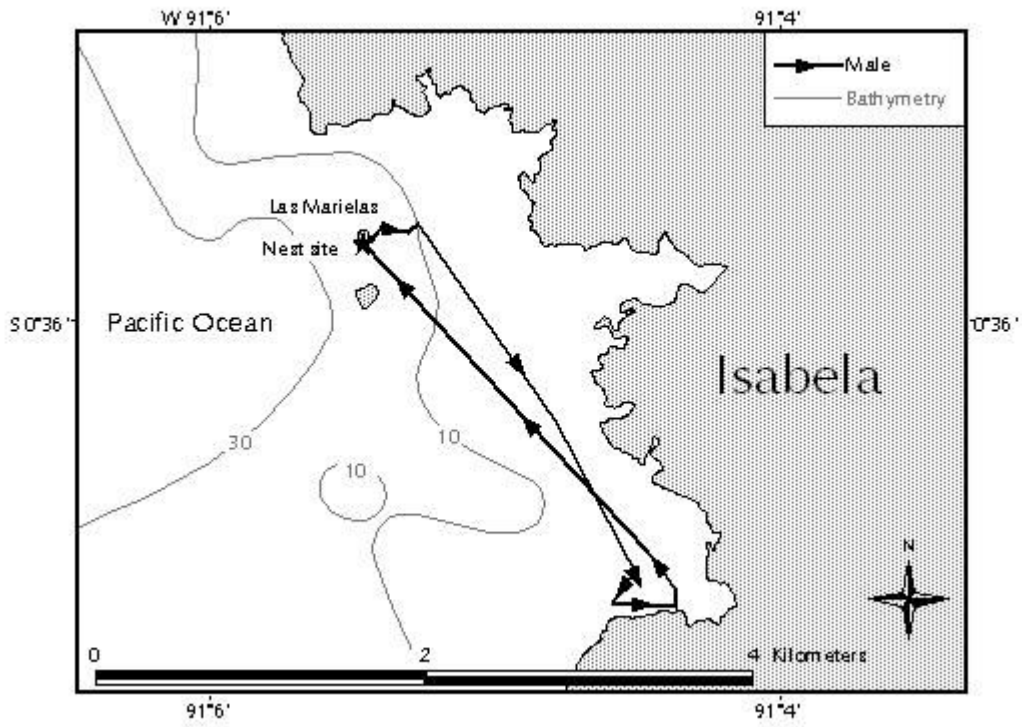


Fig. 4-3b)

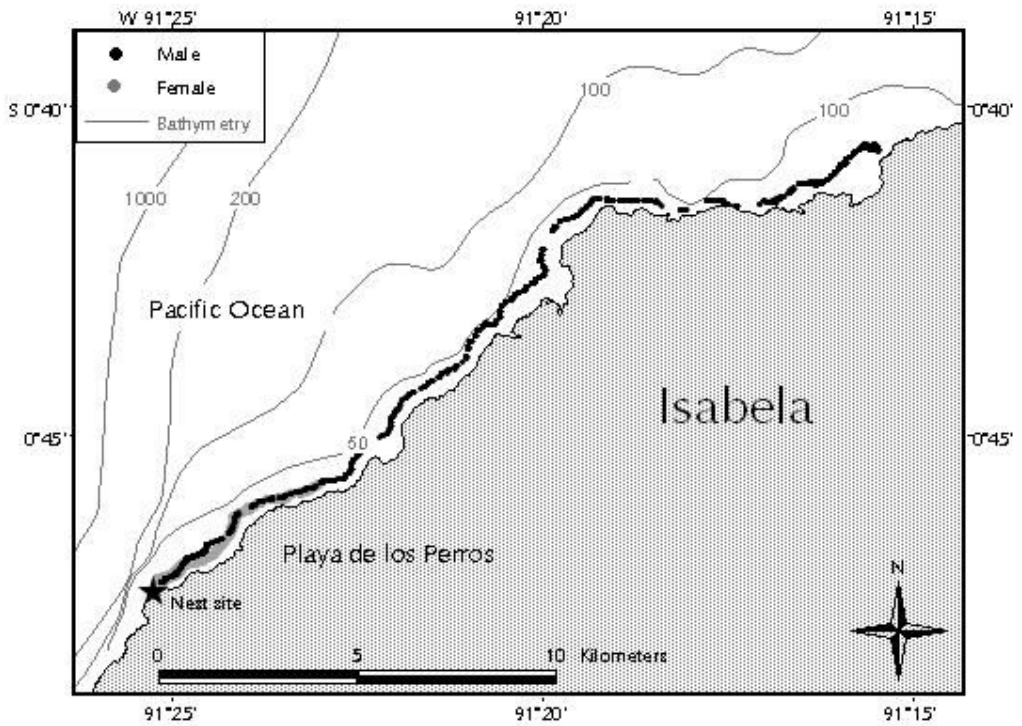


Fig. 4-3 c)

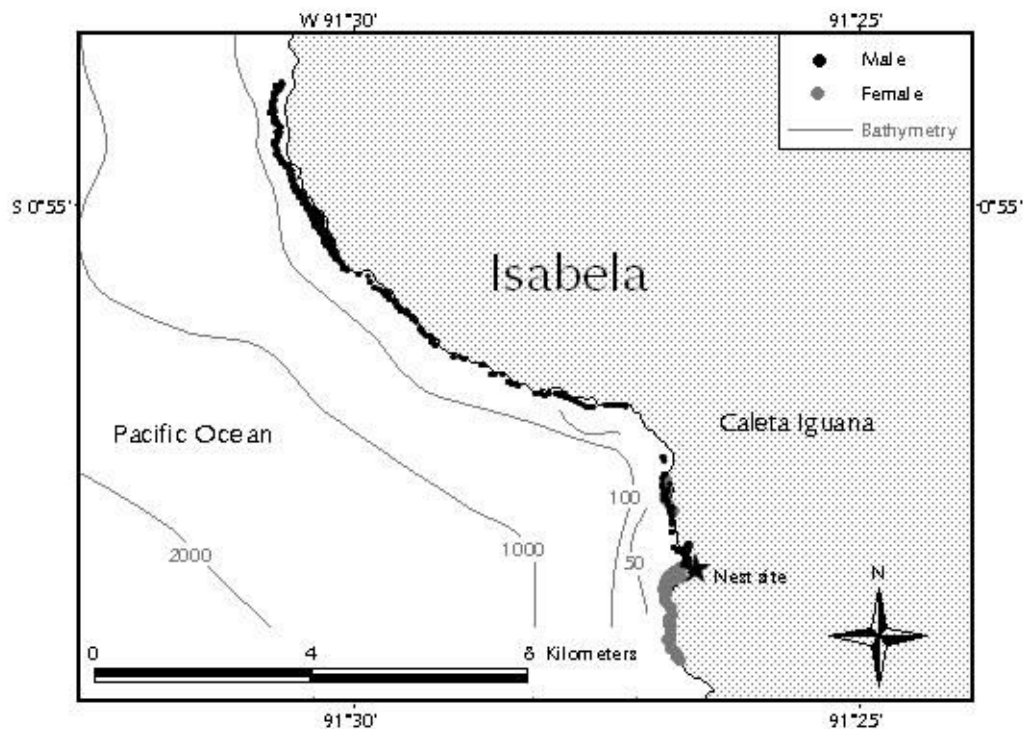


Fig. 4-3 Examples of movements of penguins at (a) Las Marielas (one bird) (b) Playa de los Perros (two birds) and (c) Caleta Iguana (two birds). Also showing bathymetry.

Diving behaviour

All of the successful device deployments delivered data from one foraging trip. Foraging trips lasted a mean of 8.4 ± 2.0 hours ($n = 12$ birds) with penguins leaving the nest to go to the sea between 5:11 and 5:48 h and returning between 11:04 and 17:00 h. Penguins foraged predominantly in surface waters, spending a decreasing amount of time with increasing depth (Fig. 4-4a). The maximum dive depth recorded for any individual was 52.1 m by a female foraging from Caleta Iguana although overall mean dive depth was $3.0 \text{ m} \pm 2.2 \text{ m}$. Mean limits for 90 % of time spent diving occurred at 8.5 m depth for males and 4 m for females (Fig. 4-4b). There were no significant differences in foraging trip duration between sexes or sites or number of brooding chicks ($p > 0.05$).

Fig. 4-4a)

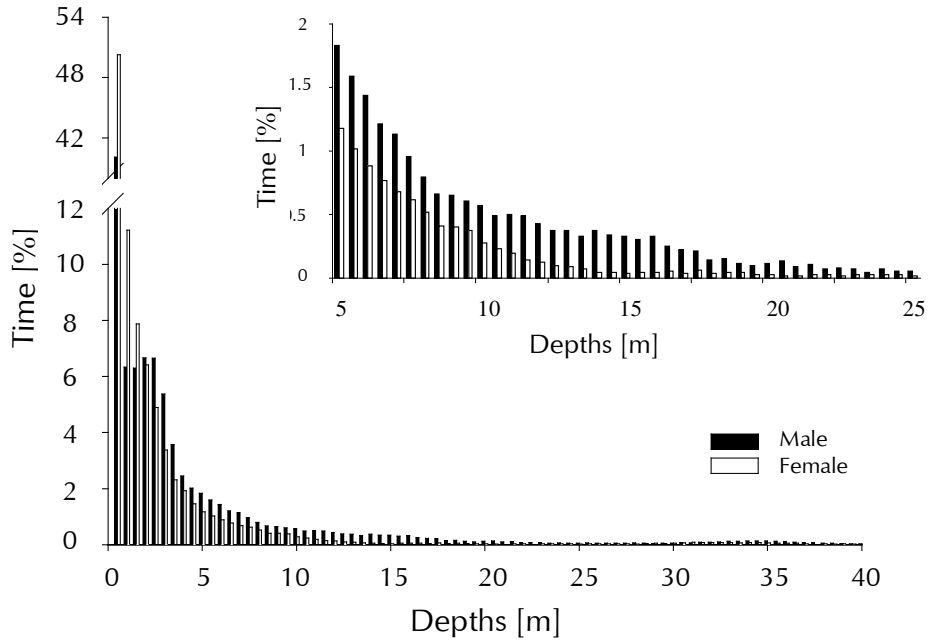


Fig. 4.4b)

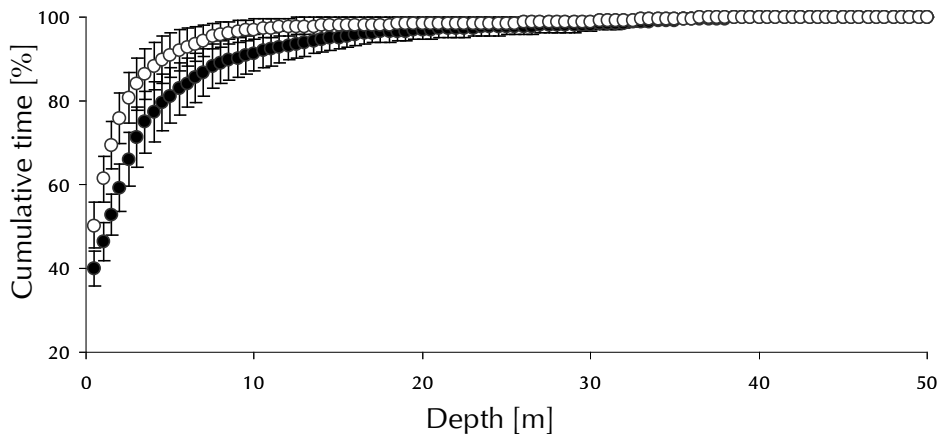


Fig. 4-4 (a) Mean percentage time spent per metre water depth by male (dark bars) and female (white bars) Galapagos penguins. The insert shows relationships for 5 to 25 metres in greater detail (b) shows the mean cumulative (percentage) time spent with increasing water depth for male (filled circles) and female (white circles) Galapagos penguins. Bars show SE.

4.4 Discussion

Device effects and potential biases associated with GPS tracking instruments

The attachment of external devices to free-living animals is known to affect behaviour (Wilson et al. 1986, Wilson et al. 1990, Culik and Wilson 1991, Bannasch et al. 1994, Taylor et al. 2001) so particular attention was paid to bird handling and the precise placement of our GPS-depth units. The GPS devices used in our study were relatively large, although still just below the threshold value of 5% body mass (Wilson and Culik 1992). Nevertheless, increased drag associated with the device deployment is inevitable, tending to reduce penguin swim speed (Wilson et al. 1986), dive performance (Wilson et al. 1991b, Ropert-Coudert et al. 2007) and likely food intake (Wilson et al. 2004) and cognisance needs to be taken of this. Despite this, and although no control study was carried out, we could detect no deleterious effects on either adult well-being or chick-rearing performance during the study.

Several potential biases might have also occurred in the interpretation of GPS tracking data: Although the device was programmed to record positions continuously, the number of locations acquired varies according to diving behaviour because positional fixes can only be obtained when the birds were at the water surface long enough to receive the relevant information from the satellites (Ryan et al. 2004). Thus, there were short periods when no positional data could be derived which could potentially affect both estimates of trip range and distance from the coast.

For the purpose of this manuscript, no differentiation was made between travel and foraging dives during penguin excursions to sea.

Foraging ranges, depths and volumes of water exploited

Greater foraging ranges are tenable in larger species for two reasons; firstly, chicks can be provisioned for extended periods by larger brooding adults because they have comparatively larger stomachs to store food, a process that is facilitated by food conservation mechanisms in the gut (Thouzeau et al. 2003). This is advantageous with respect to foraging range because where a single adult can provision the brood for long periods it allows the partner time to range farther because foraging duration correlates strongly with foraging range (e.g. Petersen et al. 2006). Secondly, both larger chicks and adults can fast for longer periods (Groscolas and Robin 2001) so that brooding adults and the chicks from larger species contend better with extended absences from the parent at sea.

