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Foraging ecology of Masked Boobies: The importance of intrinsic and extrinsic factors

by

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Declaration of originality

I hereby declare that this thesis contains no material which has been accepted for the award of any other degree or diploma in any tertiary institution, and that, to the best of my knowledge and belief, the thesis contains no material previously published or written by another person, except where due reference is made in the text of the thesis.


Julia Sommerfeld

June, 2013

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ZUSAMMENFASSUNG

Um ein fundiertes Verständnis über die Ernährungsökologie mariner Top-Prädatoren zu erlangen, ist es erforderlich, sowohl die Effekte intrinsischer Eigenschaften des Tieres zu untersuchen, als auch extrinsische, umweltbedingte Faktoren präzise zu bestimmen.

In der vorliegenden Arbeit wurden dazu die Bewegungs- und Aktivitätsmuster kükenaufziehender Maskentölpel *Sula dactylatra* über zwei Brutzeiten auf Phillip Island (Norfolk Island Gruppe), Australien (Südpazifik) mit Hilfe von GPS- und Tauch-Beschleunigungs-Datenloggern aufgezeichnet.

Ziel dieser Arbeit ist es Folgendes zu bestimmen: (I) Beeinflussen intrinsische Faktoren, wie zum Beispiel unterschiedliche Körpergewichte und Größe innerhalb desselben Geschlechts, die Bewegungsmuster, Flug- und Tauchverhalten von Männchen und Weibchen? (II) Verändern Adulttiere ihre Bewegungsmuster und ihr Tauchverhalten im Laufe der Untersuchungszeit und falls ja, steht dies im Verhältnis zu den Änderungen in der Nahrungsverteilung? (III) Die Bestimmung der Genauigkeit der First-Passage Time (FPT) Analyse – eine Methode die zunehmend verwendet wird, um spezifische Nahrungssuchgebiete (Area-restricted-search (ARS) Zonen) anhand von GPS-Daten zu identifizieren.

(I) Maskentölpel weisen einen umgekehrten Geschlechtsdimorphismus auf (d.h. Weibchen sind größer als Männchen). Die Ergebnisse der vorliegenden Studie belegen, dass der Wechsel zwischen kurzen und langen Beutezügen bei Weibchen abhängig vom Körpergewicht ist und wahrscheinlich dazu dient, abwechselnd Nahrung für das Küken zu erbeuten (kurze Beutezüge) bzw. zur Selbsternährung dient (lange Beutezüge). Weibchen mit einem größerem Körpergewicht tendieren zu kürzeren Beutezügen als leichtere, während bei Männchen kein Zusammenhang zwischen dem Körpergewicht und der Dauer der Beutezüge festgestellt werden konnte. Die Größe der Tiere hat keinen Einfluss auf die untersuchten Parameter. Während kurzer Beutezüge schlagen schwerere Weibchen signifikant häufiger mit ihren Flügeln und verbringen weniger Zeit ruhend auf der Wasseroberfläche als leichtere Weibchen. Im Gegensatz dazu schlagen schwerere Männchen seltener mit ihren Flügeln und ruhen öfters auf der Wasseroberfläche als

leichtere Artgenossen, voraussichtlich um Energie zu sparen. Maskentölpel weisen zudem unterschiedliche Elternrollen auf. Weibchen füttern größtenteils ihr Küken, während Männchen vorrangig das Nest verteidigen. Die Ergebnisse dieser Studie verdeutlichen, dass es erforderlich ist, die Effekte unterschiedlicher Körpergewichte innerhalb desselben Geschlechts, sowie das Vorkommen von unterschiedlichen Elternrollen, zu berücksichtigen, wenn die Effekte extrinsischer, umweltbedingter Faktoren untersucht werden.

(II) Marine Prädatoren erbeuten oftmals ihre Nahrung in einer Reihe mehrerer aufeinander folgender Tauchgänge. Anhand der Anzahl einzelner Tauchgänge innerhalb dieser Tauchperioden, sowie anhand der zurückgelegten Distanz zwischen einzelnen Tauchgängen, lassen sich präzise Aussagen über die Qualität und Dichte von Beuteschwärmen treffen, während Entfernungen zwischen einzelnen Tauchperioden detailliert Auskunft über die Begegnungshäufigkeit der Tiere mit ihrer jeweiligen Beute geben. Das Tauchverhalten und die Bewegungsmuster von Maskentölpeln wurden über drei Untersuchungszeiträume untersucht (am Anfang (*E1*) und Ende (*L1*) der ersten Brutsaison, sowie am Anfang der darauffolgenden Brutsaison (*E2*)). Des Weiteren wurden die Meeresoberflächentemperatur (SST) und die Chlorophyll *a* Konzentration (CHL) gemessen. Adulttiere suchten in zwei unterschiedlichen Habitaten nach Nahrung, nämlich in nahe gelegenen, flachen Gewässern entlang der Schelfkante, sowie in entfernten, tiefen Gewässern. Individuen weisen eine hohe Gebietstreue entlang der Schelfkante auf, jedoch nicht in entfernten, tiefen Gewässern. Dies lässt darauf schließen, dass die Tiere das Nahrungssuchgebiet entlang der Shelfkante mit verlässlichen Beutebegegnungen verbinden. In *E1* benutzten die Tiere ausschließlich die Shelfkante zum Erbeuten von Nahrung, obwohl die CHL-Konzentration relativ niedrig war, während in *L1* (ähnliche CHL wie in *E1*, höchste SST) und vor allem in *E2* (höchste CHL, ähnliche SST wie in *E1*) zusätzliche, entfernte Beutezüge stattfanden. Die durchschnittliche Qualität der angetroffenen Beuteschwärme war in entfernten Gewässern höher, wenn auch variabler. Die zurückgelegten Entfernungen, sowohl zwischen einzelnen Tauchgängen innerhalb einer Tauchperiode, als auch zwischen aufeinanderfolgenden Tauchperioden, waren in beiden Habitaten ähnlich, allerdings signifikant variabler in tieferen Gewässern. Die Analyse stabiler Isotope ergibt, dass die Adulttiere sich in *E1* weiter oben in der trophischen Nahrungskette ernähren, aber nicht in *L1* und *E2*. Die Ergebnisse

belegen, dass Maskentölpel in *E1* ausreichend Nahrung über dem nahe gelegenen Shelf für sich und ihr Küken erbeuten können, während ein Nahrungsmangel in diesem Gebiet in *L1* und *E2* durch zusätzliche Beutezüge in entfernte, aber produktivere Gewässer ausgeglichen wurde.

(III) Auf GPS-Daten basierende, deskriptive analytische Methoden können durch die Dauer eines Beutezuges oder durch Wasser-Ruheposition zu Fehlbestimmungen und Fehlinterpretationen von ARS-Zonen führen. Dies wurde bei Maskentölpeln durch das simultane Erfassen von GPS-Daten und Aktivitätsmustern untersucht. In 19 % aller durch FPT-Analyse berechneten ARS-Zonen verbrachten die Vögel mehr als 70 % ruhend auf der Wasseroberfläche, d.h. diese ARS-Zonen wurden aufgrund von Wasser-Ruhepositionen fälschlich bestimmt. Solche fehlerhaften ARS-Zonen wurden vorwiegend in kurzen Beutezügen nahe der Kolonie erfasst und beinhalteten wenig bis keine Tauchaktivität. Dies belegt, dass es unabdingbar ist, Wasser-Ruhepositionen in deskriptive analytische Methoden einzubeziehen, um bedeutende Nahrungshabitate mariner Prädatoren zu identifizieren. Jedoch sind identifizierte ARS-Zonen in entfernten Gewässern mit einer erhöhten Tauchaktivität verbunden, was darauf schließen lässt, dass erfasste ARS-Zonen zu einem Großteil dazu benutzt werden können, um wichtige Nahrungssuchhabitate von Maskentölpeln zu bestimmen.

Die Ergebnisse dieser Studie belegen, dass die Ernährungsökologie von Maskentölpeln sowohl vom Körpergewicht, als auch von umweltbedingten Faktoren beeinflusst wird, die zu Änderungen in der Verteilung von Nahrung führen und dass daher intrinsische, sowie extrinsische, umweltbedingte, Faktoren berücksichtigt werden müssen, wenn die Ernährungsökologie mariner Prädatoren erforscht wird. Des Weiteren sollten Schlussfolgerungen deskriptiver analytischer Methoden mit in Betracht gezogen werden, da bestimmte Verhaltensweisen der Tiere, die nicht im Zusammenhang mit aktiver Nahrungssuche stehen, zu Fehlerfassungen und Fehlinterpretationen von ARS-Zonen führen können.

ABSTRACT

The foraging ecology of marine top predators is intricately linked to intrinsic characteristics of the individual, as well as extrinsic, environmental factors. Analysing both the effects of these intrinsic and extrinsic factors is important to better understand the foraging ecology of animals that are constrained in their foraging time due to the need to return to a specific location during reproduction.

In this thesis, foraging movements and activity patterns of chick-rearing Masked Boobies *Sula dactylatra* breeding on Phillip Island (Norfolk Island Group), Australia (South Pacific) were investigated over two breeding seasons using GPS and depth-acceleration loggers, to determine (I) how intrinsic factors, such as body mass and size, influence individual foraging behaviour, (II) if adults show differences in diving behaviour and foraging movements throughout the study period, and whether this may be related to changes in prey availability and distribution in a tropical marine environment, and (III) the accuracy of first-passage time analysis (FPT) to determine area-restricted search behaviour in a central-place forager.

(I) Masked Boobies exhibit reversed sexual dimorphism. In this study, alternations between short and long trips were related to body mass in females, but not in males, and were presumably used to provision the chick and for self-maintenance, respectively. In this species, females are the parent in charge of provisioning the chick. During short trips, heavier females spent higher proportions of their flight time flapping and less time resting at the water surface than lighter females during long trips. Conversely, heavier males spent less time flapping, potentially to save energy during locomotion, and relatively more time resting. These findings underline the importance of accounting for the effects of body mass differences within the same sex, as well as different parental roles, when the influence of extrinsic, environmental factors are investigated.

(II) Marine predators often forage in bouts and both bout length and distances between dives within a bout have been related to the quality and density of prey patches, whereas distances between bouts is thought to reflect prey encounter rates. This study compared adult diving behaviour and foraging movements over three study periods (early (*E1*) and late (*L1*) phase of the first breeding season and the following early season (*E2*)) under varying

oceanographic conditions through depth-acceleration (in *L1* and *E2*) and GPS loggers. Adults showed high foraging site fidelity over the nearby shallow shelf ('local foraging area') but not over distant, deeper waters ('distant foraging area') between trips and study periods. In *E1*, although chlorophyll *a* concentration (CHL) was relatively low, adults concentrated their foraging activities within the local area, whereas in *L1* (similar CHL as in *E1*, highest sea-surface temperature (SST)) and *E2* (highest CHL, similar SST as in *E1*), numerous long displacements into the distant foraging area were observed, indicating that prey was scarce near the colony. Local trips presumably ensure that chicks are fed more frequently, but the yield of these trips appears to be insufficient (except in *E1*) for adults to maintain their own body reserves in addition to providing regular meals for the chicks. This forces individuals to forage in more distant waters for self-feeding. Prey patch quality was higher in distant waters, as indicated by increased dive rate and bout size. Prey encounter rates, although similar between both foraging areas, were more variable, indicating less predictable prey encounters. Stable isotope analysis of whole blood indicated that birds were feeding on higher trophic level prey items in *E1*, but not in *L1* and *E2*. This study revealed that, when food was scarce, birds experienced a trade-off between local foraging trips, where prey encounters were predictable but of lower quality, in order to deliver more energy to the chick, and presumably self-feeding distant trips, where prey patch quality was higher, but prey encounters less predictable.

(III) Area-restricted search (ARS) behaviour is used to better understand animal foraging behaviour. However, track-based descriptive analyses used to detect ARS behaviour may be biased by factors such as foraging trip duration as well as non-foraging behaviours (*i.e.* resting on the water). This potential bias was investigated in Masked Boobies using FPT analysis in combination with detailed foraging behaviour provided by depth-acceleration logger. In 19 % of 57 detected ARS zones, birds spent more than 70 % of total ARS duration resting on the water, suggesting that these ARS zones have been falsely detected (*i.e.* that the birds were not primarily foraging during that time). False ARS detection occurred mostly during short trips in close proximity to the colony, with very low or no diving activity. This clearly demonstrates the need to account for resting on the water positions when determining ARS behaviour based on foraging locations in marine animals. However, the

adoption of ARS behaviour at greater distances from the colony was linked to enhanced foraging activity, suggesting that ARS behaviour may be used to identify important feeding areas in this species.

These results reveal that the foraging ecology of Masked Boobies is influenced by adult body mass, as well as by changes in the distribution and availability of prey. This indicates that both intrinsic and extrinsic factors should be considered in conjunction when analysing the foraging ecology of central-place foragers. In addition, inference from track-based analyses on animals foraging strategies should be drawn carefully, as specific non-foraging behaviours may lead to an inaccurate detection and interpretation of ARS behaviour.

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Akiko Kato (Université de Strasbourg, CNRS) provided depth-acceleration data loggers, assistance with the analysis of depth-acceleration data and guidance with manuscript preparation.

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GENERAL INTRODUCTION

Marine predators, such as seabirds, marine mammals and fish, are important components of marine ecosystems. They can consume large quantities of prey (Furness and Cooper 1982, Duffy and Schneider 1994, Croll and Tershy 1988), influence the distribution and abundance of lower trophic level prey species (Birt et al. 1987, Ainley et al. 2007), and may serve to structure marine communities (Estes and Palmisano 1974, Oliver and Slattery 1985, VanBlaricom and Estes 1988).

Understanding the foraging ecology of marine predators within an ecosystem is important to assess how populations cope with natural or anthropogenic-induced environmental variability (Ashmole 1971, McCafferty et al. 1998), how organisms respond to environmental heterogeneity (Pinaud and Weimerskirch 2007), for the development of management and conservation plans (*e.g.* Schofield et al. 2007, Costa et al. 2012), and for modelling energy flow and predator–prey interactions (Bradshaw et al. 2003, Woodward and Hildrew 2002). In addition, a better understanding of predator foraging ecology can provide insights about unintended changes in the structure and functioning of marine ecosystems, directly or indirectly induced by declines of upper trophic level predators in ecosystems worldwide (Baum et al. 2003, Lotze 2004).

Pelagic predators forage in vast, rapidly changing three-dimensional marine environments (Croxall 1987), where food resources are often patchily distributed (Longhurst and Pauly 1987), and their accessibility is influenced by their remoteness or by environmental factors (Jaquemet et al. 2008, Navarro and González-Solís 2009). It is generally assumed that the foraging ecology of marine predators is a function of extrinsic factors, such as the spatial and temporal distribution of their prey, prey quality, risk of predation and environmental stochasticity (*e.g.* Oaten 1977, Stephens and Charnov 1982, Staniland et al. 2006). Seasonal and inter-annual differences in foraging trip duration, range and diving behaviour within, but also between, populations have been directly linked to changes in the distribution and abundance of prey in a range of species (*e.g.* Antarctic Fur Seals *Arctocephalus gazella*, Boyd et al 1994; Thick-billed Murres *Uria lomvia*, Falk et al. 2002; Rockhopper Penguins *Eudyptes chrysocome*, Tremblay and Cherel 2003).

However, variation in trip duration and foraging range, as well as diving behaviour, can also be determined by intrinsic factors such as body mass, size and sex (*e.g.* Southern Elephant Seals *Mirounga leonina*, Hindell et al. 1991; Harbour Seals *Phoca vitulina*, Thompson et al. 1998; Grey Seals *Halichoerus grypus*, Beck et al. 2003; Little Penguins *Eudyptula minor*, Kato et al. 2008). Intra-specific differences in the foraging behaviour between sexes are found in species across many taxa (*e.g.* Williams 1980, Clutton-Brock et al. 1982, Petit et al. 1990, LeBoeuf et al. 2000). The most common hypotheses to explain the occurrence of sex-specific foraging behaviours are sexual size dimorphism, different parental roles of each sex during the reproductive cycle and reduced intersexual competition for food (Beck et al. 2003). For instance, feeding niche segregation is common in sexually dimorphic species, with the larger sex generally foraging closer to the colony and consuming larger prey items (Selander 1966, González-Solís et al. 2000, Spear et al. 2007). These findings demonstrate that the foraging ecology of marine predators is a complex interweaving of intrinsic and extrinsic factors. It is therefore essential to analyse these effects in combination in order to better understand the foraging ecology of marine predators.

Seabirds are interesting models for studying foraging ecology. They are highly mobile, fast-moving predators, capable of travelling tens to thousands of kilometres in search of prey. During reproduction, both sexes share chick provisioning duties, and are thus constrained in their foraging behaviour due to the need to commute between feeding and breeding grounds (Orians and Pearson 1979). At this time, the proximity of prey to colonies, or the ability to forage efficiently to reach distant prey patches at low energetic costs, become critical for the parent in providing enough food to the chick, while maintaining their own body condition (Orians and Pearson 1979, Granadeiro et al. 1998, Navarro and González-Solís 2009). The study of dimorphic seabirds is particularly interesting because differing body mass may favour sex-specific foraging behaviours.

Foraging in tropical waters

Tropical waters are generally considered to lie between the latitudes of 23°27' north and south of the equator (Ashmole 1971, Ballance and Pitman 1999). In addition, zones with sea surface temperatures $\geq 23^{\circ}\text{C}$ for at least one season of the year are also defined as tropical

waters (Ashmole 1971, Ballance and Pitman 1999). The challenges to seabird foraging imposed by the marine environment are thought to be especially severe in tropical waters. Compared with temperate and polar waters, tropical waters exhibit a much lower seasonal signal and have lower phytoplankton densities, resulting in reduced energy availability for subsequent trophic levels (Nybakken 2001, Brewer and Hertel 2007). For upper level marine predators such as seabirds, the reduced productivity creates an environment where prey occurs in relatively low abundance at most spatial and temporal scales (Ainley and Boekelheide 1983). The availability of prey in tropical waters is consequently regarded as less predictable than in temperate and polar waters (Ainley and Boekelheide 1983, Weimerskirch 2007). It is therefore a paradox that tropical waters support massive populations of top predators such as tuna and billfish, marine mammals and seabirds (Harrison et al. 1983, Longhurst and Pauly 1987, Le Corre and Jaquemet 2005). This implies that seabirds, as well as other marine predators, have evolved specific foraging behaviours to cope with diminished feeding opportunities (Jaquemet et al. 2008). Habitat or diet partitioning may further allow multiple species to cohabit the same environment (Pianka 1981, Martin 1996, Navarro et al. 2013). Sympatric species may partition resources on a temporal (Croxall and Prince 1980) and/or spatial scale (Mori and Boyd 2004, Robson et al. 2004) and/or by type of prey (González-Solís et al. 2000, Zavalaga et al. 2007, Waite et al. 2012). Niche partitioning is particularly important in tropical marine environments, where resources are limited (Cherel et al. 2008).

Bio-logging and Area-restricted search behaviour

Bio-logging allows researchers to measure key parameters that form the basis for the network of variables influencing the foraging ecology, life history and behaviour of animals (Ropert-Coudert and Wilson 2005). Recent advances in data logger technology have revolutionised the quantitative measurements of animals in their natural habitat that would otherwise be difficult or impossible to obtain. The miniaturisation of data loggers, improved attachment methods, the ability to simultaneously collect behavioural, physiological and environmental data, as well as enhanced battery life and memory capacity, are just some

examples of the recent advances (Ropert-Coudert and Wilson 2005, Rutz and Hays 2009). For example, global positioning systems (GPS, Grémillet et al. 2004) can be used to study how animals move through space and time in search for prey at a very fine scale, which is crucial for understanding their foraging ecology (Pyke 1984, Staniland et al. 2006). The attachment of data loggers recording two-dimensional high-frequency acceleration and also incorporating a pressure sensor (referred to as ‘depth-acceleration loggers’ in this thesis) allows the quantification of specific animal behaviours by type, frequency and intensity (Ropert-Coudert et al. 2004).