Accordingly, published data for 13 species of penguin (brooding small to medium chicks) show that there is a general trend for foraging ranges to increase with body mass following;

$$\text{Range} = 24.73e^{0.1395\text{Mass}} \quad (r^2 = 0.76, F = 120.3, P < 0.05) \quad (\text{Fig. 4-5}).$$

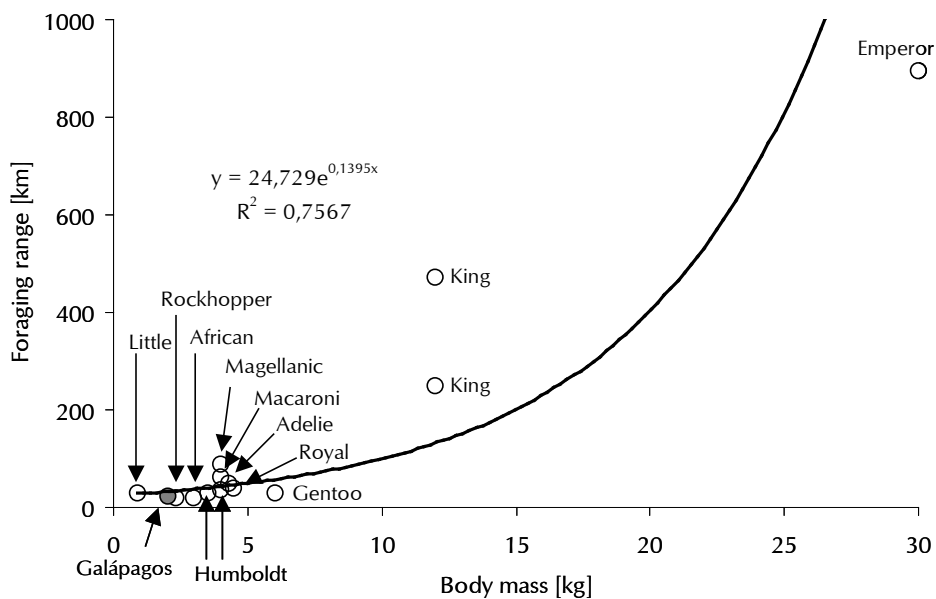


Fig. 4-5 Relationship between maximum foraging range and body mass of 13 species of penguins provisioning small or medium chicks. Note that the likelihood of species approaching a maximum foraging range will depend critically on the sample size and that conditions determining actual foraging range will vary accordingly to locality and circumstance so that values can only be considered to be approximate.

Foraging range data from Ainley et al. (2004), Sadleir and Lay (1990) (Adelie penguin), Ancel et al. (1992) (Emperor penguin), Barlow and Croxall (2002) (Macaroni penguin), Boersma et al. (2002) (Magellanic penguin), Collins et al. (1999), Norman (1992) (Little penguin), Culik and Luna-Jorquera (1997) (Humboldt penguin), Hull et al. (1997) (Royal penguin), Jouventin et al. (1994), Pütz et al. (1998) (King penguin), Lescroel and Bost (2005) (Gentoo penguin), Schiavini and Rey (2004) (Rockhopper penguin), Petersen et al. (2006) (African penguin), and mass data from Williams (1995). Two values are shown for the King penguin since the literature indicates considerable variation for this species (Charrassin and Bost 2001).

According to this regression, the Galápagos penguin, with a body mass of ca. 2 kg, is predicted to have a foraging range of 30.7 km. Our derived maximum range of 23.6 km is markedly less than this and even lower than that of the little penguin *Eudyptula minor*, a species half the mass of the Galápagos penguin, which may range over 30 km during chick provisioning (e.g. Norman 1992, Collins et al. 1999).

In addition, the data presented for all species other than the Galápagos penguin refer to general foraging range, which usually entails movement directly away from the foraging site and away from the coast (e.g. Culik and Luna-Jorquera 1997, Barlow and Croxall 2002, Ainley et al. 2004, Petersen et al. 2006). The observation that none of the GPS-depth recorder-equipped Galápagos penguins ranged farther than 1.0 km from the nearest coast indicates that the actual area of sea that they utilise is even smaller than their range would suggest. This can be illustrated by a simple model that assumes that all other penguin species during foraging radiate over a semi-circle. We consider that a semi-circle is a reasonable general approximation (cf. Wilson et al. 1988, Wilson et al. 1995a,b, Wilson

1995, Boersma et al. 2007 etc.) although the arc over which different species may forage varies between as little as 35° (Barlow and Croxall 2002) but may extend to virtually a full circle (e.g. Jouventin et al. 1994 for king penguins). Based on this general assumption, the area that can be exploited translates into $(\pi r^2)/2$, where r is the foraging range, so that the regression of foraging range versus mass can be altered into foraging area versus mass via;

$$\text{Area} = (\pi(24.73e^{0.1395})^2)/2.$$

The limits on this lie between $\text{Area} = (\pi(24.73e^{0.1395})^2)/(35/360)$ and $\text{Area} = (\pi(24.73e^{0.1395})^2)$ if the movement arcs taken for Macaroni and king penguins are taken as minima and maxima, respectively. By contrast, the sea area available to the Galápagos penguin is only effectively given by the distance from the coast multiplied by twice the range (since the foraging bird may normally move in one of two directions when leaving the colony). Using 95% confidence limits on the data gleaned from the GPS data, these only amounted to about 24 km², markedly less than the postulated mass-specific area used by penguins and even lower than that of macaroni penguins with their highly restricted foraging arc.

Putative foraging areas exploited by breeding penguins are modulated by the depths that the birds can exploit. In this regard regressions of absolute maximum depth *versus* body mass in Wilson (1995) predict that the Galápagos penguin should be able to dive to a maximum of 85 m which substantially exceeds the recorded maxima of 52.1 m. However, such measures are of limited value since they are highly dependent on sample size (since the chances of an individual executing an exceptional dive are correspondingly increased) and, in any case, tend to represent physiological maxima rather than anything of ecological relevance.

If we assume that the Galápagos penguin dive data are typical, it is possible to determine the volume of water that can be exploited by this bird by simply multiplying the maximum recorded depth (52.1 m, itself an outlier compared to other values) by the exploitable area (24 km²). Similar calculations using other penguin species demonstrate the huge discrepancy that there may be between this species and the others in the volume of water searched by breeding birds (Fig. 4-6). Indeed, even if the volume of water available to penguins is corrected to become mass-specific, the Galápagos penguin exploits about one thousand times less volume of water than other penguin species.

The primary factor in reducing the potential volume comes from the coast-hugging behaviour of the species. There are a number of possible explanations for this.

Firstly, their primary prey may be located inshore. In fact, to date, there are few data on the feeding habits of the Galápagos penguin. Both Boersma (1974) and Vargas et al. (2006) report that it takes mullet (*Mugilidae*) and Mills (1998) notes that the species is occasionally seen feeding with aggregations of seabirds exploiting what are assumed to be sardines *Sardinops sagax*. Vargas et al. (2006) also noted that the Galápagos penguin feeds on piquitangas (*Lile stolifera*) around Fernandina Island. Finally, 9 stomach samples of non-breeding adults collected during 2005 using a water-offloading method (Wilson 1984)

revealed that these individuals were feeding predominately on larvae or juvenile anchovies (*Engraulis* sp) (and fish most likely stemming from sardines and/or mullet (*Mugil* spp.)) (mean size 26 mm). Both sardine and anchovy are typical of upwelling systems, and their larvae and juvenile phases inhabit the surface inshore waters but migrate off-shore when adult (www.fishbase.org). Similarly, the local mullet are schooling fish that inhabit sand, mud and rock bottoms of shallow waters near the coast (www.fishbase.org).

Fig. 4-6a)

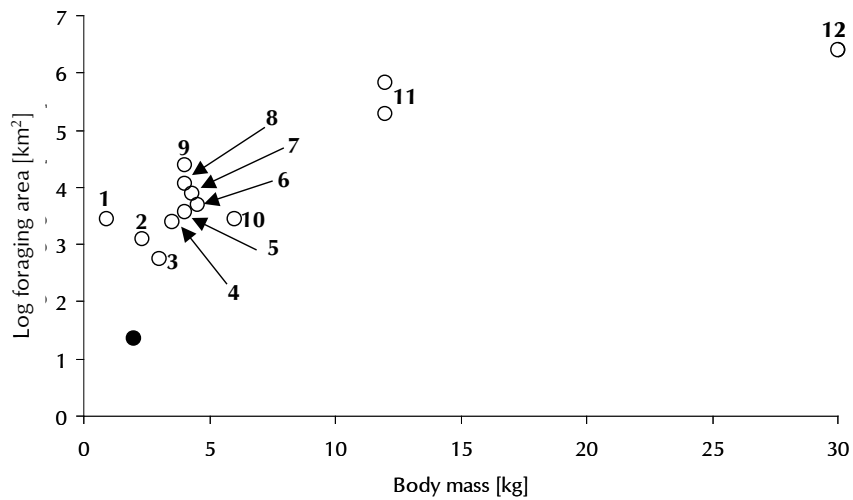


Fig. 4-6b)

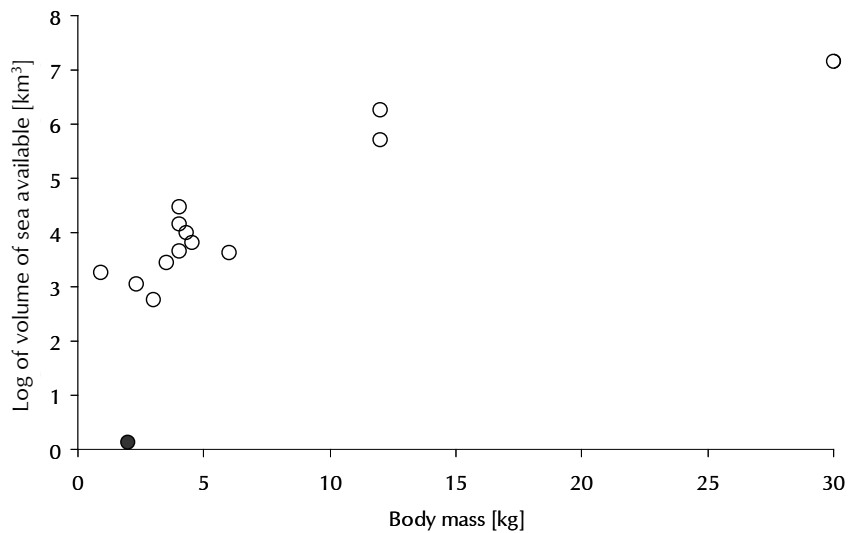


Fig. 4-6c)

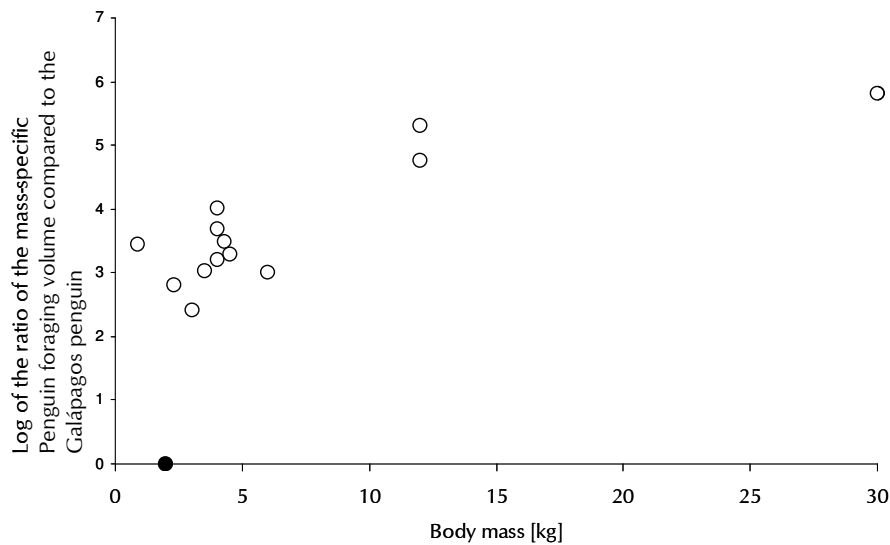


Fig. 4-6 (a) Relationship between the putative foraging area available to different penguin species hunting for small or medium chicks as a function of body mass (for calculations see text). The Galápagos penguin is denoted by the dark circle, other penguin species are indicated by following numbers: Little penguin = 1, Rockhopper penguin = 2, African penguin = 3, Chinstrap penguin = 4, Humboldt penguin = 5, Adelie penguin = 6, Royal penguin = 7, Macaroni penguin = 8, Magellanic penguin = 9, Gentoo penguin = 10, King penguin = 11, Emperor penguin = 12. (b) Relationship between the foraging volume available to different penguin species as a function of body mass (for calculations see text) – the Galápagos penguin is denoted by the dark circle. Maximum depth data derived from references given in (1) Montague (1985), (2) Tremblay et al. (1997), (3) Wilson (1985b), (4) Mori (1997), (5) Taylor et al. (2004), (6) Arai et al. (2000), (7) Hull (2000), (8) Croxall et al. (1993), (9) Walker and Boersma (2003), (10) Robinson and Hindell (1996), (11) Pütz and Cherel (2005), (12) Kooyman and Kooyman (1995) (c) Ratio between the mass-specific volume of sea available for foraging for different penguin species and that available to the Galápagos penguin (dark circle).

Another possible explanation relates to predation. It has been suggested that the paucity of non-volant pursuit divers in the tropics is related to increased predation by sharks (Au and Pitman 1986, Schreiber and Burger 2001, Weimerskirch et al. 2005). Fifteen species of shark have been recorded from the Galápagos archipelago (Humann 1993) so Galápagos penguin foraging ecology could be influenced by predator avoidance (Heithaus and Frid 2003).

These first data on the space use of the Galápagos penguin, which were taken over an extensive period of the year, suggest that the foraging habitat used by the penguins is only a small fraction of the upwelling zone and thus the potential marine habitat available to them. It is unclear why the foraging areas and volumes of this species are so much smaller than other penguin species at a similar stage of breeding. If food were abundant at the time the study was conducted, the population may not need to forage farther afield than it did, even if the birds were capable. However, the extremely aberrant coast-hugging

behaviour of the Galápagos penguin, which is shown by no other penguin species, indicates that some factor other than food limits the range. Where factors other than food distribution act to compromise potential foraging volumes, we would expect overall food availability to be similarly compromised and indeed this state of affairs alone might explain why Galápagos penguins are the only member of its genus to occur exclusively in small colonies.

Future studies need to examine the area and depth use of Galápagos penguins during the non-breeding season in order to be able to explain observed patterns more definitively. Certainly, an understanding of what limits area use by foraging Galápagos penguins has important implications for estimates of the distribution at sea and habitat used by Galápagos penguins as well as for assessments whether expanding anthropogenic activities, including commercial fisheries, may be potentially capable of harming penguin populations.

Future work should address the precise conditions that determine penguin foraging success and nesting requirements since the birds can clearly only breed in areas close to appropriate marine conditions. The likelihood of both conditions occurring together may already be reduced but further man-induced deterioration in either of these could prove critical to this species survival.

5 The diet of non-breeding Galápagos penguins, *Spheniscus mendiculus*, at Caleta Iguana, Isabela Island, Galápagos

5.1 Introduction

The foraging strategies of breeding seabirds are constrained by the dispersion and availability of different prey resources, the energetic costs of foraging, and by the rate at which food must be delivered to the nest during breeding (Lack 1968, Weimerskirch et al. 1994). Thus, prey selection has an important influence on bird biology, affecting activity, distribution, energetics, competitive abilities, breeding success and survival (e.g., Furness and Monaghan 1987, Montevecchi et al. 1988, Garthe et al. 1999). Knowledge of feeding ecology and diet composition, therefore, is fundamental towards understanding avian biology.

Although the Galápagos penguin (*Spheniscus mendiculus*) is an important marine predator in the western Galápagos archipelago, little is known about its feeding preferences (Boersma 1977, Mills 1998). No systematic dietary study has yet been conducted on this species and thus, almost nothing is known about the diet of the Galápagos penguin. The only observations have been incidental, of penguins apparently feeding on South American pilchard (*Sardinops sagax*) (Boersma 1977, Mills 1998), piquitangas (*Lile stolifera*) (Vargas et al. 2006) and mullet (*Mugil* sp.) (Nicolaides and Murillo 2001). These fish are epipelagic shoaling species (families Clupeidea and Engraulidae) and are characteristic of upwelling environments (Palacios 2003). This accords well with the penguin's distribution in the archipelago because approximately 98 % of the Galápagos penguin population is found in the western part of the archipelago which has been shown to be the primary area of upwelling, and the most productive waters of the archipelago, caused by the Equatorial Undercurrent (EUC; also known as Cromwell Current) (Palacios 2004, Jiménez-Uzcátegui et al. 2006).

The precarious population status of the endemic and endangered Galápagos penguin (Jiménez-Uzcátegui et al. 2006), poor understanding of the bird's ecology and the expanding latter day human activities affecting the Galápagos islands (e.g., Anderson et al. 2003), make a good case for urgent studies to obtain basic ecological information for this species. In particular, commercial fisheries are considered to be potentially capable of harming penguin populations due to entanglement and drowning in nets (Simeone et al. 1999) as well as competing directly for food, especially during El Niño events (e.g., Hays 1986).

This study was initiated as a first step to examine the diet of the Galápagos penguin using stable-isotopes of penguin tissues to provide a proxy for diet that can be compared to results obtained using more conventional direct diet sampling techniques of stomach contents (Wilson 1984).

The application of the stable-isotope technique to ecological studies has steadily increased since the 1970s (Hobson 1987, 1990, 1995, Hobson and Montevecchi 1991, Hobson et al. 1994, 2002, Sydeman et al. 1997, Hodum and Hobson 2000, Cherel et al. 2002, Forero et al. 2002). In studying seabirds, stable-isotopes of nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) have been mainly used to address questions on diet and foraging behaviour (Hobson 1995, Hobson et al. 2002, Sydeman et al. 1997). This approach relies on the fact that food-web isotopic signatures are reflected in the tissues of the consumer since, in general, seabirds have enriched nitrogen when feeding in higher trophic levels and have increasingly enriched carbon when feeding primarily from off-shore, or in pelagic zones, as opposed to coastal and inshore zones (Hobson et al. 1994). Thus, investigation of stable-isotopes in seabird tissue is a valuable and simple means to assess dietary behaviour. However, the amount of time that the isotopic signature of a particular diet remains in the tissues of the consumer depends on the metabolic rate of the particular tissue involved (Tieszen et al. 1983). In contrast to traditional diet sampling techniques (Wilson 1984, Gales 1987), which give a snapshot of diet at a particular time, stable-isotope analysis provides the opportunity to give a time-integrated average of diet, with the extent of the time window being dependent upon the tissue examined:

Analyses of **bone collagen** for example can provide a lifetime average dietary signal (Hobson et al. 1994) if the collagen is not remobilized during periods of stress, and if it accumulates at a known rate. Bones of chicks will obviously represent a very short interval during the breeding season, while those of adults will be averaged over years. **Feathers** have been used in a variety of studies to determine diet as well as to track migratory movements (see summary of studies by Forero and Hobson 2003). Analyses of feathers can provide dietary information for the post-breeding period in penguins. Once grown, a feather is no longer nourished by the blood system, and will retain an isotopic signature representing diet during the time of moult and regrowth only. Galápagos penguins moult all their body and tail feathers during a two to four week period (Williams 1995) so stable-isotope analyses of feathers should provide information on diet during this pre-moult period. Moreover, due to carbon, oxygen and nitrogen isotopes incorporated into the carbonate from recently-consumed food (Schaffner and Swart 1991), the use of **eggshells** in these studies also provides valuable information on the diet of breeding females during a critical stage in the breeding cycle (Schaffner and Swart 1991). Analysis of these tissues thus provides a seasonal and annual dietary profile of this species that should be useful in assessing dietary shifts and the trophic position of major prey.

This combined approach of stable-isotope analysis and conventional dietary sampling of stomach samples, is a first attempt to conduct a systematic dietary study on the Galápagos penguin in order to characterise penguin's basic diet preferences and to assess the potential for interactions with local and commercial fisheries. This work complements my study on the foraging behaviour of this species (for details see chapter 4) and should enhance understanding of how oceanographic parameters affect the foraging patterns of Galápagos penguins and possibly how the birds change strategy according to circumstance.

However, to date, neither of the two proposed methodologies has been used on the Galápagos penguin. So, in view of the precarious population status of this bird, the Galápagos National Park Service and the Charles Darwin Foundation requested a pilot study to test the feasibility of the proposed methodologies. The study presented below details the results of this work, which nevertheless goes well beyond a simple pilot study involving only a handful of individuals.

5.2 Material and Methods

Data collection

Stomach samples

Between May and July 2005 (inclusive), stomach samples were obtained from birds at the penguin's main breeding site, Caleta Iguana (S 0.98/W 91.45). Birds were caught as they returned in the late afternoon (17:00 to 18:00) from foraging. Birds were weighed to the nearest 100 g with a 5 kg spring balance (Pesola®, Baar, Switzerland) and sexed by bill measurements (length, depth, and width) using callipers to the nearest 0.1 mm (Boersma 1977). Additionally, birds were individually marked with a PIT- (Passive Integrated Transponder) tag in their left leg. The wound was closed with surgical glue (Vetbond, 3M). Penguin's stomachs were flushed once using the wet offloading technique described by Wilson (1984). This involved pumping water into the stomach down a tube inserted through the bill, which induces a vomit reflex. Bird handling for the whole procedure took approximately 20 minutes. For transportation and later analysis, samples were stored in 95 % isopropanol in individual "Ziplok" plastic bags marked with the collection date and the location. After this treatment, penguins were observed from the distance to assure that there were no apparent negative effects on bird well-being.

In accordance with the Galápagos National Park Service designated protocol, no sampling was carried out on breeding birds to preclude possible nest desertion or induction of breeding failure (see Wilson et al. 1989a).

Stable-isotope samples

Penguin bones, eggshells, feathers and tissues that were needed for the stable-isotope analysis were collected between May and July 2005 (inclusive) at the penguin's two main breeding sites in the Galápagos archipelago; at Caleta Iguana (S 0.98/W 91.45) and Playa de los Perros (S 0.79/W 91.43) on Isabela Island. Each tissue sample was separately stored in a "Ziplok" plastic bag that were marked with the collection date and the location.

These samples were salvaged only from tissue remains found at nest sites. Thus, no live birds or eggs were collected, handled, or disturbed for this sample collection.

Sample preparation and analysis

Stomach samples

The analyses of the stomach samples were conducted in the laboratory of the Charles Darwin Foundation (CDF) in Puerto Ayora, Santa Cruz, Galápagos.

The digested part of the stomach content was separated from the undigested, still identifiable material such as whole fish, fish tails and fish heads. Otoliths that were still enclosed in fish crania were removed and collected. The semi-digested material was examined for the presence of any diagnostic prey remains such as otoliths, vertebrae, cephalopod beaks or crustacean carapaces. Diet composition was assessed from each stomach sample in recording frequency of occurrence (loose otoliths were paired by size and species), number of individuals and length of undigested prey. All prey items were identified to the lowest possible taxonomic level by direct comparison with a reference collection compiled for this purpose (obtained from fresh fish samples) as well as with help from the CDF, SPC (Secretariat of the Pacific Community, New Caledonia), local fishermen and according literature (Rivaton and Bourret 1999).

Common and scientific fish names follow those suggested by Fish Base (<http://www.fishbase.org>).

Stable-isotope analysis

The stable-isotope analysis of these samples was undertaken between May 1st and May 15th 2006 at the University of Saskatchewan, Department of Geological Science in Saskatoon, Canada under the supervision of Dr. Bill Patterson.

Samples were divided into eggshell, eggshell-membrane, feather shaft and rami, toenails, bone, bone tissue and scale tissue. Each sample was treated individually following guidelines regarding material-specific characteristics e.g. to remove lipids or / and water.

Stable-isotope values of organic $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were obtained by mass spectrometry using a Thermo Finnigan Flash 1112 Elemental Analysis coupled to a Thermo Finnigan Delta Plus XL through a Conflo III.

0.5 mg of the sample, filled-up in a tin capsule was dropped, in a helium atmosphere, into an oxidation furnace packed with chromium (VI) oxide and silvered cobaltic/cobaltous oxide (to remove any halogens) at 1000°C. This process ensures that all organic material is oxidized to carbon dioxide and various nitrogen gases. Afterwards, this gas was passed through a reduction furnace packed with elemental copper at 680°C to reduce all nitrogen-bearing compounds to pure gaseous nitrogen. The resulting gases were then passed through a water trap to eliminate moisture. A gas chromatograph column at 50°C was then used to unmix the carbon dioxide and nitrogen gases for analysis in the mass spectrometer. Carbon isotope ratios were corrected for O^{17} contribution and reported in per mil notation relative to the V-PDB (Vienna-Pee Dee Belemnite) standard. Nitrogen isotope ratios are reported in per mil notation relative to air. Precision and accuracy of data were monitored through routine analyses of in-house standards which were stringently calibrated against IAEA (International Atomic Energy Agency) standards. Accuracy of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ measurements were 0.2‰ and 0.3‰, respectively. Percent C and N measurements had an accuracy of 1%.

Stable-isotope values of inorganic $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ were obtained from the eggshells by running the samples in a Finnigan GasBench II which was connected to the Isotope Ratio mass spectrometers. Precision and accuracy of data were monitored through routine analyses of a lab internal calcium carbonate standard. An overall precision of 0.06‰ for $\delta^{18}\text{O}$ and of 0.08‰ for $\delta^{13}\text{C}$ was achieved.

Actual sample errors may be greater than these due to heterogeneity, and more accurate data may be obtained for such through repetition.

Statistics

Tests for significant differences in the stable-isotope values between the tissues was carried out using SPSS 11.0 for Windows.

5.3 Results

Data analysis and interpretation

Stomach samples

The stomach contents of eight non-breeding adult birds (three females and four males) were collected. Mean \pm SD body mass was significantly higher in males (2.4 ± 0.2 kg) than females ($2.0 \text{ kg} \pm 0.7$) ($p < 0.001$).

In all samples, fish was the predominant prey item in terms of frequency of occurrence. A cephalopod beak was found in one sample while there was no evidence of crustaceans in any of the stomach samples.

Although not all prey items could be identified, stomach samples showed that penguins fed predominantly on pelagic prey species. The major prey item was represented by anchovies (likely Pacific anchoveta *Cetengraulis mysticetus*) followed by South American pilchard (*Sardinops sagax*) and mullet (*Mugil* spp). Other prey species found in the stomach samples could only be related to the families Sphyraenidae and Carangidae (Allain pers. comm.).

Overall, results obtained from un- and semi-digested fish showed that Galápagos penguins fed almost exclusively on prey items less than 30 mm, while a sardine of 60 mm size was found only once.

Since all loose otoliths (with two exceptions) found in the stomach samples represented the same size class as the otoliths obtained from the undigested fish, this suggests that the fish sizes should be comparable. Otoliths of our reference collection that were taken from fresh adult fish (6-10 cm in length) were much larger and emphasises our assumption.

Since otoliths of juvenile fish or even larvae often represent a different shape than in later stages, the identification of all prey items without having an appropriate reference collection was not possible. Also, a regression relating otolith length to fish length to allow estimation of the original fish size and mass could not be undertaken. Correspondingly vertebrae were not used to identify species.

For necropsy, the Galápagos National Park Service provided a juvenile penguin that was found drowned in a gill net. This stomach sample contained fourteen herrings, with an average size of 87 mm.

Stable-isotope analysis

Penguin feathers (8 samples), bones (6 samples), toenails (3 samples) and eggshells (12 samples) were collected at numerous active nests. C and N values of eggshell and eggshell-membrane, feathers, bone, scales, toenails, and tissue varied from 8 to 11 permil and from -20 to -14 permil, respectively (Fig. 5-1), while C and N differed significantly in eggshell and eggshell-membrane (Wilcoxon test, both $T = 66$, both $n = 11$, both $p < 0.001$). C differed significantly in organic and inorganic eggshell samples (Wilcoxon test, $T = 66$, $n = 11$, $p = 0.001$) (Fig. 5-2).