In seabirds, one of the most common foraging movements is commuting flights (Weimerskirch 2007), where individuals leave the colony in a particular direction, travelling at higher speeds until reaching an area where they decrease their travel speed and increase their path sinuosity in search of prey (Fauchald 1999, Fauchald and Tveraa 2003). This behaviour has been termed area-restricted search (ARS) behaviour and is based on the hypothesis that animals should increase their search effort in areas where resources are plentiful rather than in areas where resources are scarce (Kareiva and Odell 1987). The adoption of ARS behaviour has been demonstrated in many seabird species (*e.g.* Black-browed Albatrosses *Thalassarche melanophris*, Pinaud 2008; Cory’s Shearwaters *Calonectris diomedea*, Paiva et al. 2010) and in marine mammals (*e.g.* Southern Elephant Seals, Thums et al. 2011, Dragon et al. 2012).

Several track-based analytical methods have been developed to determine ARS behaviour in animals (*e.g.* First-passage time (FPT) analysis Fauchald and Tveraa 2003; Fractal landscape analysis, Nams 1996, Tremblay et al. 2007; State-space models, Kareiva and Shigesada 1983, Marsh and Jones 1988). In this thesis, FPT analysis is applied to determine ARS behaviour. Briefly, FPT is by definition the time an animal requires to cross a circle of a given radius along a foraging trajectory (Fauchald and Tveraa 2003). First, FPT is calculated along a foraging track for increasing radii. The log-transformed variance as a function of the radius size is then plotted and ARS scales identified as the maximum peak in the log-transformed variance (Fauchald and Tveraa 2003).

In all of these analytical approaches, travel speeds and turning rates are used to detect the areas in which animals increase their search effort (Benhamou and Bovet 1989, Bartumeus et al. 2008). However, the detection of ARS behaviour based on these methods can be biased by factors such as foraging trip duration, as well as non-foraging behaviours such as resting on the water (Weimerskirch et al. 2008, Pinaud 2008). The shorter a foraging trip, the lower the number of locations that are available to identify ARS behaviour. Locations recorded while resting at the sea surface can be mistaken as searching or foraging locations (depending on the species and its feeding techniques), because location-only data cannot differentiate between simple roosting behaviour and potential in-water positions that may be associated with foraging (*i.e.* searching for prey and/or diving). The potential bias induced by non-foraging locations needs to be accounted for when analysing foraging movements to avoid false interpretation of the presence of ARS zones. This can be achieved by investigating the foraging movements of individuals recorded by GPS in combination with time-activity budgets recorded by depth-acceleration loggers (see Ropert-Coudert et al. 2004). The frequency and intensity of specific behaviours can then be examined in relation to the adoption of ARS behaviour determined by FPT analysis and *false* ARS zones due to resting on the water locations identified.

The Masked Booby

Masked Boobies *Sula dactylatra* are colonial seabirds that breed on tropical oceanic islands. They belong to the family Sulidae, which includes three species of gannets (temperate or cold water foragers) and a total of six tropical booby species (Nelson 1978). Masked Boobies are divided into six subspecies based largely on geographical and morphological variations (Nelson 1978, O'Brien and Davies 1990).

Masked Boobies are the largest of all boobies with adult body mass ranging from 1.5 – 2.9 kg, but body masses can vary considerably between subspecies and within sexes (Nelson 1978, Marchant and Higgins 1990, this study). This species exhibits reversed sexual dimorphism (RSD), where females are larger than males (Fig. 1.1). This occurs among seabirds only in boobies, skuas *Catharacta* and *Stercorarius* spp. and frigatebirds *Fregata*

spp. (Lormee et al. 2005). Females lay two eggs, but generally only one chick is reared through obligate siblicide (Dorward 1962). The mean incubation period is 43 days (range 40 – 49 days for the first egg and 38 – 47 days for the second egg) and chicks fledge after approximately 115 – 124 days, depending on the population (Nelson, 1978, 2005). Both sexes share breeding duties, but a division of labour was found in Masked Boobies from Clipperton Island in the eastern tropical Pacific, with the larger female mainly responsible for chick-provisioning (Weimerskirch et al. 2009). Foraging ranges of 245 km recorded in chick-rearing Masked Boobies from Clipperton Island in the eastern tropical Pacific revealed that this species is the most wide-ranging of all boobies (Weimerskirch et al. 2008). However, foraging movements recorded in breeding adults on Palmyra Atoll in the central Pacific Ocean were < 30 km (Young et al. 2010), indicating that foraging movements are highly variable between populations, most likely due to differences in prey availability.



Figure 1.1. Masked Booby pair with a young chick on Phillip Island (Norfolk Island Group). The difference in size is clearly evident, with the more slender male in the left of the photograph and the larger female on the right.

Masked Boobies are an ideal species to investigate how intrinsic and extrinsic, environmental factors influence the foraging ecology of a marine predator. Differences in body mass and size within and between sexes, the presence of RSD, as well as the vast differences in foraging movements between populations thought to be driven by changes in prey availability, in addition to the constraints imposed by tropical waters (which are especially severe during reproduction) make them an ideal candidate for a study of this nature.

This thesis examines the foraging ecology of Masked Boobies breeding on Phillip Island (part of the Norfolk Island Group, Australia, see below) in the south-western Pacific Ocean (Fig. 1.2, Fig. 1.3.). This subspecies is currently referred to as *Sula dactylatra fullagari* (but see Steeves et al. 2010 for taxonomy) and breeds only in the Norfolk Island Group, on Lord Howe Island and in the Kermadec Islands (Nelson 1978, Priddel et al. 2005, 2010, Garnett et al. 2010). The subspecies comprises fewer than 1500 breeding pairs (Priddel et al. 2005, 2010, Garnett et al. 2010) and is distinguished from its conspecifics by its longer wing lengths and sepia, not yellow, irides (O'Brien and Davies 1990).

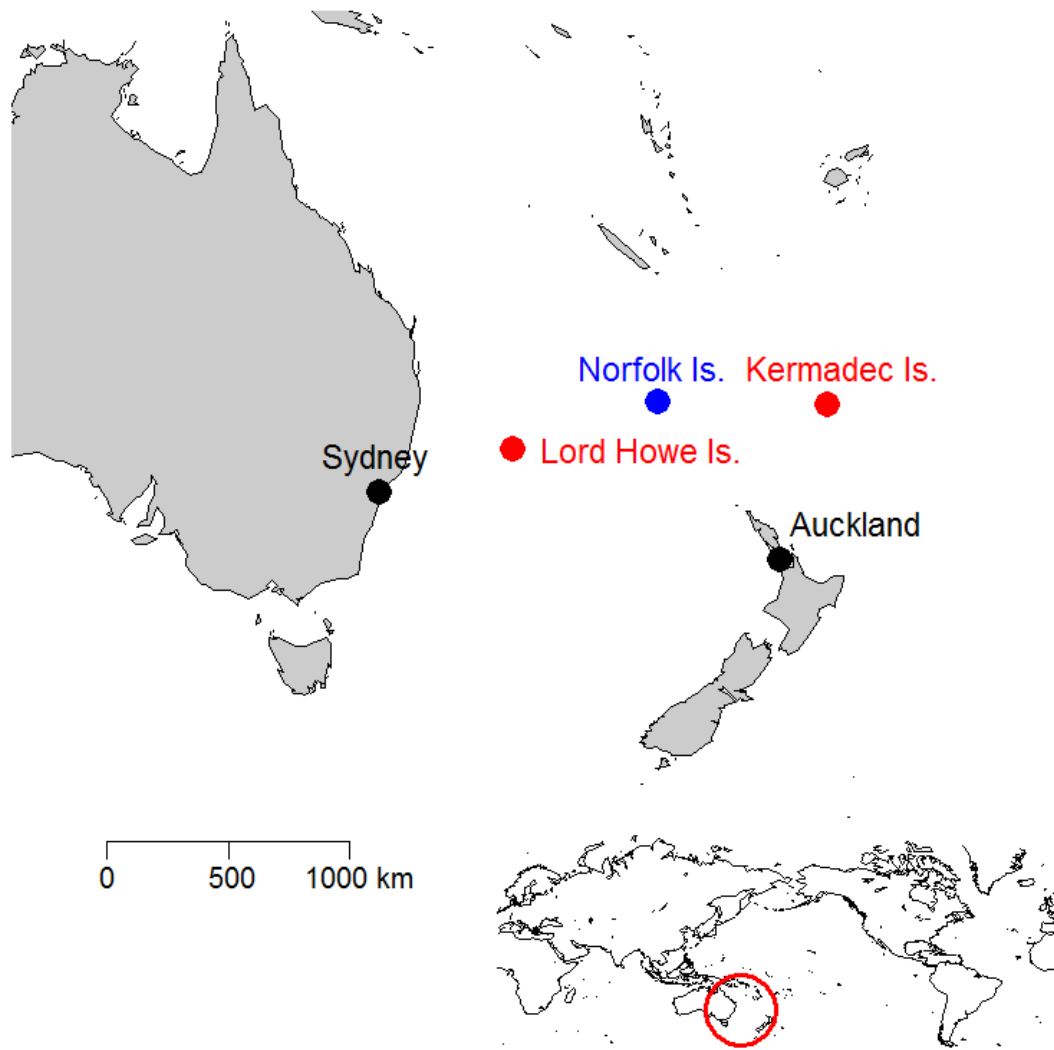


Figure 1.2. Distribution map of Masked Boobies *Sula dactylatra tasmani* and location of the study area (Norfolk Island Group) in the south-western Pacific Ocean. In red are shown the two other breeding sites of *S. d. tasmani*.



Figure 1.3. Phillip Island of the Norfolk Island Group in the south-western Pacific Ocean.