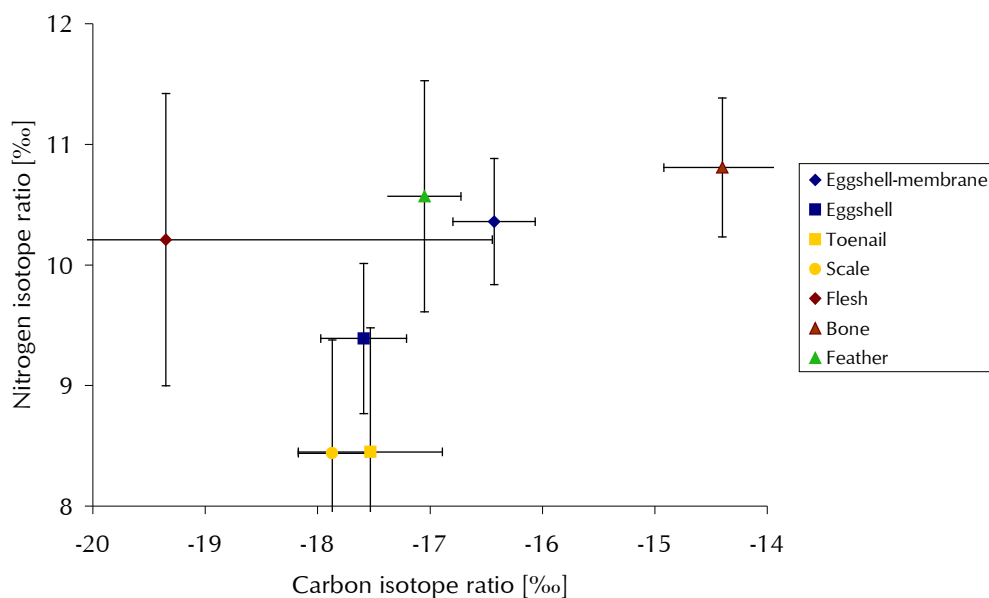


Fig. 5-1 Mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ (+/-SE) values and samples sizes of different tissues of the Galápagos penguin.

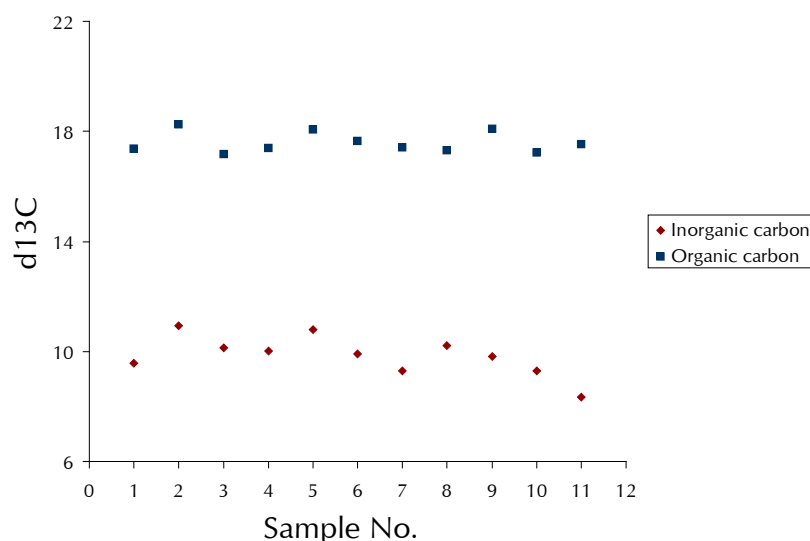


Fig. 5-2 Organic and inorganic $\delta^{13}\text{C}$ in penguin's eggshells.

5.4 Discussion

Methodology assessment, errors, biases and caveats in this study

The advantages of the isotope methodology for studying seabird trophic ecology are numerous. Previous conventional studies of seabird diet relied upon examination of stomach contents of birds (Wilson 1984) with all its attendant biases (see review in Duffy and Jackson 1986 and González-Solis et al. 1997). In fact, unsurprisingly, no method of assessing the stomach content of marine animals is free from bias or error of one kind or another (Hyslop 1980).

The major problem is that prey is digested at different rates, even if they are ingested at the same time (Wilson et al. 1985a). This is particularly obvious with respect to soft-bodied prey within the stomach contents. Fortunately the otoliths of fish and the beaks of squid tend to be more persistent than other body parts and can be used to calculate the size of the original prey items, although even these are subject to digestive erosion (Herling et al. 2005), and corrective factors may need to be applied (Gales 1988).

In addition, there are some ecological problems where conventional studies of the diet perform poorly (e.g., quantifying trophic level) for which the stable-isotope technique provides solutions. For example, in contrast to traditional diet sampling techniques, which give a snapshot of diet at a particular time, stable-isotope analysis gives a time-integrated average of diet, with the amount of time depending upon the tissue examined.

Furthermore, in the particular case of the Galápagos penguin as an endangered species, the stable-isotope methodology provides the additional advantage, that information can be obtained while not involving either bird handling, or disturbance.

To reliably collect all the stomach contents, the stomach-pumping procedure needs to be repeated several times on the same individual (Gales 1987). While this technique is not without its own problems, it has been used successfully on almost all penguin species in the world and, only after careful consideration was this methodology proposed to the Galápagos National Park Service. Because a collection of the stomach contents of parents during chick rearing would deprive their chicks a meal, the Galápagos National Park Service gave permission to carry out this study under the premise of 1) capturing up to 10 non-breeding birds and 2) birds should be flushed no more than once.

These restrictions, which resulted in the small sample size, mean that the results presented here are necessarily preliminary, but serve as a good broad outline of dietary preferences. It should also be noted that, since stomach sample collection was carried out during a very short time period at only one site, this work cannot pretend to address either temporal nor spatial differences in diet.

Although there is no doubt that stable-isotope analysis has helped to revolutionise the way we study ecology, in many cases the correct interpretation of the results obtained from wild studies depends on laboratory experiments to clarify assumptions on which these studies rely (Cherel et al. 2004). There is still much left to be learnt about the interactions between isotope ratios and animal physiology and further research is also required into natural variation in isotopic patterns.

Thus, I believe that combined approaches used are complementary, with biases in one technique being partially corrected by the other. For the future, measurements of multiple isotopes in multiple tissues that integrate diet over various temporal scales in conjunction with conventional dietary sampling could provide an unparalleled opportunity to disentangle the complex trophic relationships of dynamic food webs.

Prey composition

The upwelling habitat on the western side of the archipelago is created by the surfacing of the EUC. The waters are nutrient-rich, cold, well oxygenated (Anderson 1977, Lukas 1986) and thus providing suitable habitat to different euphausiid assemblages (*E. eximia*, *E. paragibba*, and *Nyctiphanes simplex*) (Cornejo de González 1977, Brinton 1979), myctophids (*Myctophum nitidulum*), several squid species (Palacios 2003), and Panamá lightfish (*Vinciguerra lucetia*) (García et al. 1993) among the mesopelagic organisms, and South American pilchard (*Sardinops sagax*), Pacific anchoveta (*Cetengraulis mysticetus*), and round herring (*Etrumeus teres*) (García et al. 1993, Grove and Lavenberg 1997) among the epipelagic schooling fishes. Other schooling fishes that occur in high abundance in Galápagos' coastal waters are the black-striped and the white salema (*Xenocis jessiae* and *Xenichthys agassizi*, family Haemulidae), the yellow-tailed and the Galápagos mullet (*Mugil rammelsbergii* and *M. galapagensis*, respectively) (Palacios 2003).

Thus, while the penguin's marine environment offers a variety of different prey items, the results within this study show, even despite of all the problems and biases, that fish were the dominant prey in the Galápagos penguin's stomach samples. There was no contribution of crustaceans in the diet detectable and a cephalopod beak was found among all samples only once. Since in general the keratinous cephalopod beaks are more liable to retention than the calcareous otoliths and thus tend to accumulate in the stomach the findings should present rather overestimates than underestimates. Therefore, we can assume that cephalopods can be neglected as a diet component at least in non-breeding penguins, at this time of the year and at that specific site.

The diet composition mainly occurred of neritic, pelagic species typical of upwelling systems, dominated by Engraulidae (here likely represented by Pacific anchoveta *Cetengraulis mysticetus*). These schooling fishes generally grow to up 10 cm in the first year of life (Hobday 1992) which is within the range of prey taken by other *Spheniscus* penguins (Scolaro et al. 1999, Herling et al. 2005, Ludynia 2007) as well as little penguins (Cullen et al. 1992).

However, the study provides strong evidence that penguins were feeding almost exclusively on very young fish or even larvae of these species since they were consuming individuals of up to 30 mm in size (<http://www.fishbase.org>). Adult fish, that was expected to be an important component of the penguin's diet, was almost absent.

Larvae and juvenile phases of the penguin's principal prey species inhabit the surface inshore waters and migrate offshore when adult. This corresponds well with the results obtained in the study on the Galápagos penguin's foraging behaviour (see chapter 4). Data obtained on diving behaviour of chick-rearing Galápagos penguins confirm that foraging is concentrated in a strip of sea up to only 1.0 km from the coast while dives occur in 90 % of their time at depths less than 6 m.

However, while for some species at certain localities or seasons the diet may consist of largely a single species, it is more likely that breeding Galápagos penguins represent generalists that, within limits, eat what is available in their limited foraging range at chick-rearing stage.

The non-breeding adult and juvenile birds, however, may feed outside the average foraging range of breeding birds at Caleta Iguana and thus, it can be that these results do not reflect the diet consumption of penguins during the breeding period.

The stomach content of the juvenile penguin in this study was found in a gill net in the harbour of Villamil, a village in the south of Isabela Island. Here, gill nets, though an illegal fishing technique in the archipelago, are regularly used on the purpose for bait fishery.

Although the penguin's stomach was filled with herring, it is likely that this sample rather mirrors a good food availability (in the net) than prey preference, which would support the idea of Galápagos penguins being opportunists.

Stable-isotope

This study was a first approach to examine the stable-isotope ratios of different penguin tissues in order to assess potential dietary shifts and trophic position of major prey.

However, although the samples provide preliminary isotope values on the different tissues, the interpretation of these proxies is, however, very limited. Nevertheless, the isotope values obtained in this study can serve as a base to discuss potential scenarios and help to improve data collection in further studies.

For example, although having essentially the same diet (anchovy) (Scolaro et al. 1999), nitrogen isotope values for Magellanic penguins are considerably higher, leading to the assumption that the Galápagos penguin is feeding on a lower trophic level. An explanation for the difference in N values between the Magellanic and the Galápagos penguin therefore could come from feeding on different sizes and age classes of the same prey species.

But, across the equatorial Pacific there is a high variation in $\delta^{15}\text{N}$ values, ranging from 12 to 15 permil. Most of this variation can be explained by changes in the $\delta^{15}\text{N}$ at the base of the food web with lesser variation due to trophic level and ontogenetic shifts in diet. Changes in the isotopic composition of nitrogenous nutrients affect the $\delta^{15}\text{N}$ of phytoplankton and that isotopic signal is propagated up the food web.

Thus, differences the $\delta^{15}\text{N}$ value of birds is likely driven by differences in the $\delta^{15}\text{N}$ of the prey fish (probably reflecting a change in the $\delta^{15}\text{N}$ of the food source for the fish) rather than due to different trophic levels.

In addition, the waters in the Galápagos islands are fed by upwelling of deep-water nitrate whereas the nutrients around the Falklands and the southern coast of Argentina and Chile originate from the Southern ocean. Nitrate in upwelled water has a $\delta^{15}\text{N}$ of deep-water nitrate (~5 permil) whereas the $\delta^{15}\text{N}$ of nitrate in surface waters of the Southern ocean can be quite variable and most likely much higher than 5 permil (Sigman et al. 2000).

For this reason $\delta^{15}\text{N}$ values of fish from the Atlantic ocean can hardly be used as being representative of a fish from the Pacific, even they are the same species (Popp pers. comm.).

Comparison with congeners

Penguins breeding at low latitudes, such as the *Spheniscus* penguins, are mainly fish-eaters with their main prey of small fish such as anchovy, sardines and sprat. The bills of these penguins species are therefore often hooked at the end of the top mandible, a feature that helps holding the prey. Accordingly, the penguins of the genus *Spheniscus* are reported to be specialised on pelagic school fish such as anchovies (*Engraulis* spp.), pilchards (*Sardinops* spp.), sprats (*Sprattus fuegensis*), hake (*Merluccius hubbsi*), silversides (*Odontesthes* spp.) and pelagic goby (*Sufflogobius barbatus*) (African penguin *S. demersus* Crawford and Shelton 1981, Randall and Randall 1986; Magellanic penguin *S. magellanicus* Frere et al. 1996, Scolaro et al. 1999; Humboldt penguin *S. humboldti* Wilson et al. 1989b, Wilson et al. 1995a, Herling et al. 2005) and only to a lesser extent on cephalopods (like *Loligo* spp.) and krill (euphasiids).

However, several studies on *Spheniscus* penguins show that feeding preferences differ considerably over their breeding range (Crawford and Shelton 1981, Randall and Randall 1986, Wilson et al. 1989b, Wilson et al. 1995a, Frere et al. 1996, Scolaro et al. 1999, Herling et al. 2005) and thus, inter-site variability can be significantly greater than inter-specific differences in diet (Wilson et al. 1995a, Scolaro et al. 1999).

Oceanographic conditions

Seasonality

Furthermore, oceanographic conditions like sea surface temperature and salinity have a significant influence on distribution and availability of marine resources (e.g., Castillo et al. 1996, Hansen et al. 2001). Some fish species show seasonal variation in their spatial distribution and thus makes them differently available throughout the year (e.g., Parrish et al. 1989, Castillo et al. 1996). Even in regions with frequent and strong upwelling fish species like pilchards (*Sardinops* spp.) show migratory behaviour (Parrish et al. 1989). Due to this seasonality, changings in prey abundance are reflected in differences in the diet of *Spheniscus* penguins and has already been documented in various studies, except for the Galápagos penguin (Wilson 1985a, Scolaro et al. 1999).

Interannual variation

While seasonal variability only has a slight effect on the productive upwelling habitat in the western archipelago, the strongest impacts occur at the inter-annual and intra-seasonal timescale. The upwelling system in the western archipelago is regularly affected by frequent periods of the anomalous climatic conditions of the El Niño phenomenon (ENSO = El Niño-Southern Oscillation) (Palacios et al. 2006), where the nutrient-rich surface waters are replaced by warm, nutrient-poor waters (Colling 2001). These events are known to reduce primary productivity and disrupt marine food webs (Arntz and Fahrbach 1991, Palacios et al. 2006). Epipelagic schooling fish such as Pacific anchoveta (*Cetengraulis mysticetus*) and Round herring (*Etrumeus teres*) (García et al. 1993, Grove and Lavenberg 1997) migrate away from the Galápagos archipelago, and thus are unaccessible to penguins as well as to other marine animals that depend on this prey. The impacts of poor fish availability during El Niño on penguins are widely studied (e.g., Hays 1986, Duffy et al. 1987, Boersma 1998). Although the continuous recurrence of warm and cold events in

the tropical east Pacific suggests that long-lived animals such as penguins should be adapted to different food availability and adjust prey composition accordingly (Duffy et al. 1987), during the El Niño events in 1982-83 and 1997-98, the Galápagos penguin population underwent dramatic population declines of 77 % and 65 %, respectively (Boersma 1977, 1998, Robinson 1987, Valle et al. 1987, Valle and Coulter 1987, Trillmich 1991, Chavez et al. 1999, Vargas et al. 2006). Boersma (1998) and Vargas et al. (2007) linked these dramatic population declines of Galápagos penguins mainly to starvation.

Fisheries

In contrast to Chile, anchovies and pilchards are not commercially harvest species in the Galápagos islands and thus it seems unlikely, that penguins compete with man for food (Simeone et al. 1999).

However, local fishing boats operating in inshore waters in the western part of the archipelago are documented as incidentally drowning Galápagos penguins due to floating nets and illegally-used bait fisheries in gill nets (Cepeda and Cruz 1994).

Despite ongoing efforts aimed by the Galápagos National Park Service at bringing illegal fisheries under control, the monitoring of their activities in the Galápagos Marine Reserve due to its logistical and financial difficulties is a challenging task and precise measures of the species magnitude of net-mortality remains uncertain.

Species like the Galápagos penguin that only occur in low population numbers are particularly susceptible to the effects of increased mortality (Vargas et al. 2007), and recent plans as to establish longlining fisheries in the Galápagos islands raise even more concern (Altamiro (CDF) and (Chavez) GNPS pers. comm.). Only recently an experimental pilot project on longlining fisheries has been carried out in the Galápagos islands with 155 launchings of longlines of between 80 and 350 hooks each one, the so called “green” longlining. Apart from the well-known impact of by-catch caused by this technique (Weimerskirch et al. 2000) an additional, and in the case for the penguins eventually even more critical, aspect could be an increasing demand in bait fish that cause a dramatic increase in inshore bait fisheries.

Despite all caveats associated with the data collection and obtained data sets, this preliminary study provides a first step towards a systematic dietary study of the Galápagos penguin and gives a broad outline of the diet composition with an adequate assessment of the used methodologies.

However, as mentioned above, since our sampling was carried out during a very short time period and additionally at only one site, neither temporal nor spatial differences in diet preferences of the Galápagos penguin could be investigated.

Detailed knowledge of feeding preferences and diet composition of the Galápagos penguin will be beneficial towards understanding better the role of the Galápagos penguin in its marine environment and thus could do much to alert authorities to changes in the marine ecosystem on which these birds depend and help to improve fisheries management to avoid undue competition between man and penguins (e.g., Anderson et al. 2003).

A continued monitoring of the Galápagos penguin's diet could indicate the extent to which oceanographic parameters (and changes) affect foraging patterns in terms of prey predictability and thus may help to estimate any difficulties of penguins meeting their energetic demands e.g during El Niño years.

For this reason, for further diet studies it is necessary to include the possible effects of inter-annual (i.e. ENSO) and seasonal variability as well as spatial variation in the diet in the western archipelago considering the high variability in the study area with "average" conditions being less common (Trenberth 1997).

6 The predatory impact of cats (*Felis catus*) on the Galápagos penguin (*Spheniscus mendiculus*) at Caleta Iguana, Isabela Island, Galápagos

6.1 Introduction

The geographic isolation of oceanic islands when combined with recent appearance, late human colonisation and an absence of native terrestrial carnivores, has repeatedly led to the evolution of a unique insular flora and fauna with a high degree of speciation and endemism (Grant 1999). However, the naivety of the islands' fauna to predation, resulting from lack of antipredator behavioural, morphological, and lifehistory responses (Stone et al. 1994), means that the impact of introduced mammals has been devastating on many oceanic islands (e.g., Diamond and Veitch 1981, King 1984, Moors and Atkinson 1984, Fitzgerald 1988, Atkinson 1989, Stone et al. 1994, Holdaway 1999, Groombridge and Jenkins 2000, Atkinson 2001, McNeely et al. 2001).

In these insular environments, feral cats (*Felis catus*) are, in particular, recognized as a significant threat to the island fauna (Nogales et al. 2004).

As human commensals, cats have travelled on ships around the world with explorers, sealers, whalers and other seafarers, and thus gained easy access to some of the most remote oceanic islands (Todd 1977). In addition to the cats that escaped ashore during stopovers, many cats actually arrived and stayed at these places with colonists. Although such cats have been mainly introduced in small numbers, the ease with which they proliferate in the favourable conditions found on many of the islands (often being virtually exempt from natural enemies and surrounded by defenseless prey - as well as introduced prey such as rodents), these opportunistic predators (Jones 1977, Konecny 1987, Rodriguez-Estrella et al. 1996) have been able to survive under even the most inhospitable conditions (Tabor 1983, Apps 1986, van Aarde 1986, Fitzgerald 1988, Atkinson 1989) and, as a result, often established feral populations soon afterwards (Todd 1977). Accordingly, feral cats have been directly responsible for numerous extinctions and extirpations across multiple insular taxa worldwide (Iverson 1978, Moors 1985, Moors and Atkinson 1984, Kirkpatrick and Raution 1986, Cruz and Cruz 1987, Towns et al 1990, Witthaker 1998, Donlan et al. 2000, Veitch 2001, Keitt et al. 2002) which finally led to the inclusion of cats into the list of the 100 worst invasive species (Lowe et al. 2005).

It is probably the life-history characteristics of many seabirds, such as low annual productivity, long reproductive cycles, delayed reproductive maturity and low adult mortality (Warham 1990, Russell 1999) that made them particularly vulnerable to predators introduced on islands (Pascal 1980, Jouventin et al. 1984, Rodriguez-Estrella et al. 1991, Monteiro et al. 1996).

Not surprisingly, therefore, cats have caused severe damage at seabird colonies worldwide (Stonehouse 1962, Jones 1977, Van Aarde 1980, Moors and Atkinson 1984, Fitzgerald and Veitch 1985, Veitch 1985, Fitzgerald 1988, Keitt and Tershy 2003). Indeed, Lever (1994) describes the impacts of cats on birds with “the list of species they have helped to exterminate or endanger reads like a roll-call of avian disaster”.

Although it is uncertain when house cats were introduced in the Galápagos islands, Salvin (1876) had reported a well-established feral cat population by 1869 at Tagus Cove, Isabela Island, this being the largest and one of the four inhabited island within the archipelago. Despite of the harsh climatic conditions that the cats have to face, they now range all over this island (Jiménez-Uzcátegui et al. 2006).

The Galápagos penguin (*Spheniscus mendiculus*) is one of the endemic seabirds in the Galápagos islands and, due to its small population size, considered to be of serious conservation concern (BirdLife International 2005). Certain characteristics, however, notably the fact that it is endemic, endangered and flightless, make this species particularly vulnerable to introduced predators compared to other seabirds. Of particular note is that:

1. While other seabirds usually breed on more than one island, the Galápagos penguin breeds in a geographically highly-restricted range (91.3 % of the breeding sites are located along ~ 400 km of the coast of Isabela Island).
2. The Galápagos penguin shares all of its main breeding locations with introduced mammals such as rats and/or cats.
3. In contrast to volant birds, the flightlessness of penguins makes them particularly vulnerable to terrestrial predators.

It is, therefore, unsurprising, that cats are considered to exert a considerable negative effect on the penguin’s population with the implications for the penguin’s conservation being likely to be significant. Despite this general belief, there is little actually known of the extent of the threat. Although feral cats on Isabela Island have been investigated by Konecny’s (1983), this work focuses mainly on the behavioural ecology, food habits and energetics of feral house cats in the Galápagos islands (Konecny 1987) rather than on the predatory impact on endemic and endangered species. Konecny (1983) found that by far the most important food for feral cats in the Galápagos islands is black rats although they do eat, to a lesser extent, birds, insects, crustaceans, and lizards. Konecny’s study was carried out at a non-penguin breeding site where penguins only land infrequently, so any results from Konecny’s work cannot be used to make deductions about the possible impact of cats at penguin breeding sites.

We managed to confirm the presence of cats at the two of the main breeding sites of the Galápagos penguin, Playa de los Perros and Caleta Iguana, in the southwest of Isabela Island (see chapter 3), both by direct observation and indirect evidence (by finding cat excrement) during my regular visits. However, we did not find any evidence of a negative impact until April 2005.

During the field trip, conducted from April 24th to May 6th 2005, for the first time, we found depredated penguins by cats at Caleta Iguana and observed a (black) cat feeding on them.

Although it was not clear whether this cat had killed these birds or was scavenging on them. Given that Galápagos penguin breeding sites are so critical with respect to population stability (Vargas et al. 2007), these observations precipitated a decision to initiate a cat monitoring trip (under the guidance of the Galápagos National Park Service) at this particular site on Isabela Island. The determination of the extent to which cats posed a threat on the penguin population caused by cats was crucial for formulation of an appropriate control strategy in terms of scale and location of implementation (Rollins et al. 2006).

The objectives of this study described in this chapter were, therefore, to

- examine the diet of feral cats at Caleta Iguana so as to determine the predation pressure on penguins.
- evaluate the best methodologies for trapping cats in this area.
- trap cats, if necessary, so as to reduce their population and therefore predation pressure.

6.2 Material and Methods

Study site

The predatory impact of cats on the Galápagos penguin was studied between the 24th of May and the 2nd of June 2005, at Caleta Iguana (S 0.98/W 91.45), the main breeding site of the Galápagos penguin (43 breeding pairs) on Isabela Island.

Located in the south-western part of Isabela Island, Caleta Iguana is an isolated site and located about 36 km from the nearest human settlement.

For data collection, the coastline which made up the breeding area of the Galápagos penguin (0.5 km) was divided into five sections based on distinctive features of the area:

- (I) Camp site (even ground with high vegetation),
- (II) Bahía I (rocky shore formed by basaltic boulders),
- (III) Platform (around 200-300 m in altitude, is relatively flat and dominated by many different plant species),
- (IV) Bahía II and (V) Bahía III (both rocky shores formed by basaltic boulders but separated from each other by a steep cliff).

Feral populations of cats, rats (*Rattus rattus*), pigs (*Sus scofra*) and cattle (*Res taurus*) all occur at Caleta Iguana.

Trapping

Cats were systematically trapped in live-capture Tomahawk traps ($n = 7$) (measuring 80 X 20 X 20 cm) baited with tuna and foothold ($n = 6$) traps. While Tomahawks could be deployed in almost all areas with relatively even ground, foothold traps need to be covered with soil and thus could only be deployed on soft ground. For this reason their deployment could only be undertaken on sandy walking tracks around the camp site as well as on the plateau (this precluded areas of Bahia I, II and III).

All traps were deployed within a 0.5 km range north of the camp site and each location was recorded with a hand-held Garmin 12 CX Global Positioning System (GPS) receiver and mapped using ArcView3.2. Since cats are known to re-use the same walking tracks in their territory, the locations for trap deployment were selected after careful observation of signs of area usage by cats as denoted by spoor or scats.

Traps were prepared daily and deployed between 16:00 and 18:00 to function overnight when cats are most active. We inspected traps in the early morning (between 6:00 and 8:00) daily in the areas I-IV but traps were then closed during the day to prevent heat stress in caught animals resulting from extended periods exposed to high temperatures and insolation.

The crossing to Bahía III (area V) was dependent on the tide and thus only possible once a day. For this reason, both control and renewed deployment was undertaken at the same time.

Trapped cats were euthanised with ketamine hydrochloride.

Cats were described by colour, sexed and weighed to the nearest 100 g with a 5 kg spring balance (Pesola®, Baar, Switzerland). Body length, measured to the nearest millimetre in a straight line from nose to tail tip, was taken using a steel tape. In a subsequent dissection, the reproductive status of females was recorded.

Cat's diet

Diet was determined by examination of the digestive parts of feral cats trapped at Caleta Iguana. Stomachs were cut open along the concave side and intestines were opened along their entire length. Prey items were sorted into prey types (e.g., small mammals, invertebrates, birds) and identified to the lowest taxonomic level. We did not quantify non-prey items such as plant material, bait and parasitic worms. Unmacerated grass blades and shrub leaves were assumed to be consumed as an aid in digestion, a means to eliminate tapeworms in the digestive tract (Neale and Sacks 2001). For each prey type, its frequency of occurrence was recorded and the minimum number of individuals present was estimated from the numbers of unique identifiable parts. The samples were weighed and stored in 98 % ethanol in individual "Ziplok" plastic bags marked with the collection date and location.

Predatory impact of cats on penguins

Two methods were used in order to quantify the rate of penguin predation by cats: 1) direct counts of penguin mortality using carcass deposition rate and 2) an energetic approach.

1) Penguin mortality

To assess current levels of penguin mortality from feral cats, all penguin carcasses found were removed and the cause of death determined wherever possible. This included specific examination for evidence of cat predation by recording penguin body parts that were missing, as well as wounds and the manner in which the carcass had been dismembered. Additionally, the presence of tracks and other evidence at the corpse site were noted. The location of each carcass was recorded with a GPS receiver (see above) and mapped using ArcView3.2.

Measurements of bill length, depth, and width were taken with callipers to the nearest 0.1 mm to determine the sex of the individual (Boersma 1977). Birds were also checked to see if they had been marked with a PIT- (Passive Integrated Transponder) tag in their left leg (birds were individually marked as part of a separate study (Vargas unpublished data)).

2) Energetic model

To evaluate mortality from cats, daily biomass consumption was calculated, based on cat field metabolic rate (Nagy 1987) and an estimation how much of cat diet came from penguins. Figures were scaled up to estimate how many penguins an individual cat needed to consume each month to satisfy field metabolic rates.

Daily consumption of biomass (b) [g] by a feral cat was estimated using the allometric equation (Nagy 1987):

$$b = 3.35 \times (\text{predator weight})^{0.813} \times 2.86/18$$

This equation provides an estimate for the biomass needed to maintain a free-living eutherian mammal for one day. In this formula, 2.86 is included to account for the 65 % water content of seabirds and 18 is the estimated mean metabolizable energy content of the prey in kilojoules of metabolizable energy per gram of dry matter (Nagy 1987).

We used the calculated cat metabolic demand and penguin weight to calculate the mean monthly consumption (n_c) of penguins by cats. Minimum and maximum estimates are from the 95 % confidence limits provided by Nagy (1987):

$$n_c = b \times 30 \text{ days} / 1000 \text{ g/bird}$$

6.3 Results

Trapping

During the study, the seven Tomahawk traps were deployed a cumulative total of 54 times, the six foot-hold traps forty-four times. Five cats were caught in the Tomahawk deployments and two during the foot-hold traps.