Study site and field work

The Norfolk Island Group (29°02'S, 167°57'E), including Norfolk Island (3455 ha), Phillip Island (190 ha), Nepean Island (10 ha) and a number of smaller islets, is located approximately 1670 km north-east of Sydney, Australia and 1070 km north-west of Auckland, New Zealand. This group of islands lies on the Norfolk Ridge in the south-eastern Coral Sea, on the north-eastern edge of the Tasman Front (Fig. 1.4). The Norfolk Island Group is part of a unique marine ecosystem. It is surrounded by a high number of seamounts, which lie within the so-called 'Norfolk Island Seamounts Area' (NISA) (Williams et al. 2006). The NISA is a distinct regional-scale bioregion, meaning its ecosystem has different components to those in all other provinces within the Australian Marine Jurisdiction (Williams et al. 2006).

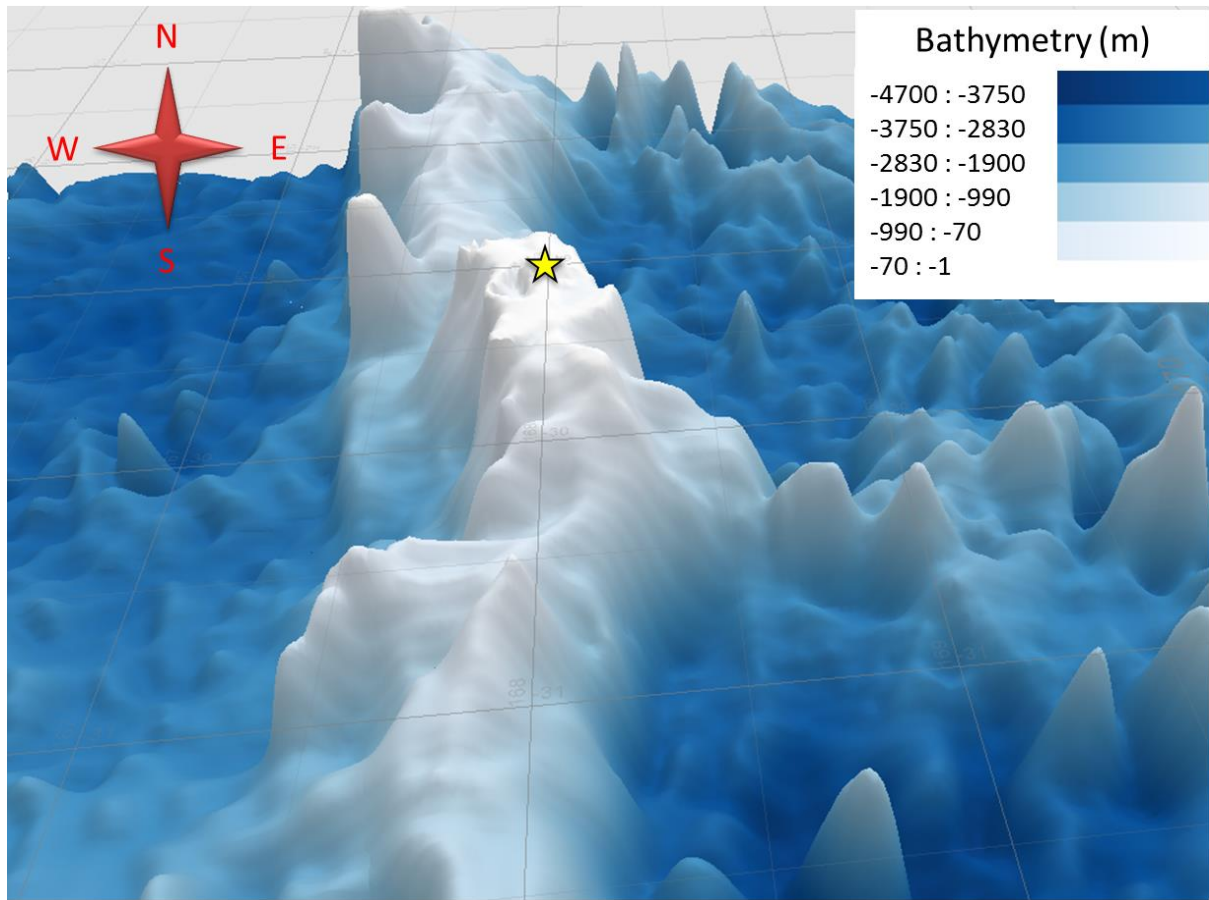


Figure 1.4. Bathymetry of the Norfolk Island Ridge located in the south-western Pacific Ocean. The Norfolk Island Group is represented by the yellow star.

Phillip Island is located 6 km south of Norfolk Island. This island rises to a narrow summit of 280 m above sea level at its southern peninsular and consists mainly of basaltic lava and tuff that erupted from the submerged Norfolk Ridge almost three million years ago (Jones and McDougall 1973). Approximately 300 Masked Booby pairs breed in open habitats thinly dispersed over the island (Priddel et al. 2010). Their breeding season is protracted, with chicks hatching between early September and late March. The majority of chicks hatch between October and December and generally fledge between January and March (Hermes et al. 1986, Priddel et al. 2010).

This study was conducted over three fieldtrips in two successive breeding seasons: (1) between 28 October 2009 and 07 November 2009, corresponding to the early phase/peak of the breeding season, (2) between 12 February 2010 and 03 March 2010, corresponding to

the late phase of the same breeding season, and (3) between 27 October 2010 and 10 November 2010, corresponding to the early phase/peak of the following breeding season.

Aims and thesis outline

Using Masked Boobies as a model, the aim of this research project is to examine how intrinsic characteristics of the individual, as well as extrinsic, environmental factors influence the foraging ecology of a central-place forager in a tropical marine environment. This thesis further seeks to determine which factors influence the detection and interpretation of ARS behaviour using FPT analysis, and whether ARS behaviour can be used as a proxy for important feeding areas. These main objectives were achieved through the simultaneous deployment of GPS and depth-acceleration loggers to provide information on the foraging movements and time budgets of Masked Boobies during the energy-demanding chick-rearing period, and by taking morphological measurements of study animals. Data obtained are specifically used to:

- (I) Analyse how body mass and size differences within sexes influence key foraging parameters such as foraging trip duration, flight patterns, foraging time spent resting at the water surface and diving behaviour in Masked Boobies.
- (II) Determine differences in diving behaviour and foraging movements of adults during the chick-rearing period, and assess relationships between these parameters and changes in prey availability and distribution in a tropical marine environment.
- (III) Examine the effects of foraging and non-foraging behaviours on the accuracy of FPT analysis to determine ARS behaviour, and assess whether the adoption of ARS behaviour can be used as a proxy for identifying important feeding areas.
- (IV) Incorporate the findings of this thesis to present a comparative overview of the foraging ecology of temperate, polar and tropical seabird species.

This thesis is designed to elaborate each of the above aims. A brief outline of each chapter is presented below:

Chapter 2 – The individual counts: within sex differences in foraging strategies are as important as sex-specific differences in masked boobies *Sula dactylatra*

This chapter analyses how differences in body mass and size within sexes influence foraging trip duration, flight patterns (*i.e.* proportions of flight time spent flapping and gliding), foraging time spent resting at the water surface and diving behaviour in Masked Boobies. The results reveal differences within sexes in these key parameters due to varying body masses, in addition to differential parental roles. The results are discussed in relation to the findings of other studies investigating the foraging behaviour of dimorphic seabird species.

Chapter 3 – Response of a marine predator, the Masked Booby, to spatial and temporal changes in the availability and distribution of prey

In this chapter, intra- and inter-seasonal changes in prey availability and distribution, and their effect on foraging behaviour, are examined by determining dive bout length and distances between dives within a bout, as well as distances between dive bouts. These characteristics are considered to be related to the quality and density of prey patches, and to reflect prey encounter rates, respectively. Foraging movements of Masked Boobies are further analysed within and between seasons, and in relation to sea surface temperature (SST) and chlorophyll *a* concentration (CHL). The results reveal differences in prey quality in relation to the distance between the foraging grounds and the colony, with higher quality prey patches found at greater distances from the colony. Findings further show that individuals show strong foraging site fidelity at a coarse scale between trips, over a shallow shelf-edge located near the colony. Differences in foraging trip duration and ranges between seasons suggest that adults adjust their foraging behaviour according to prey availability. These findings are discussed in relation to other studies investigating the effects of changes in prey on the foraging behaviour of seabirds.

Chapter 4 – Foraging parameters influencing the detection and interpretation of Area-restricted search behaviour in marine predators: a case study with the Masked Booby

The potential bias of factors such as foraging trip duration and resting at the sea surface locations, when FPT analysis is used to determine ARS behaviour, is investigated. This chapter also examines if the adoption of ARS behaviour coincides with adult diving locations to determine if ARS behaviour can be used as a proxy for important feeding areas. The findings reveal that resting on the water locations lead to a false detection of ARS behaviour and incorrect interpretation of ARS zones. The importance of these findings for studies investigating the adoption of ARS behaviour in seabirds, and also in other marine species, is discussed.

Chapter 5 – General discussion

In this final chapter, the findings of this research study are discussed while incorporating them into a comparative overview of the foraging ecology of temperate, polar and tropical seabird species during the energy-demanding chick-rearing period with respect to foraging movements and behaviour, foraging habitat and site-fidelity, as well as foraging strategies employed by tropical species.

Individual chapters (2 – 4) in this thesis were written and formatted for future submission to scientific journals. Julia Sommerfeld was senior author for each chapter and responsible for collection, analysis and interpretation of data and manuscript preparation. However, co-authors contributed to the facilitation of this project, data analysis and preparation of the manuscripts. These co-authors are listed in the statement of publication and co-authorship.