Of the seven cats (Tab. 6-1), one was a juvenile male, two were adult males and four were adult females, in the areas I, III and V. One trapped female was accompanied by a young kitten (juvenile, also trapped). Of the four female cats, three were pregnant. Of all cats encountered, all but one were tabby, while one male cat was black. Of all the trapped cats, mean \pm SD body mass (size) was 3.0 ± 0.5 kg (body length 44.5 ± 0.7 cm) for males and 2.4 ± 0.2 kg (body length 43.0 ± 0.0 cm) for females.

All trapped cats appeared to be in good physical condition, although the one black male's head was covered with scars and wounds. No dead cats were found in the controlled area. In one case a black rat was trapped accidentally.

Cats were most often observed by team members near sunset and during the night, only occasionally being seen during daylight. They were least often observed around midday when the ambient temperature was the highest.

The rate of cat sightings did not change over the course of the trip. When cats saw humans they quickly sought cover, using the numerous lava crevices along the coastline. However, at night, cats were detected close to the camp site at distances of up to only few metres.

Tab. 6-1 Information on the cat trapping realised at Caleta Iguana, Isabela Island between 24th of May and 2nd of June 2005.

Trapping			Cat							
ID	Area	Date	Colour	Weight [kg]	Body length [g]	Sex	Age	Diet	Diet [g]	Reproductive status
1	Camp site	26. May '05	tabby	2.65	45	male	adult	empty	~	~
2	Camp site	26. May '05	tabby	1.0	32	female	juvenile	rat	6	~
3	Platform	26. May '05	tabby	2.3	43	male	adult	rat	10	~
4	Camp site	28. May '05	tabby	2.3	43	female	adult	rat	46	pregnant
5	Bahia III	29. May '05	tabby	2.7	43	female	adult	rat	40	pregnant
6	Camp site	30. May '05	tabby	2.5	43	female	adult	rat	89	pregnant
7	Bahia III	30. May '05	black	3.4	44	male	adult	penguin	~	~

Cat's diet

Details of prey eaten by cats and weights of the stomach and intestine contents are listed in Tab. 6-1.

Rat remains were found in all of the samples except in one, and thus formed the major diet component in six of seven cats. No invertebrate prey items such as insects etc. were found. The only other food items found in these samples included tuna and meat from cattle (while the tuna was used as bait in the traps, the beef had been taken from our camp site, having been derived from a hunt of cattle and pigs by the National Park Warden during the day).

Penguin feathers were recovered from the digestive tracts of one cat and represented the only prey item in this sample. Since penguin feathers differ significantly from other bird feathers in colour and size of the feathers and aftershafts, there is no doubt about their correct identification.

Effect of cat predation

Penguin mortality

We observed mortality in seven adult penguins, 6 of which showed evidence of predation by cats: 1) three carcasses were found with the head separated, 2) the breast and the clavícula in all the dead birds were destroyed, 3) carcasses were all found at the same sites, indicating that the predator cached its food as is typical for cats (Stahel and Gales 1987), 4) the cat trapped at that site (no. 7) (Tab. 6-1) provided a stomach sample full of feathers, 5) all the dead penguins were found in Bahía III and thus in a restricted area, 6) in penguins that were freshly depredated the head, spine, part of the skin and legs were left uneaten (Konecny 1987).

Aside from these findings, we found another dead penguin floating in the bay. The condition of this animal did not permit us to determine cause of mortality of this bird.

Although, during this work, we only found penguins at the end of their breeding stage, with mainly big chicks, there was no evidence of chick or juvenile mortality due to predation.

Tab. 6-2 Information on the penguin carcasses found at Caleta Iguana, Isabela Island between 24th of May and 2nd of June 2005.

Carcass-ID	Locality	Date	PIT-tag No.	Physical appearance	Sex	Age	Bill			Wing
							Length [mm]	Width [mm]	Depth [mm]	Length [mm]
1	Bahia III	25. May '05		decomposed		adult	52.7	10.5	16.5	130
2	Bahia III	25. May '05	052-567-269	decomposed		adult	55.8	10.6	16.6	
3	Bahia III	25. May '05		decomposed		adult	55.8	8.4	10.2	
4	Bahia III	25. May '05	041-875-322	decomposed	male	adult	57.6	11.5	19.7	
5	Bahia III	27. May '05		decomposed		adult	56.3	10.0	16.5	
6	Bahia III	27. May '05				adult	56.2	9.6	11.7	150
7	Bahia III	29. May '05	041-827-035	recently dead	female	adult	54.4	10.1	14.8	154

Since all dead carcasses found during our previous visit were removed, it was possible to calculate the time window over which these new dead birds had been depredated. Using this information we estimated the total number of penguins killed per month at this colony at 6.6.

Based on the annual census data of 2006 (Jiménez-Uzcátegui et al. 2006), the penguin population in the Caleta Iguana area comprises 188 birds (183 adults, 5 juveniles) and thus, cats would cause an increase in the mortality rate of the penguin population of up to 42 % (43 % only adults) per year.

Energetic model

Using the energetic model, a 2.6 kg (mean of our data) cat needs to consume 318 g of food per day (minimum 184 g , maximum 438 g).

The field observations indicated that cats ate around 60 % of the weight of a penguin, leaving behind bones, feathers, skin and the head. Since a Galápagos penguin weighs on average 2.0 kg, a cat consumes ~ 1.2 kg of tissue per penguin.

Thus, a cat eating exclusively penguins needs to consume one penguin every four days or 7.5 birds per month to meet its metabolic requirements. Based on the penguin population estimates from the last census trip (Jiménez-Uzcátegui et al. 2006), a single cat could be responsible for an increase in penguin mortality of 47 % (49 % only adults) per year at Caleta Iguana.

6.4 Discussion

The principal threats to seabirds breeding in the Galápagos islands are human disturbance including tourism, commercial fisheries and marine pollution (Cepeda and Cruz 1994). However, a recurrent past and present, problem relates to introduced alien mammals.

Predatory impact of cats on penguins

This study was a first attempt to evaluate the predatory impact of cats on the Galápagos penguin at their main breeding site of Caleta Iguana, in the southwest of Isabela Island. The number of dead penguins found shows that in a very short time an even small number of cats can lead to dramatic reductions in annual penguin population. The potential threat to the penguin's population viability on Isabela Island is, therefore, serious.

Using data from the carcass monitoring to estimate penguin mortality rates, it was possible to calculate that seven penguins were predated per month from cats. The energetic approach indicated a monthly mortality rate of eight penguins per cat. The similarity in these two independent mortality assessments suggests that one cat was responsible for killing all the penguins. This assumption is supported by the fact that after kill-trapping this individual, predation at Caleta Iguana stopped. However, it still remains possible that the predator(s) responsible for the mortality left the area, or that predation is sporadic, so there is no guarantee that the trapping was the reason for the cessation in predation.

In the assessment of the mortality rate caused by cats, sources of possible experimental bias should be considered, for example, the assumption (based on the information obtained from the diet samples) that the cat preyed exclusively on penguins and thus satisfied 100 % of its energy needs via this food source.

Therefore, the mortality estimates from this calculation should be considered as an upper limit of mortality caused by a single cat.

There are several estimates for the daily food requirements of feral cats available in the literature (see Keitt et al. 2002), and our estimates of 318 g day⁻¹ falls somewhere in the middle of these. Using the calculated minimum (184 g) and maximum (438 g) values for the cats' daily food requirement (see results 1.3) the mortality rate at Caleta Iguana accordingly would range between 29.5 % and 71.8 %.

Although there are shortcomings to the approach used and inaccuracies present in these calculations stemming from a number of assumptions (e.g., the use of literature values) to generate the predatory impact of cats on the penguin population, the derived information should (1) stimulate discussion on the effects of introduced predators on native avian island species, and (2) provide basic data that are of use for the managers of the Galápagos National Park to establish a monitoring and control programme of cats at Caleta Iguana, Isabela Island.

Cat diet

There are many factors that affect the extent of predation on seabirds at their colony and it is important that land managers understand the dynamics of differing scenarios on the survival of the impacted birds (see Moors and Atkinson 1984, Courchamps et al. 1999).

1) The availability of prey throughout the year can greatly affect how many cats survive from year to year. Although there are two main breeding peaks in the annual cycle of Galápagos penguins, breeding penguins can be found at the colony year-round (see chapter 3) and thus may provide a constant prey source that may help maintain the cat population.

2) Feral cats at Caleta Iguana are not limited to using Galápagos penguins as a prey source and data on the diet composition of the seven trapped cats suggests that rats are the most important food item. This likely reflects the high abundance of these rodents in the environment, this phenomenon having been described by a number of authors (Coman and Brunner 1972, Konecny 1987). Nonetheless, although generally opportunistic (Bonner 1984, Pearre et al. 1998), feral cats may also feed on select species disproportionately (Konecny 1987) choosing some food items preferentially over others (for ref. See Konecny 1987) almost irrespective of abundance. Thus, although there may be some taxonomic bias towards vertebrates, and especially mammals, prey preference is likely determined, at least in part, by abundance, accessibility, ease of handling, energy contained in prey, and concentrations of some nutrients. Abundance will directly affect the encounter rate and the information of a search image for prey species. Accessibility and ease of handling involve roosting places, daily habits, size, strength and defensive behaviour which will determine whether a capture attempt can be made and the net benefit of capturing a prey type. Therefore, cats appear able to assess the net energy reward in a prey species (total calories less capture expenses) and assess the potential net benefit of a capture attempt on larger prey (Jones 1977, Jaksic et al. 1993, MacDonald and Rogers 1984). Thus, related to their size, the reward to catch a penguin is proportionately much greater than, for example, that gained by capture of rodents.

3) Although Leyhausen (1979) stated that cats cannot kill anything larger than themselves, cats have been reported as predators (or scavengers) on penguins in the past (Jones 1977, Van Aarde 1980, Karl and Best 1982, Berruti 1986, Alterio and Moller 1997, Massaro and Blair 2003), albeit taking mainly chicks and juveniles rather than adults. The differential predation on exclusively adult Galápagos penguins found in this study could be partly explained by the bird's smaller size compared to the other penguin species (Williams 1995) and is thus, perhaps simply easier to catch. However, in the Galápagos islands the defensive behaviour of many species has been reduced or lost and cats have been observed attacking frigate birds (*Fregata* spp.), pelicans (*Pelecanus* spp.), and flightless cormorants (*Phalacrocorax harrisi*), all of which are larger than cats (Konecny 1987).

Also, for the cat, other factors may have played a role to prey-switch. For instance, although juveniles are likely more defenceless and less aggressive than adults, at night juveniles sit on rocks close to the water. When approached by a cat or some potential danger, they are likely to retreat to the sea for safety. Adults, however, return at night to their nest-sites formed of lava crevices and caves, even when they are not breeding, and thus may be encountered fairly predictably. Although Yorio and Boersma (1994) stated that covered nests present a formidable defence against most predators, once the nest is detected Galápagos penguins are likely easy prey for cats since the birds cannot leave the vicinity with exposing themselves. When attacked, *Spheniscus* penguins bite powerfully (Wilson pers. comm) and can inflict considerable damage (pers. observation). The marks and wounds observed on the black cat's head likely stem from predation on penguins. This animal, which was the largest of those trapped by 0.5 kg, would presumably have been the best equipped to capture penguins. In this regard it is notable that Berruti (1986) found in his study on Dassen Island, South Africa that cats (> 3 kg) ate penguins, rabbits and mice.

4) When both bird and mammal prey are available, it is believed that the domestic cat diet will include mainly mammals (Konecny 1987, Nogales et al. 1992). Indeed, in some island ecosystems, cats may maintain rodent populations at low levels (Courchamp et al. 1999). However, because cats may prey upon endangered species, it is believed that, in some ecosystems at least, the beneficial effects of reducing the rodent population could be outweighed by the damage done to the endemic species (Fitzgerald et al. 1991). Strategies to reduce cat populations may cause a commensurate increase in the number of rats to the detriment of the ecosystem (Courchamp et al. 1999). This process, termed "mesopredator release" (a sudden burst of mesopredators, once the superpredator pressure is suppressed) applies well for many insular foodwebs. Conversely, the fluctuation in rodent population (e.g. due to eradication, natural causes or seasonal variation) first might induce cats, as an opportunistic predator, to switch prey, resulting in a dramatic increase in predation pressure on threatened endemic species (Davis 1957, Moors and Atkinson 1984).

The effect of alien invasive species may be simple or very complex, especially since a large array of invasive species, mammals and others, can be present simultaneously and interact among themselves, as well as with the native species. Therefore, the influence of introduced predators can cascade through trophic levels and severely change community structures. Recently, functional models have linked introduced predators to both native

and exotic prey, suggesting that the introduction of a novel prey can indirectly cause the extinction of native prey species (Courchamp et al. 1999, 2000). This form of apparent competition, termed hyperpredation, occurs when a native prey species (e.g., penguin) experiences an increase in predation pressure caused by an introduced predator (e.g., cat) that is sustained by an abundant exotic prey (e.g., rat). Thus, although eradication of cat populations is desired in many cases, paradoxically, in some particular situations, the presence of a controlled population of cats might be, at least temporarily, more beneficial to their endemic prey than its eradication. Such is the case on many islands where rodents have also been introduced (Courchamp et al. 1999).

Implications for penguin conservation

Although we can assume that a large proportion of the cat prey is likely to consist of rats, we do not know why the cat prey-switched to penguins or at least supplemented its typical diet with an alternative prey item. The numbers of penguins killed by presumably this one cat was much greater than the penguin population could have sustained, and interactions such as this show how quickly cat predation may have resulted in a substantial short-term population decline and have been reflected in other studies (Estes et al. 1998, Roemer et al. 2001, Roemer et al. 2002).

The reproductive value of adults for maintaining the population stability is far greater than that of juveniles or chicks (PHVA 2005). During the PHVA (Population and Habitat Viability Analysis) workshop held in the Galápagos islands in 2005, a computer simulation (Vortex) showed that an increase in adult mortality in the short- or long-term could reduce the reproductive success and cause an irreversible impact for the population, eventually leading to the extinction of this species in less than 100 years (Vargas et al. 2007).

Although the annual penguin census shows a relative stable and even slightly increasing population trend over the last years (Jiménez-Uzcátegui et al. 2006), the vulnerability of this population to even small changes in mortality rates is well known (Weimerskirch et al. 1992, Crawford et al. 1999, Ratcliffe et al. 2002) and these results reveal that the situation of the Galápagos penguin is more precarious than previously assumed. Clearly, greater attention should be paid to the impact of introduced species that are increasingly affecting this species.