Chapter 2 – The individual counts: within sex differences in foraging strategies are as important as sex-specific differences in masked boobies *Sula dactylatra*

ABSTRACT

Understanding how animals allocate their foraging time is a central question in behavioural ecology. Intrinsic factors, such as body mass and size differences between sexes or species, influence animals' foraging behaviour, but studies investigating the effects of individual differences in body mass and size within the same sex are scarce. We investigated this in chick-rearing Masked Boobies *Sula dactylatra*, a species with reversed sexual dimorphism, through the simultaneous deployment of GPS and depth-acceleration loggers to obtain information on foraging movements and activity patterns. Body mass ranged from 2120 – 2870 g in females and from 1685 – 2465 g in males). Heavier females performed shorter trips closer to the colony than lighter females. During these shorter trips, heavier females spent higher proportions of their flight time flapping and less time resting on the water than lighter females did during longer trips. In contrast, body mass did not affect trip duration of males, however heavier males spent less time flapping and more time resting on the water than lighter males. This may occur as a result of higher flight costs associated with body mass and allow conservation of energy during locomotion. Body size (i.e. wing length) had no effect on any of the foraging parameters. Dive depths and dive rates (dives h⁻¹) were not affected by body mass, but females dived significantly deeper than males, suggesting that other factors are important. Other studies demonstrated that females are the parent in charge of provisioning the chick, and maintain a flexible investment under regulation of their own body mass. Variation in trip length therefore seems to be triggered by body condition in females, but not in males. Consequently, shorter trips are presumably used to provision the chick, while longer trips are for self-maintenance. Our findings underline the importance of accounting for the effects of body mass differences within the same sex, if sex-specific foraging parameters in dimorphic species are being investigated.

INTRODUCTION

Foraging behaviour in marine predators is intricately linked to extrinsic, environmental factors. For instance, the complex interactions between bathymetry and sea surface temperature (Yen et al. 2004, Hamer et al. 2009, Paiva et al. 2010) and other physical and biological processes promoting growth and retention of plankton, leading to higher productivity zones (Haury et al. 1978) and concentrations of prey, the latter being key determinant of foraging success. Yet factors intrinsic to the individual are also paramount in determining foraging performance and cannot be easily dissociated from extrinsic factors (Zimmer et al. 2011). Sex-specific foraging strategies in seabirds often result from intra-specific competition (Lewis et al. 2001, Phillips et al. 2004), sex-specific nutrient requirements (Lewis et al. 2002, Zavalaga et al. 2007) and/or sex-specific foraging abilities (Kato et al. 1999). But body mass and size also play important roles in dimorphic species (e.g. Kato et al. 1999, Velando and Alonso-Alvarez 2003, Lewis et al. 2005, Weimerskirch et al. 2009). Body size is often evolved to adapt to different ecological niches (Shine 1989, Sandercock 2001), favouring dimorphic species to exploit a wider range of resources than monomorphic ones (Figueroa 1999). The larger sex is often more competitive and dominant (reviewed for seabirds in Lewis et al. 2002). Sexual selection is further thought to favour small body size in species that perform aerial displays (Andersson and Norberg 1981, Blomqvist et al. 1997), while a larger size is often present in species that display or fight on the ground (Clutton-Brock et al. 1982, Lindenfors et al. 2002).

Flight performance in birds is strongly constrained by body mass and size. As an illustration, flapping flight has been associated with high energy expenditure (Pennycuik 1989), which increases substantially with body mass (Pennycuik 1972), whereas gliding and soaring are considered to be energetically efficient flight methods (Norberg 1986). The energetic costs of locomotion are therefore likely to be an especially strong selecting force for efficient flight (Ballance 1995). This will be particularly important during the high-energy demanding chick-rearing period in which parents must sustain their chicks in addition to themselves.

Some seabird species adopt a bimodal foraging strategy during this high-energy demanding period (e.g. Chaurand and Weimerskirch 1994, Weimerskirch 1998, Weimerskirch and Cherel 1998, Sommerfeld and Hennicke 2010, Saraux et al. 2011). During short foraging trips, individuals forage near the colony to maintain a high feeding frequency of the chick at the expense of their own body mass, while longer foraging trips to more distant, but highly productive, areas are for self-provisioning (e.g. Granadeiro et al. 1998, Thalmann et al. 2009). In environments where resources are abundant, or in other seabird taxa (e.g. Lewis et al. 2004, Zavalaga et al. 2011), this alternation strategy disappears (Phillips et al. 2009).

Adult body mass further plays an important role in the regulation of parental effort (e.g. Chastel et al. 1995, Erikstad et al. 1997, Dearborn 2001). Sex-specific foraging strategies in species with reversed sexual dimorphism (RSD) often occur during the chick-rearing period as a result of differing parental roles – larger females exhibit a flexible breeding investment under regulation of their own body mass, whereas males present a fixed investment (e.g. Guerra and Drummond 1995, Velando and Alonso-Alvarez 2003, Weimerskirch et al. 2009). Deeper dives and consumption of different types and/or sizes of prey were found in individuals of the larger sex (Kato et al. 1999, Zavalaga 2007), suggesting size-specific, vertical feeding niche segregation. Plunge-diving seabirds, such as Sulidae (gannets and boobies) use the momentum of their fall to attain depth (Ashmole 1971, Nelson 1978, but see Ropert-Coudert et al. 2004, 2009 for alternative hunting strategies and use of wing flapping underwater). As such, heavy individuals are thought to attain deeper depths during plunge-diving from passive mechanisms mediated by gravitational acceleration (Ropert-Coudert et al. 2004). Accordingly, the larger sex may be advantaged during diving (Kato et al. 1999, Lewis et al. 2005, Zavalaga et al. 2007), while the smaller sex may have higher flight efficiency in light winds (Shaffer et al. 2001). Consequently, the larger sex may dominate intra-specific competition near the colony, forcing the smaller and thus less competitive sex to use its higher flying efficiency to forage in more distant grounds. Such a case has for instance been found in Northern Giant Petrels *Macronectes halli* (González-Solís et al. 2000) and Brown Boobies *Sula leucogaster* (Gilardi 1992).

Surprisingly, although sex-specific and species-specific foraging strategies due to body mass and size differences have been found in several species, studies investigating the effects of individual differences in body mass and size within the same sex still remain scarce (but see Kato et al. 2008, Zimmer et al. 2011). This is an important component of intrinsic influences on behaviour as it helps to disentangle the potentially confounding effects of body mass, size and sex.

We investigated this in Masked Boobies *Sula dactylatra* breeding on Phillip Island (Norfolk Island Group) in the south-western Pacific. Masked Boobies are the largest of all boobies and display a moderate RSD (Nelson 1978). The aim of the study was to examine the effects of individual differences in body mass and size within the same sex on four key foraging parameters: (I) foraging trip duration, (II) flight time spent flapping, (III) foraging time spent sitting on the water surface, and (IV) dive depth and dive rate (dives h⁻¹).

MATERIAL AND METHODS

Study site and species

Masked Boobies were studied on Phillip Island (29°02'S, 167°57'E) in the south-west Pacific Ocean. Phillip Island (190 ha) is part of the Australian Norfolk Island Group, located approximately 1670 km north-east of Sydney, Australia and 1070 km north-west of Auckland, New Zealand. The study took place between 12 February 2010 and 03 March 2010 and 27 October 2010 and 10 November 2010, corresponding to late and early breeding seasons, respectively.

Approximately 300 Masked Booby pairs breed on Phillip Island (Garnett et al. 2010, Priddel et al. 2010). Females lay two eggs, but generally only one chick is reared through obligate siblicide (Dorward 1962). All individuals in the present study were rearing chicks between 3 and 11 weeks of age during February and March 2010 and between 2 and 7 weeks of age during October and November 2010.

Data loggers and deployment

Activity patterns and time budgets of Masked Boobies were studied using cylindrical, four channel data-loggers (M190-D2GT, 12 bit resolution, 53 x 15 mm, 17 g, Little Leonardo, Tokyo, Japan), which simultaneously recorded depth (1 Hz), temperature (1 Hz) and acceleration (16 Hz) along two axes. The relative accuracy for the depth sensor was 0.1 m. The loggers contain an acceleration sensor measuring both dynamic (vibration) and static (gravity) accelerations. The depth-acceleration loggers were attached using TESA® tape (Beiersdorf AG, GmbH, Hamburg, Germany), positioned underneath three central tail feathers in order to measure acceleration along two axes: surging acceleration along the longitudinal body axis and heaving acceleration dorso-ventrally (see below for details).

Individuals were simultaneously equipped with GPS data loggers (46 x 32 mm, 20 g, Earth & Ocean Technologies, Kiel, Germany) to study foraging movements. GPS loggers were attached on top of three central tail feathers using TESA® tape. Total attachment weight including tape was approximately 55 g (range 45 – 60g, n = 27), corresponding to 2.2 % and 2.7 % of female and male mean body mass respectively. This was below the generally accepted 3 % of mean body mass threshold for attachment of GPS loggers (Phillips et al. 2003, Wilson and McMahon 2006, but see Vandenabeele et al. 2012).

Adults were sexed by voice and by measurements: males have a distinctive higher pitched voice than females and are the smaller bird within a pair (Nelson 1978). Either the female or the male of a chick-rearing pair was captured with a noose-pole and weighed using a spring balance (Pesola®, maximum deviation ± 0.3 % of load). Prior to deployments, nests were monitored throughout the day (or during the previous day, if deployments occurred at night). This maximised our chances of attaching data loggers on individuals that spent the day at the nest and were thus likely to depart on a foraging trip and, to avoid potential biased body masses due to full stomach contents. Birds were colour-marked on the breast with a green or blue biological dye (sheep crayon) at first capture. Non-banded adults were banded with a metal leg band (Darvic®, Australian Birds and Bats Banding Scheme). After attachment of the data loggers, individuals were released immediately onto their nests. Loggers were retrieved after 1 – 4 days, recording 1 – 4 successive foraging trips. Wing

length, an index for body size (see Weimerskirch et al. 2009a for the use of wing length as an index of body size in Brown- *Sula leucogaster* and Blue-footed Boobies *S. nebouxii*), was measured as the distance from the distal portion of the carpus to the tip of the longest primary feather, using a ruler to the nearest 1 mm, upon retrieval of the data loggers. To minimise disturbance and possible device-related effects, only one adult of a pair was instrumented with data loggers and individuals were never studied twice within or between seasons. No nests were deserted during the entire duration of the study.

Data analysis

Depth-acceleration data were analysed with IGOR Pro 6.21 (Wavemetrics software, Portland, USA). First, the component of the gravity acceleration along the surging and heaving axes (*i.e.* measured along the longitudinal body axis and dorsoventrally, respectively) was separated from the high-frequency component resulting from wing beat activity, using a low-pass filter (Tanaka et al. 2001). Next, the following types of behaviour were identified from the depth-acceleration logger signals: (1) on land, (2) take-off, (3) in flight (flapping/gliding), (4) sitting on the water surface and (5) plunge-diving (Fig. 2.1). Diving threshold was set to 0.2 m. Flapping activity within each flight session was identified as an oscillating pattern present simultaneously on both axes, with each propulsive stroke recorded on the heaving axis resulting in a forward acceleration recorded on the surging axis (Fig. 2.1, see Ropert-Coudert et al. 2004 for details). Birds were considered to be gliding when these distinctive oscillation patterns within a flight bout were absent. On-land behaviours were excluded from the analysis.

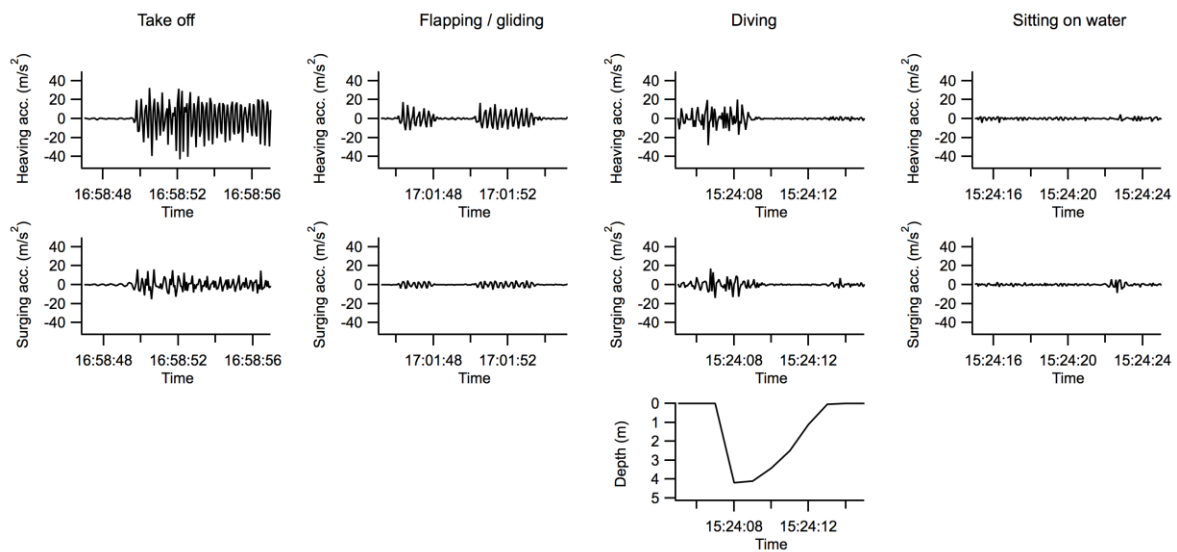


Figure 2.1. Dive depth, high-frequency components of heaving and surging acceleration data recorded for take-off, flapping and gliding flight, plunge-diving and sitting on the water surface in a Masked Booby.

Flight time was calculated as the sum of the total time spent flapping and gliding per foraging time (total trip duration minus nocturnal time, see results). The proportion of flight time spent flapping was accordingly the amount of time spent flapping within the total flight time. The proportion of time spent sitting on the water was the time sitting at the water surface within the total foraging time. Dive rates were calculated as the total number of dives within an hour of the total foraging time (dives h^{-1}). For statistical analysis, foraging time, foraging trip duration (used as a continuous variable), body mass, wing length and dive rates were \log_{10} transformed. Proportion values were logit transformed.

Statistical analysis

All statistical analyses were performed using R 2.15.0 (R Development Core Team 2012). Non-linear mixed models (Faraway 2006) were applied using the function *lme* in R package *nlme* (Version 3.1-104, Pinheiro et al. 2012), with respective foraging parameters as response variables and interactions *sex* \times *body mass* and *sex* \times *wing length* as fixed effects to account for individual differences in body mass and wing length within the same sex. As several foraging trips were recorded for the same individual, and data were collected over two breeding seasons, bird ID nested within season was included as a random effect to

account for pseudo-replication. When effects of interactions were not significant, we tested whether any of the single terms *sex*, *body mass* or *wing length* had a significant effect on respective foraging parameters. We further tested, in two separate models, whether the interaction *sex* \times *flapping* \times *body mass* and *sex* \times *sitting* \times *body mass* had an effect on foraging time.

To test the influence of single terms or interactions in a model, the function *drop1* in R was used. This function tests every term in the model as if it is the last entering the model, so that it omits every term in the model in turn. The reduced model was then compared with the full model using a likelihood ratio test under 1 degree of freedom (test *Chisq* in R). Before drawing inference, model assumptions were checked following Crawley (2007).

Significant interactions were plotted using function *allEffects* of package *effects* in R (Fox et al. 2012). From these interaction plots, we drew inference about the directions of the significant interactions. Correlations were calculated using Spearman's rank correlation or Pearson's product moment correlation. To test for body mass and wing length differences between sexes, a Welch's t-test was performed. All tests were two-tailed, with a significance level of $p < 0.05$. Mean (\pm SD) results are reported.

RESULTS

A total of 61 foraging trips from 27 individuals (17 males and 10 females) containing both position and activity data were recorded. Of the 27 birds, three females and four males stayed overnight at sea (one male spent two nights at sea). Three of these foraging trips were excluded from the data analysis because battery-exhaustion of the depth-acceleration loggers occurred before the birds returned to the colony. Our sample size was too small to test whether birds staying overnight at sea differed from birds that made single-day trips, therefore the nocturnal portions of the overnight trips were excluded (birds spent most of the nocturnal period sitting on the water surface for long hours without any significant activity). Overnight trips – without the nocturnal period – were subsequently pooled with single-day trips. Consequently, foraging time as used in the present study corresponded to the total foraging trip duration minus the nocturnal period.

Morphological comparison

Females were on average 16.6 % heavier than males, but only 2 % larger in terms of wing length (Table 2.1). Mean body mass and wing length differed significantly between males and females (*Welch's t-test* $t = 7.13$, $df = 45.21$, $p < 0.001$ and $t = 6.05$, $df = 43.45$, $p < 0.001$, respectively). Body mass and wing length showed a significant positive correlation in males (*Spearman* $r_s = 0.50$, $S = 5732.61$, $p = 0.001$, $n = 17$), but not in females (*Spearman* $r_s = -0.39$, $S = 810.01$, $p = 0.088$, $n = 10$).

	Males	n	Females	n	<i>Welch's t-test</i>
Body mass (g)	2059.1 \pm 225.8 (1685 – 2465)	17	2470.2 \pm 220.2 (2120 – 2870)	10	$t = 7.13$, $p < 0.001$
Wing length (mm)	460.3 \pm 6.0 (443 – 474)	17	469.5 \pm 5.3 (460 – 479)	10	$t = 6.05$, $p < 0.001$

Table 2.1. Body mass and wing length of male and female Masked Boobies from Phillip Island. Values are presented as mean \pm SD. Ranges in parentheses. Sample sizes (n).

Foraging trip duration and range

Both mean foraging trip duration and total distance travelled were highly variable (Fig. 2.2, Fig. 2.3), but not significantly different between males and females ($\chi^2_1 = 1.93$, $p = 0.165$, $\chi^2_1 = 2.92$, $p = 0.093$, respectively) (Table 2.2). Mean maximum distances from the colony were greater in females than males (Table 2.2), but the difference was not significant ($\chi^2_1 = 1.76$, $p = 0.185$). Not surprisingly, foraging trip duration was strongly and positively correlated with both the total distance travelled (*Pearson* $r = 0.91$, $t_{56} = 16.11$, $p < 0.001$) and the maximum distance from the colony (*Pearson* $r = 0.86$, $t_{56} = 12.62$, $p < 0.001$). Foraging movements of both sexes showed considerable overlap (Fig. 2.3).

Foraging parameters	Males	n	Females	n
Trip duration (h)	7.03 ± 8.16 (0.15 – 41.79)	41	8.18 ± 7.61 (0.52 – 37.19)	20
Total distance travelled (km)	148.6 ± 143.4 (3.2 – 577.7)	39	213.9 ± 174.0 (10.4 – 602.3)	19
Maximum distance from colony (km)	57.9 ± 54.9 (2.2 – 226.7)	39	77.6 ± 64.4 (4.5 – 230.8)	19
Foraging time spent in flight (%)	67.9 ± 17.0 (19.9 – 95.9)	41	63.5 ± 17.9 (13.9 – 83.9)	20
Flight time spent flapping (%)	57.5 ± 8.3 (38.8 – 78.7)	41	48.3 ± 12.9 (20.9 – 71.5)	20
Foraging time spent sitting on water (%)	28.0 ± 15.6 (2.8 – 62.6)	41	34.7 ± 18.1 (12.2 – 84.8)	20
Dive depth (m)	2.46 ± 1.35 (0.24 – 5.96)	540	2.9 ± 1.4 (0.2 – 6.3)	256
Dive rate (dives ^{-h})	0.88 ± 1.0 (0.15 – 4.69)	35	1.4 ± 1.9 (0.2 – 6.5)	19

Table 2.2. Foraging parameters of male and female Masked Boobies during chick-rearing. Values are presented as mean ± SD. Ranges in parentheses. Sample sizes (n).

The interaction *sex* × *body mass* on foraging trip duration was significant ($\chi^2_1 = 4.46$, $p = 0.034$), indicating that the effect of sex on foraging trip duration changed with individual body mass (Table 2.3). Heavier females conducted shorter foraging trips, while lighter females performed longer foraging trips (Fig. 2.4). Males showed a weak and opposing effect, with heavier males undertaking longer foraging trips and lighter males shorter foraging trips (Fig. 2.4). The interaction *sex* × *wing length* had no effect on foraging trip duration ($\chi^2_1 = 2.61$, $p = 0.106$), as was also the case for the single term *wing length* ($\chi^2_1 = 0.72$, $p = 0.393$).