Obviously, the best thing is to prevent species introduction in the first place. Unfortunately, a great number of introductions already exist, forcing us to adopt an appropriate strategy to minimise or alleviate problems caused by introduced species: exclusion, control and eradication (Courchamp et al. 2003). The three major approaches all involve reduction of the numbers of the animals causing problems. Globally, feral cats have been removed from at least 48 islands, however the majority of these islands are small ($< 5 \text{ km}^2$). The largest successful eradication campaign took place on Marion Island (290 km^2), but cats have been successfully removed from only 10 islands $\geq 10 \text{ km}^2$ (Nogales et al. 2004)

Although eradication of all cats on Isabela Island would be the best management strategy, and should be a conservation priority (Tershy et al. 2002, Keitt and Tershy 2003), it is currently an economic, political, and social impossibility. Isabela island is the largest and probably the topographically most complex of all the Galápagos islands (4588 km^2).

Feral cats in these remote areas are solitary, elusive, hard to capture, and inhabit areas that are difficult to survey, making the application of traditional methods to understand population dynamics and identify source population problematic. Dispersal patterns of feral cats and the inaccessibility of remote locations also make the effective management of feral cat population logistically difficult (Rollins et al. 2006). Furthermore, the presence of domestic cats in Villamil, Isabela island, may be acting as a source population from which feral cats can originate (Donlan and Keitt 1999, Abdelkrim et al. 2005, Hansen et al. submitted). Thus, the success of control programmes will require and depend on the participation of the local community in a collaborative approach to limit the number of domestic animals.

A control programme therefore, might be the best strategy to regularly reduce the cat population on Isabela island. However, such programmes are not definitive requiring constant and/or repeated actions, to keep the population at low density after the initial decline.

We strongly recommend the following priority specific conservation actions:

- The establishment of permanent programmes for the monitoring of penguin mortality and control of cats at the main breeding sites of the Galápagos penguin on Isabela Island, supported by applied research on cat density, movement and migratory patterns, as well as dietary preferences to better understand the predation-prey dynamics of this species and thus, to refine and maximise control strategies.
- An intensified control of the cat population in the islands' villages to avoid reinvasion of feral cats.

7 General conclusions

Natural sciences play a fundamental role in the conservation of species, habitats and ecosystems, as they help to understand fundamental principles of life history, to predict population variation, and to identify conservation demands. Thus, scientific research is crucial for conservation practice, as no effective long-term conservation strategies and management plans can be formulated and implemented without this knowledge.

The Galápagos penguin (*Spheniscus mendiculus*) is one of the endemic birds in the Galápagos archipelago and, with a population of around 2000 individuals, one of the rarest bird species in the world (Birdlife International 2005). The penguin's small population, restricted distribution, and vulnerability to ever-increasing human threats in the form of tourism, fisheries and national and international shipping, combined with severe population fluctuations due to natural marine perturbations such as the El Niño - Southern Oscillation, led to its classification as endangered by BirdLife International in 2000 and to its inclusion in the IUCN (International Union for the Conservation of Nature and Natural Resources) Red List of Threatened Species (Boersma et al. 2007, BirdLife International 2000, 2005).

While all *Spheniscus* penguins are temperate in distribution and occur in much warmer climates than the other penguin genera (Williams 1995), the Galápagos penguin constitutes the northernmost end of penguin distributions (with even some breeding activities occurring in the northern hemisphere).

Although located on the equator, and thus exposed to high insolation and an excessive temperature regime on land, the Galápagos penguin's distribution is expected to be strongly associated with cold and nutrient-rich waters that provide a high density of food (chapter 1). Accordingly, approximately 98 % of the Galápagos penguin's population is found in the western part of the archipelago along the western coast of Isabela and around Fernandina Island, which coincides with the primary areas of upwelling and the most productive waters of the archipelago caused by the Equatorial Undercurrent (EUC, also known as Cromwell Current) (Palacios 2004, Jiménez-Uzcátegui et al. 2006). While generally these oceanographic conditions provide a high density of prey (Palacios 2003), this upwelling system is regularly affected by frequent periods of the anomalous climatic conditions of the El Niño phenomenon (ENSO = El Niño-Southern Oscillation) (Palacios et al. 2006, Vargas et al. 2006, 2007), where the nutrient-rich surface waters are replaced by warm, nutrient-poor water masses (Colling 2001). Oceanographic conditions have a significant influence on distribution and availability of marine resources (e.g. Castillo et al. 1996), and are known, to reduce primary productivity and disrupt marine food webs (Arntz and Fahrbach 1991). Epipelagic schooling fish such as Pacific anchoveta (*Cetengraulis mysticetus*) and round herring (*Etrumeus teres*) migrate away from the Galápagos archipelago (García et al. 1993, Grove and Lavenberg 1997), which make them

inaccessible to penguins as well as to other land-based marine animals that depend on this prey. Now, food availability has an important influence on bird biology (Lack 1955), as it affects activity, distribution, energetics, competitive abilities, breeding success and survival (e.g., Furness and Monaghan 1987, Montevecchi et al. 1988, Garthe et al. 1999) and indeed, all seabirds ultimately rely on a predictable food availability within their species-specific foraging range (Lack 1968, Weimerskirch et al. 1994). Seabirds exhibit huge variation in their foraging ranges, with the range being largely dependent on cost of transport. Albatross and petrels, for example, can cover hundreds of kilometers on their foraging trips (Weimerskirch et al. 1993, Waugh et al. 2002) exploiting food sources distant from their breeding sites (Davis and Cuthbert 2001) while penguins are much more restricted in their foraging range, generally feeding within a few tens of km of their nests (chapter 4, cf. Wilson 1985). Since the cost of swimming is more expensive and slower than flying (Pinshaw et al. 1977, Schmidt-Nielsen 1999), flightlessness in penguins imposes limits on their foraging capabilities compared to volant seabirds and thus foraging ranges are correspondingly reduced (Wilson 1985). This, coupled with the high variability in the oceanographic environment around Galápagos caused by the frequent recurrence of El Niño events, suggests that the Galápagos penguin should have a breeding and foraging biology adapted to deal with the temporal and spatial variation in oceanographic conditions which affects prey availability (Boersma 1974). Clues as to how the Galápagos penguin might deal with its environment might be given by examination of the biology of other *Spheniscus* penguins (Magellanic *S. magellanicus*, Humboldt *S. humboldti* and African penguin *S. demersus*), species that have been assumed to be similar in a great many ways (cf. Wilson & Wilson 1995, and refs therein). However, the paucity of information on the foraging ecology of the Galápagos penguins (chapter 4) means that this supposition has never been demonstrated.

This thesis outlines several important aspects of the marine ecology of the Galápagos penguin which should help to understand how it survives in its particular habitat. Within this study four main questions were addressed:

- Do Galápagos penguins forage in predictable oceanic habitats, characterised by specific oceanographic features and does habitat use change regionally?
- How is penguin's diet composition related to foraging behaviour and oceanographic parameters?
- How is the penguin's breeding activity, in terms of locations and breeding patterns, related to oceanographic conditions?
- What are the main current threats faced by the penguin population in their marine and terrestrial environments?

To answer the questions raised in this thesis, the three-dimensional habitat use of the Galápagos penguin at sea during chick-rearing periods was investigated and characterised by regional oceanographic parameters of their environment. These results were complemented by information obtained by studying diet preferences as well as investigating the breeding activity of the penguins.

1) Distribution at sea and habitat use

The use of miniaturised monitoring technology (GPS-TD recorders) delivered evidence that the dispersal pattern of Galápagos penguins during chick-rearing ranges less than previously expected. Birds moved an average of no more than 5.2 ± 4.9 km (range 1.1 - 23.5 km) away from the nest. On all recorded tracks the device-equipped penguins left and returned along the same track, concentrating foraging in a strip of sea of only up to 1.0 km of the shore.

Typically, foraging trips of other penguin species follow a so-called 'looping' course which usually entails movement directly away from the foraging site and away from the coast (e.g. Culik and Luna-Jorquera 1997, Barlow and Croxall 2002, Ainley et al. 2004, Petersen et al. 2006) which makes the coast-hugging behaviour observed in Galápagos penguins particularly unusual.

While Magellanic penguins, during chick-rearing, forage more than 150 km from the colony), Humboldt penguins tend to stay in 90 % of their foraging time within a 25 km radius around their colony. Taking the farthest range recorded by a Galápagos penguin (23.5 km) the foraging range of a Humboldt penguin does not appear to be very different. While Magellanic penguins are described as offshore foragers, our tracking results (chapter 4), as was expected, are consistent with the inshore nature described for foraging Humboldt penguin (Davis and Renner 2003). However, in contrast to Humboldt penguins that radiate over a semi-circle during foraging (Boersma et al. 2007), the observation that none of the device-equipped Galápagos penguins ranged farther than 1.0 km from the nearest coast indicates that the actual area of sea that they utilise is much smaller than their range would suggest. Since all the equipped Galápagos penguins stayed within the 50 m bathymetry line close to the coast, this behaviour may be explained by the regional bathymetry: Magellanic penguins, that breed along the Argentinian coast forage over the Patagonian shelf, one of the broadest continental shelves in the world where the shelf break (200 m isobath) is more than 400 km from shore. Productivity and prey abundance are primarily determined by widely-distributed tidal and estuarine fronts, which vary seasonally (Acha et al. 2004, Boersma et al. 2007). In contrast, along the coast of Chile and Perú, where the Humboldt penguins are found, the continental shelf is extremely narrow and thus provides only a relatively fixed region with highly productive upwelling waters (Acha et al. 1991). The Galápagos islands, formed from the emerging tips of submarine volcanoes, rise from a very shallow platform, that drops off down to 2000 and 3000 m within 1.0 km from the coast in the western part of the archipelago. Thus, if Galápagos penguins at their breeding sites, want to stay on the shelf they need to stay very close to the shore.

The diving patterns the Galápagos penguin differ considerably from those of its congeners. Although the deepest dive recorded was 52.1 m, birds spent most of their time underwater at shallow depths (< 6 m). Based on allometric regressions derived from other penguin species, those dive depths were less than those expected. Applying the maximum values for movement to calculate space use, the Galápagos penguin exploits therefore a maximum volume of water of < 1.4 km³, which is almost 90 times less than that predicted for its mass. The bird thus utilises only a small portion of the total potentially available upwelling area within the Galápagos Archipelago.

It should be noted that this study only reports data on the foraging behaviour of breeding birds (a necessity dictated by the technology used). A more complete picture is needed using data from non-breeding birds although foraging parameters are likely to be similar (cf. Rand 1960).

2) Penguin's diet composition in relation to foraging behaviour and oceanographic parameters

The diet of the Galapagos penguin was found to be mainly composed of neritic, pelagic species typical of upwelling systems, dominated by Engraulids (here represented by Pacific anchoveta *Cetengraulis mysticetus*). However, while other *Spheniscus* penguins are known to feed on adult schooling fish such as anchovies (*Engraulis* spp.), pilchards (*Sardinops* spp.) ≥ 100 mm (Herling et al. 2005), this study provides strong evidence that Galápagos penguins feed preferentially on young fish or even larvae (≤ 30 mm). Since larvae and juvenile phases of this fish species inhabit the surface inshore waters and migrate offshore when adult, this finding corresponds well with the results of the Galápagos penguin's foraging behaviour (chapter 4).

However, several studies on *Spheniscus* penguins show that feeding preferences may differ considerably on a temporal and spatial scale (Crawford and Shelton 1981, Randall and Randall 1986, Wilson et al. 1989b, Wilson et al. 1995a, Frere et al. 1996, Scolaro et al. 1999, Herling et al. 2005). For this reason, in an environment like the Galápagos islands where "average" conditions being less common (Trenberth 1997), considerable variations in diet composition during seasons, years and regions can be expected.

Unfortunately, due to the precarious population status of the Galápagos penguin (see general introduction and details given in chapter 5) as well as due to time restrictions, it was not possible to investigate either temporal or spatial differences in diet of this species. A continued monitoring of the diet of Galápagos penguins would help promote better understanding of the role of this species in its marine environment and would do much to alert authorities to changes in the marine ecosystem on which these birds depend, also helping to improve fisheries management in avoiding undue competition between man and penguins (e.g., Anderson et al. 2003)

3) Breeding activity related to oceanographic conditions

Within this study it could be shown that the Galápagos penguin's breeding habitat is strongly associated with cold and nutrient-rich waters within the archipelago.

Since the proximity of the food supply is crucial for flightless birds, particularly during breeding when birds are central place foragers (*sensu* Orians and Pearson 1979), this had been expected. To compensate for the high costs of getting the food, as well as to allow them to catch enough food to raise their chicks successfully (Croxall and Davis 1999), penguins must have a predictable food supply within their limited foraging ranges (Lack 1968, Wilson 1985, Weimerskirch et al. 1994).

In addition to spatial requirements, to maximise reproductive success, birds are also expected to adjust the timing of breeding to when environmental conditions are favourable (Lack 1954).

Thus, the breeding frequency and time of year at which it occurs are important aspects of avian reproductive strategy (Perrins and Birkhead 1983, Löfgren 1984, Paredes et al. 2002).

The extremely variable and unpredictable oceanographic conditions in the eastern Pacific caused by the frequent occurrence of El Niño events (Barber and Chávez 1983, Tovar and Guillén 1987, Valle et al. 1987, Duffy 1990, Vargas et al. 2006) probably exerted strong selection pressures on breeding and survival strategies in this area. A marked seasonal absence of breeding patterns including its ability to breed rapidly and opportunistically when conditions are favourable has been shown to be a characteristic feature in Humboldt penguins' population (Paredes et al. 2002) and were to be expected for the Galápagos penguin.

In this thesis we could show that, although breeding attempts occurred almost throughout the year, Galápagos penguins had two marked peaks of egg laying periods, one during March to May and one during July to September. The region in the western part of the archipelago undergoes (except in an El Niño years) a seasonal increase in phytoplankton biomass in the second part of the year (from June to December) which coincides well with the second period of egg-laying while the first egg-laying peak corresponds with the strengthening and shoaling of the EUC in April (Lukas 1986, Johnson et al. 2002).

Although in the two subsequent years of the study, this pattern was roughly in phase for both single and double brooders, a slight shift was detectable with an earlier egg-laying date for the second clutch in the second year. Such shifts in breeding patterns could have resulted from low breeding success from the first clutch that subsequently led to a replacement clutch (Reilly and Balmford 1975, Randall and Randall 1981, Woodell et al. 1984, La Cock and Cooper 1988, Bost and Jouventin 1990, Zavalaga and Paredes 1997). However, as birds are expected to adjust the timing of breeding to when conditions are most favourable, the shift in breeding pattern could also suggest that the penguin's behaviour was dictated by local oceanographic features and thus was a (flexible) response to the available food supply.

Data on breeding patterns also showed regional differences, which could be an indication of local variability reflected by differences in oceanographic conditions in the western archipelago which might augur for penguin response to environmental conditions on a particularly small scale. It should be noted, though, that the African Penguin also shows variability in breeding peaks according to locality and availability of prey (Wilson 1985, Crawford and Shelton 1984).

In summary, the breeding biology of the Galápagos penguin seems to be well adapted to its unpredictable environment (Boersma 1977) and their breeding strategy seems to have diverged little from that observed in Humboldt penguins in Perú (Paredes et al. 2002).

4) Current threats faced by the penguin population in their marine and terrestrial environment

Marine

Considering penguin breeding sites in light of the Galápagos Marine Reserve (GMR) zoning system raises interesting concerns. Although the nest themselves are located on the terrestrial portion of the coastline, this study found 73 % of the breeding sites to be surrounded by zone 2.3. of the GMR (designated for conservation, extractive use and non-extractive activities/fisheries zone). Thus, while most penguins are recorded in the areas set aside for fisheries, only few breeding Galápagos penguins are afforded the highest protection levels of the GMR. The implications for penguin conservation may be significant: Even though nesting penguins would not feed in this adjacent coastal area, by all means they need to pass this zone on their way to their foraging sites and while returning to their nest site.

The fishing industry, in particular, is potentially capable of harming penguin populations due to entanglement and drowning in nets (Simeone et al. 1999, CDF unpubl. data). Indeed, local fishing boats operating in inshore waters in the western part of the archipelago are documented as incidentally drowning Galápagos penguins due to floating nets and illegally-used bait fisheries in gill nets (Cepeda and Cruz 1994).

Fortunately, and in contrast to Chile, anchovies and pilchards are not commercially harvested in the Galápagos islands and thus it seems unlikely, that penguins currently compete with man for food (Simeone et al. 1999, Darby and Dawson 2000). However, recent plans to establish longline fisheries, even though proposed as “green” longlining, in the Galápagos islands raises additional serious concern. Aside from the well-known impact of by-catch caused by this technique (Weimerskirch et al. 2000), in the case of Galápagos penguins, it is likely that an increasing demand for bait fish will dramatically increase inshore bait fisheries with all its associated problems.

Since current breeding sites are important areas for penguins with regard to population stability (Vargas et al. 2007), potential threats in their marine environment are serious. Based on the spatial distribution of chick-rearing foraging penguins, we would strongly recommend that a fishery exclusion zone be set up to a distance of 24 km in each direction from a colony along the coast and extending out to sea for 1.5 km.

Terrestrial

The most obvious past and present threat to the Galápagos endemic fauna is that of introduced mammals (Cepeda and Cruz 1994). As part of this thesis, the predatory impact of cats (*Felis catus*) on the Galápagos penguin population at its main breeding site was investigated. This work indicated that one cat was responsible for an increase in adult mortality of 49 % year⁻¹ at this site.

Although the annual penguin census shows a relatively stable, and even slightly increasing, population trend over the last nine years (Jiménez-Uzcátegui et al. 2006), the vulnerability of this population to even small changes in mortality rates is widely accepted (Weimerskirch et al. 1992, Crawford et al. 1999, Ratcliffe et al. 2002, Vargas et al. 2007) and my results reveal that the situation of the Galápagos penguin is even more fragile than

previously assumed. Greater attention should be paid to the impact of introduced species that are increasingly affecting this species.

Outlook

Marine reserves and National Parks are valuable tools for marine biodiversity conservation (Hyrenbach et al. 2000). The suitability of these systems, however, depends on the requirements of the species to be protected (Boersma and Parrish 1999, Hyrenbach et al. 2000). Regardless of which of these model is appropriate for the conservation of a particular species, the design of effective conservation measures requires an understanding of the species' use of the marine (and terrestrial) environment.

Despite all the shortcomings in this thesis associated with small data sets, logistic and financial difficulties, the presented work delivers a unique dataset to help better understand the Galápagos penguin in its marine ecosystem and stimulate discussion on appropriate conservation measures. The worth of such data is particularly high since previous information on the marine ecology and life history of the Galápagos penguin was rare and anecdotal.

This project provides critical information on the penguins' use of the Galápagos Marine Reserve (GMR) which will be used to help the managers of the GMR to design the layout and protection levels of the zonation system for the reserve. In addition, the findings will assist in the formulation of long-term conservation strategies and management plans for the Galápagos Penguin, with the aim of preventing the extinction of this remarkable species.

During this project it became very obvious to me that research into nature conservation is based on far more than just biology and geoscience. It also includes engineering, economics, politics and human social science. In the main it requires a broad and effective translation of knowledge and conservation needs to both local populations and the general public so as to enhance widespread awareness and foster collaboration to e.g. discourage illegal fishing.

For the future, I believe the protection and preservation of biological diversity requires serious ongoing efforts and commitment as a shared mission - not only for the local community but on an international scale.

8 References

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9 Annex

9.1 Abbreviations

BS	Breeding success
CBSG	Conservation Breeding Specialist Group
CDF	Charles Darwin Foundation
chl	Chlorophyll
CI	Caleta Iguana, Isabela Island, Galápagos
e.g.	exempli gratia (for example)
ENSO	El Niño Southern Oscillation
EUC	Equatorial Undercurrent
GC	Gas chromatograph
GMR	Galápagos Marine Reserve
GNPS	Galápagos National Park Service
GPS	Global Positioning System
GPS-TD	Global Position System-Temperature depth logger
IAEA	International Atomic Energy Agency
i.e.	id est (that is)
ITCZ	Intertropical Convergence Zone
IUCN	International Union for the Conservation of Nature and Natural Resources
LM	Las Marielas, Galápagos
PDLP	Playa de los Perros, Isabela Island, Galápagos
PHVA	Population and Habitat Viability Analysis
PIT	Passive Integrated Transponder
PMB	Participatory Management Board
PVA	Population Viability Analysis
SD	Standard Deviation
SE	Standard Error
SEC(N)	South Equatorial Current (northern branch)
SEC(S)	South Equatorial Current (southern branch)
SPC	Secretariat of the Pacific Community, New Caledonia
SST	Sea Surface Temperature
V-PDB	Vienna- Pee Dee Belemnite (standard reference)
WGS	World Geodetic System

9.2 List of figures

Fig. 1-1 The <i>Spheniscus</i> penguins.....	1
Fig. 2-1 Map of the Galápagos archipelago with the names of the main islands	5
Fig. 2-2 Map of the Galápagos Marine Reserve zonation system. The zones are in blue: 2.1 fully-protected 'no-take'area [6.3 %], in green: 2.2 non-extractive use areas [10.8 %], in red: 2.3 regulated extractive uses [78.2 %], in black: 2.4 special zones nearby the inhabited port areas [4.7 %]	9
Fig. 2-3. Number of penguins counted between 1970-2005 in the Galápagos archipelago (blue) on Isabela (black), on Fernandina (red) and on the smaller islands (Floreana, Bartolomé, Santiago, Sombrero Chino and Rábida surveyed since 1993; green) (Vargas et al. 2005b).....	12
Fig. 3-1 Map of the Galápagos archipelago. Breeding sites of the Galápagos penguin, <i>Spheniscus mendiculus</i> found in the Galápagos archipelago between 2003 and 2006 are indicated by red dots	17
Fig. 3-2 Location of nesting sites (indicated by black circles) related to the zoning system of the Galápagos Marine Reserve. The zones are in blue: 2.1 fully-protected 'no-take'area [6.3 %], in green: 2.2 non-extractive use areas [10.8 %], in red: 2.3 regulated extractive uses [78.2 %], in black: 2.4 special zones nearby the inhabited port areas [4.7 %].....	19
Fig.3-3 Phenology of egg-laying by Galápagos penguins at the main breeding site Caleta Iguana for two different breeding categories (single brooders and double brooders) in a) 2004 and b) 2005.....	20
Fig.3-4 Comparison of time of egg-laying (month) by Galápagos penguins for double brooders at the breeding sites Caleta Iguana (CI) and Las Marielas (LM) in 2004.....	21
Fig. 3-5 Inter-annual comparison (2004 - 2005) of time of egg-laying (month) by Galápagos penguins at Caleta Iguana in two different breeding categories (single and double brooders)	21
Fig. 3-6 Distribution of Galápagos penguin egg-laying for first and second laid clutches in a) 2004 and b) 2005.....	22
Fig. 4-1 Upwelling area of the Galápagos islands showing the distribution of the Galápagos penguin (red dots) based on penguins surveyed in September 2005 in relation to direction of major flows and ramifications of the Cromwell Current (arrows) and bathymetry. Oceanographic features were adapted from Houvenaghel (1984). The black dots show the three study sites Caleta Iguana (CI), Playa de los Perros (PP) and Las Marielas (LM) where penguins were equipped with GPS-depth loggers.....	34

Fig. 4-2 (a) Maximum distances moved by penguins (measured in straight line) from the nest at Caleta Iguana (CI), Playa de los Perros (PP) and Las Marielas (LM). Note that bird PP-19 travelled nearly five times farther than the overall mean. (b) Maximum distance moved from shore by 20 penguins at Caleta Iguana (CI) and Playa de los Perros (PP)37

Fig. 4-3 Examples of movements of penguins at (a) Las Marielas (one bird) (b) Playa de los Perros (two birds) and (c) Caleta Iguana (two birds). Also showing bathymetry39

Fig. 4-4 (a) Mean percentage time spent per metre water depth by male (dark bars) and female (white bars) Galápagos penguins. The insert shows relationships for 5 to 25 metres in greater detail (b) shows the mean cumulative (percentage) time spent with increasing water depth for male (filled circles) and female (white circles) Galápagos penguins. Bars show SE 40.....40

Fig. 4-5 Relationship between maximum foraging range and body mass of 13 species of penguins provisioning small or medium chicks. Note that the likelihood of species approaching a maximum foraging range will depend critically on the sample size and that conditions determining actual foraging range will vary accordingly to locality and circumstance so that values can only be considered to be approximate: Foraging range data from Ainley et al. (2004), Sadleir and Lay (1990) (Adelie penguin), Ancel et al. (1992) (Emperor penguin), Barlow and Croxall (2002) (Macaroni penguin), Boersma et al. (2002) (Magellanic penguin), Collins et al. (1999), Norman (1992) (Little penguin), Culik and Luna-Jorquera (1997) (Humboldt penguin), Hull et al. (1997) (Royal penguin), Jouventin et al. (1994), Pütz et al. (1998) (King penguin), Lescroel and Bost (2005) (Gentoo penguin), Schiavini and Rey (2004) (Rockhopper penguin), Petersen et al. (2006) (African penguin), and mass data from Williams (1995). Two values are shown for the King penguin since the literature indicates considerable variation for this species (Charrassin and Bost 2001)42

Fig. 4-6 (a) Relationship between the putative foraging area available to different penguin species hunting for small or medium chicks as a function of body mass (for calculations see text). The Galápagos penguin is denoted by the dark circle, other penguin species are indicated by following numbers: Little penguin = 1, Rockhopper penguin = 2, African penguin = 3, Chinstrap penguin = 4, Humboldt penguin = 5, Adelie penguin = 6, Royal penguin = 7, Macaroni penguin = 8, Magellanic penguin = 9, Gentoo penguin = 10, King penguin = 11, Emperor penguin = 12. (b) Relationship between the foraging volume available to different penguin species as a function of body mass (for calculations see text) – the Galápagos penguin is denoted by the dark circle. Maximum depth data derived from references given in (1) Montague (1985), (2) Tremblay et al. (1997), (3) Wilson (1985b), (4) Mori (1997), (5) Taylor et al. (2004), (6) Arai et al. (2000), (7) Hull (2000), (8) Croxall et al. (1993), (9) Walker and Boersma (2003), (10) Robinson and Hindell (1996), (11) Pütz and Cherel (2005), (12) Kooyman and Kooyman (1995) (c) Ratio between the mass-specific volume of sea available for foraging for different penguin species and that available to the Galápagos penguin (dark circle).....45

Fig. 5-1 Mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ (+/-SE) values and samples sizes of different tissues of the Galápagos penguin52

Fig. 5-2 Organic and inorganic $\delta^{13}\text{C}$ in penguin's eggshells52

9.3 List of tables

Tab. 3-1 Breeding sites and locations of the Galápagos penguin, number of active nests and nest type found in the Galápagos archipelago between 2003 and 2006.....18

Tab.3-2 Habitat types related to numbers of nests and breeding sites.....18

Tab.3-3 Numbers (percentages) of breeding sites and active nests as related to the zoning system of the Galápagos Marine Reserve.....19

Tab. 3-4 Breeding success (BS) in [%] in the different breeding categories (single brooders and double brooders) at Caleta Iguana over two years (2004 and 2005). NA = value not available22

Tab. 6-1 Information on the cat trapping realised at Caleta Iguana, Isabela Island between 24th of May and 2nd of June 200564

Tab. 6-2 Information on the penguin carcasses found at Caleta Iguana, Isabela Island between 24th of May and 2nd of June 2005.....65

Description of the individual scientific contribution to the multiple-author paper

The forth chapter of this thesis has been accepted as a manuscript to a scientific journal with multiple authors. This serves as a clarification of my personal contribution on this publication:

Chapter 4: Space use by foraging Galápagos penguin, *Spheniscus mendiculus* during chick-rearing

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Erklärung

Hiermit erkläre ich, dass die vorliegende Dissertation selbstständig von mir angefertigt wurde. Die Dissertation ist nach Form und Inhalt meine eigene Arbeit und es wurden keine anderen als die angegebenen Hilfsmittel verwendet. Diese Arbeit wurde weder ganz noch zum Teil einer anderen Stelle im Rahmen eines Prüfungsverfahrens vorgelegt. Dies ist mein einziges und bisher erstes Promotionsverfahren. Die Promotion soll im Fach Zoologie erfolgen. Des Weiteren erkläre ich, dass ich Zuhörer bei der Disputation zulasse.

Kiel, den 29. Mai 2007

(Antje Steinfurth)