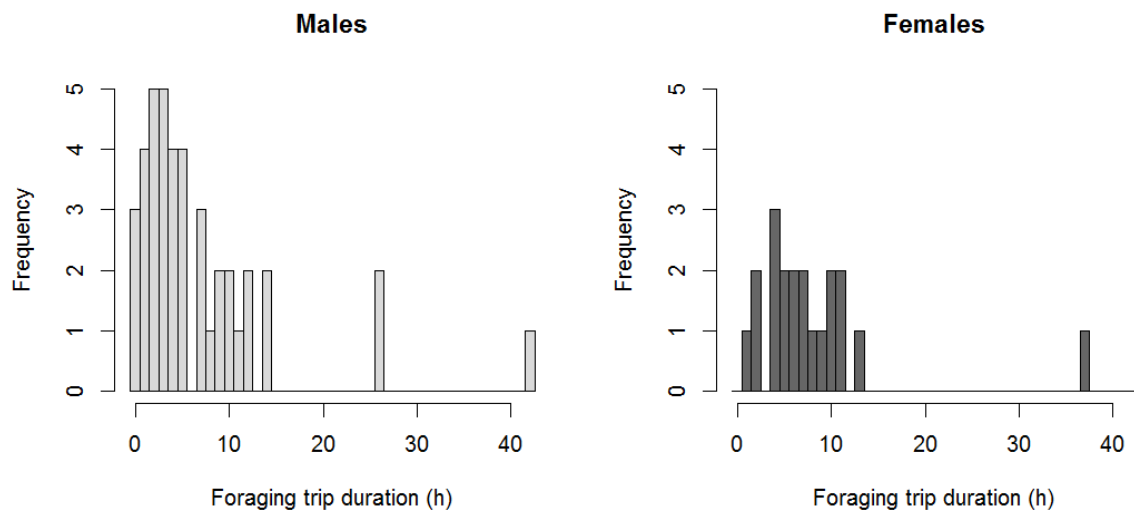


Figure 2.2. Frequency distribution of foraging trip duration (h) in male and female Masked Boobies.

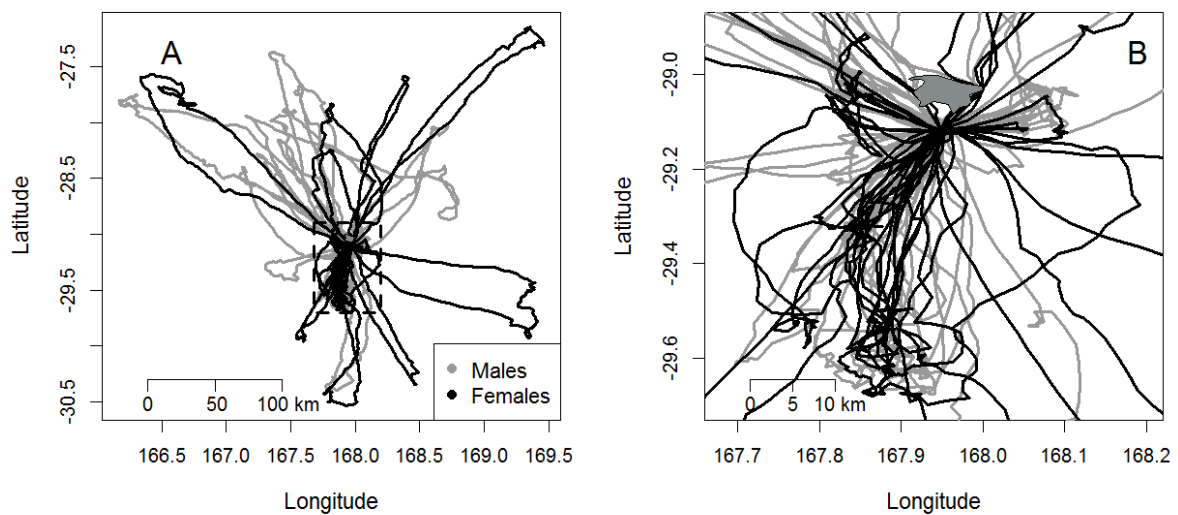


Figure 2.3. Foraging movements of male and female Masked Boobies recorded by GPS at 4 intervals. (A) All foraging movements, and (B) short foraging movements within the black rectangle. Black lines correspond to female tracks, grey lines to males. The grey area represents Norfolk Island, Australia.

Flight

The percentage of foraging time spent in flight and the total flight time spent flapping was similar between males and females (Table 2.2). The two-way interaction *sex* × *bird mass* was highly significant ($\chi^2_1 = 11.05$, $p < 0.001$), indicating that the effect of sex on the flight time spent flapping changed with individuals' body mass (Fig. 2.4, Table 2.3). Heavier females spent more time flapping than lighter females, whereas the opposite was observed in males: heavier males spent less time flapping than lighter males (Fig. 2.4). The interaction *sex* × *wing length*, as well as the single term *wing length* did not significantly improve the fit of the models ($\chi^2_1 = 0.09$, $p = 0.758$ and $\chi^2_1 = 0.10$, $p = 0.744$, respectively), indicating that wing length did not affect the amount of time individuals spent flapping (Table 2.3).

The effect of the three-way interaction *sex* × *flapping* × *body mass* on foraging time was significant ($\chi^2_1 = 4.81$, $p = 0.028$), indicating that heavier females spent more time flapping during shorter foraging trips than lighter females during longer foraging trips, but this effect was not evident in males.

	Foraging trip duration		Flapping		Sitting on the water		Dive depth		Dive rate (dives ^{-h})	
	χ^2_1	p	χ^2_1	p	χ^2_1	p	χ^2_1	p	χ^2_1	p
Fixed effects										
<i>sex</i> × <i>body mass</i>	4.46	0.034	11.05	< 0.001	8.40	0.003	0.19	0.662	0.25	0.614
<i>sex</i> × <i>wing length</i>	2.61	0.106	0.09	0.758	1.44	0.229	0.01	0.904	0.24	0.624

Table 2.3. Non-linear mixed models of foraging parameters explained by *sex* × *body mass* and *sex* × *wing length*. Chi-square under 1 degree of freedom for maximum likelihood analysis (χ^2_1). Significant results in **bold**.

Resting at the water surface

Males and females spent similar proportions of their total foraging time sitting at the water surface (Table 2.2). The two-way interaction *sex* × *body mass* was statistically significant ($\chi^2_1 = 8.40$, $p = 0.003$) (Table 2.3). Heavier females spent less time sitting at the water surface than lighter females, while heavier males spent more time sitting at the water surface than their lighter counterparts (Fig. 2.4). Again, *sex* × *wing length* or the single term *wing length*

were not significant ($\chi^2_1 = 1.44$, $p = 0.229$ and $\chi^2_1 = 0.66$, $p = 0.414$, respectively). Surprisingly, the three-way interaction *sex* \times *sitting* \times *body mass* had no effect on foraging time ($\chi^2_1 = 0.15$, $p = 0.697$), indicating that the time heavier or lighter individuals spent resting on the water was similar in both sexes during shorter trips in close proximity to the colony, as well as in longer, more distant trips.

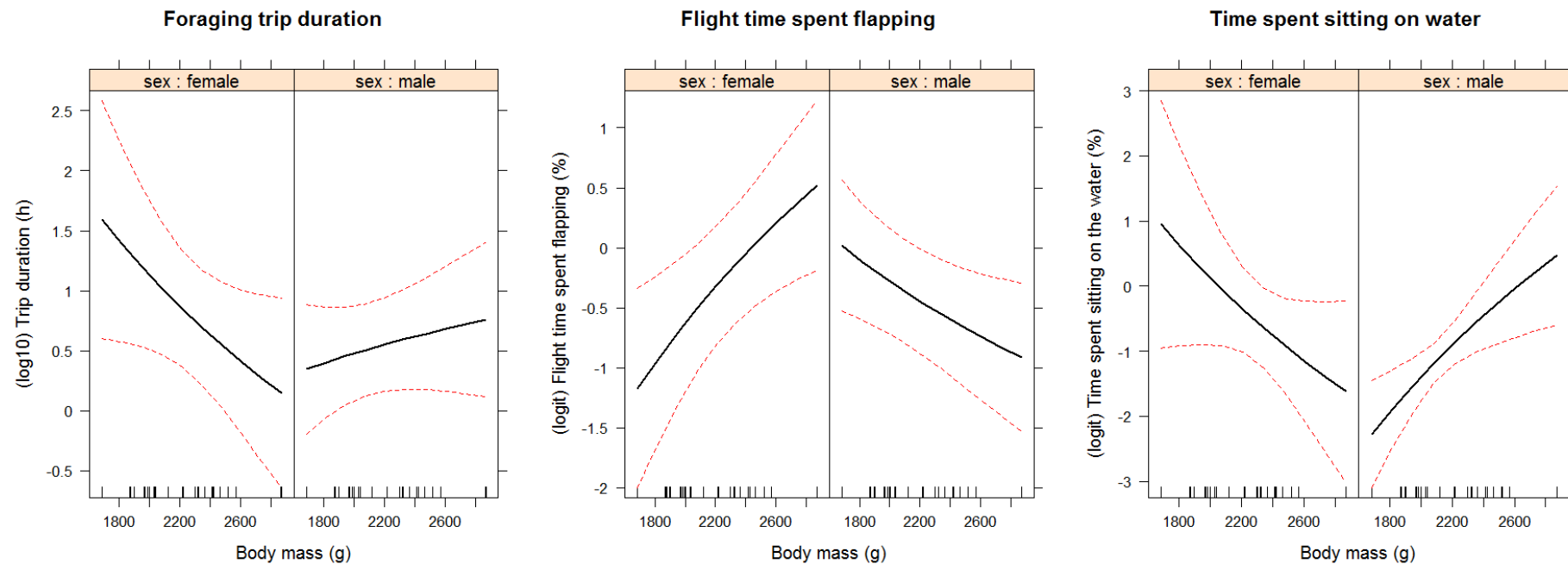


Figure 2.4. Effect display for the interaction $sex \times body\ mass$ on (left) \log_{10} foraging trip duration (h), (middle) logit transformed flight time spent flapping (%) and (right) foraging time spent sitting on the water surface (%). Red-dashed line represents the 95 % pointwise confidence interval around the estimated effect. Vertical black strokes at the bottom of each graph correspond to measured body masses.

Dive behaviour

A total of 796 dives were recorded. Overall, diving accounted for less than 1 % of the time budget of Masked Boobies. Dive depth was not affected by the two-way interactions *sex* × *body mass* or *sex* × *wing length* ($\chi^2_1 = 0.19$, $p = 0.662$ and $\chi^2_1 = 0.01$, $p = 0.904$, respectively) (Table 2.3). The single term *wing length* did not influence dive depth ($\chi^2_1 = 0.37$, $p = 0.548$). However, the difference of distribution of diving depths was statistically significant between sexes ($\chi^2_1 = 6.31$, $p = 0.012$), with greater depths more common in females than in males (Fig. 2.5).

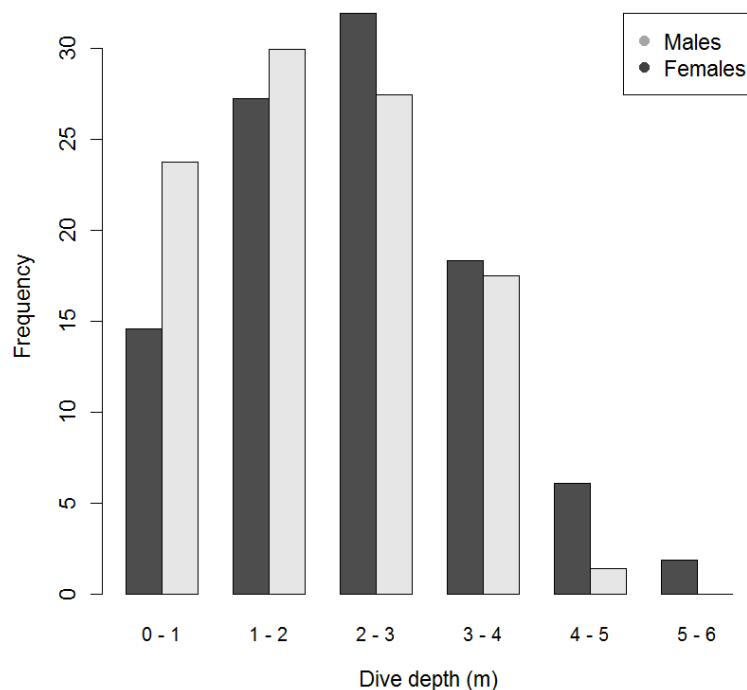


Figure 2.5. Frequency distribution of diving depths of male and female Masked Boobies.

Dive rates were not explained significantly better by the interaction *sex* × *body mass* ($\chi^2_1 = 0.25$, $p = 0.614$) or *sex* × *wing length* ($\chi^2_1 = 0.24$, $p = 0.624$) (Table 2.3) or *wing length* ($\chi^2_1 = 1.84$, $p = 0.174$) and did not differ between sexes ($\chi^2_1 = 1.52$, $p = 0.218$) (Table 2.2).

DISCUSSION

This study examined the effects of individual differences in body mass and wing length within and between sexes on several foraging parameters. Most importantly, individual differences in body mass led to contrasting foraging behaviours in males and females. Consequently, the interpretation of sex-specific foraging behaviour would be overall misleading in this species (except in dive depth and dive rate), because the effect of sex changes with individual body mass.

Wing length

Wing length did not affect foraging trip duration or any of the other foraging parameters in our study, either because there was no effect or, more likely, because wing length is not an ideal descriptive parameter for body size in this species, as indicated by the minimal differences within and between sexes. On Palmyra Atoll in the Pacific Ocean, male and female Masked Boobies differed with respect to body mass, as well as head-to-bill length, while culmen and tarsus lengths were similar between sexes (Young et al. 2010). However, wing measurements were not taken in this study. In Blue-footed and Brown Boobies, wing length used as an index of body size, had a significant effect on maximum foraging range and total distance covered, which in turn were further positively correlated with foraging trip duration (Weimerskirch et al. 2009a). However, differences between female and male wing lengths were considerably greater than in our study species (5 % and 6 % larger in female Blue-footed and Brown Boobies, respectively).

Foraging trip duration and body mass

Lighter individuals within a sex often perform longer foraging trips, reaching more distant foraging grounds due to lower flight costs, as it was found in Brown Boobies, a species with marked RSD (Lewis et al. 2005). In our study, variations in body mass in males had no evident effect on foraging trip duration, indicating that factors other than lower flight costs led males to determine the duration of their foraging trips. Weimerskirch et al. (2009), as well as studies on Blue-footed Boobies (Guerra and Drummond 1995, Velando and Alonso-

Alvarez 2003), demonstrated that a division of labour occurred within a pair. Females had a flexible investment under regulation of their own body mass, while males had a fixed investment. In the study from Weimerskirch et al. (2009), body mass at departure was negatively correlated with foraging trip duration in females, but not in males, as also found in our study. Weimerskirch et al. (2009) further showed that females were the main provisioning parent of the larger chick, i.e. females delivered larger meal masses (i.e. large quantities of energy) and spent more time at sea foraging. Smaller males in contrast, delivered smaller meal masses, but attended the nest significantly more often, suggesting that males invest more in territory defence and nest guarding (Weimerskirch et al. 2009). Meal masses delivered by adults were not measured in our study due to logistical constraints, but similar attendance patterns were observed in masked booby pairs breeding on Phillip Island (H. McCoy, pers. comm.).

From the above, we consider it very likely that Masked Boobies at Phillip Island also exhibit such a sex-specific division of labour. Shorter foraging trips undertaken by heavier females are likely to provision the chick at the expense of their body mass. In contrast, lighter females undertake longer foraging trips at greater distances from the colony to replenish their own body reserves. The evident limitation of our results is that we could not weigh the birds after their return from a foraging trip. We unfortunately cannot ascertain whether heavier females lost weight during those shorter foraging trips, closer to the colony, and if lighter females gained weight after longer foraging trips, further away from the island. However, based on results recorded in Masked Boobies from Clipperton Island (Weimerskirch et al. 2009), as well as in other seabird species (see Clarke 2001, Ropert-Coudert et al. 2004, Kato et al. 2008, Saraux et al. 2011), this seems a plausible explication.

Two explanations have been proposed to explain why foraging trip duration is independent of body stores in males (Weimerskirch et al. 2009). Firstly, males may have a lower body mass safety margin than the larger females, before reaching a critical threshold under which an individual limits its mortality by deserting its nest or by reducing parental effort (Weimerskirch 1998, Weimerskirch et al. 1999, 2009). Secondly, males may be unwilling, irrespective of body mass, to invest more in provisioning their chicks as their primary role is

nest defence, which is safer and more predictable in terms of energy expenditure than foraging (Weimerskirch et al. 2009).

Time budget

In birds, flapping costs increase with body mass (Pennycuik 1972). In addition, higher proportions of flapping have been associated with foraging flight, while there is generally a lower proportion of flapping during travelling flight (Ropert-Coudert et al. 2006). Because the functions of the foraging trips were different within females, as well as between sexes, time budget changed according to body mass. Each sex regulated differently their time budget to optimize their foraging trips. Heavier females increase their energy expenditure during shorter trips in order to maintain a high provisioning rate of the chick (i.e. more time spent flapping/foraging and less resting), while lighter females restore their body reserves during longer trips (i.e. less costly flapping flight and more resting periods). Time spent resting at the water surface might further allow lighter adults to digest and, at least to some extent, assimilate already ingested food. These physiological processes would reduce the total mass of food individuals have to carry back, or alternatively, would make space in the stomach for storing more food for their chicks, before returning to the colony (Sibly 1981, Jackson 1992, Guillemette 1994, Ropert-Coudert et al. 2004a).

Foraging trip duration of males, in contrast, is independent of body mass, suggesting that males are not willing to increase chick provisioning under expense of their own body mass (see argumentation above). Differences observed between lighter and heavier males might thus be primarily related to an energy-efficient foraging strategy due to prevailing body mass, as we would have expected. Heavier males spent less time flapping (i.e. more time gliding) and more time resting on the water to save energy, while lighter males are already flying in an energy-efficient mode. For example, within the Sulidae, the larger and heavier gannets (Lewis et al. 2004, Ropert-Coudert et al. 2004a, Garthe et al. 2007, Green et al. 2010) spend considerably more time sitting on the water than lighter, smaller boobies (Lewis et al. 2005). Resting for prolonged periods at the water surface probably allows the larger and heavier birds to recover from their energetically more costly flight in comparison

with lighter birds (Ropert-Coudert et al. 2004a, Green et al. 2010). However, we cannot exclude the possibility that differences in prey distribution may, in addition to energetic flight costs, have influenced the time budget of the individuals. Unfortunately, no data on prey distribution is available to support or reject this possibility.

Diving behaviour

Body mass and size differences between sexes and specific nutritional requirements may facilitate feeding niche segregations, including underwater niches, in seabirds with regard to foraging areas and/or diet (Kato et al. 1999, Lewis et al. 2005, Zavalaga et al. 2007). Foraging ranges overlapped extensively between sexes, and body mass, regardless of sex, had no effect on dive depths and rates in Masked Boobies. However, females dived on average deeper than males, indicating that factors other than body mass play an important role in dive depth. Such a sex-based segregation may not be so surprising since different dive depths between sexes have also been documented in monomorphic species, such as northern gannets, where females dive deeper than males (Lewis et al. 2002). By diving deeper, females may have access to different prey as shown in Blue-footed Boobies breeding on Isla Lobos de Tierra (Peru). These females dive deeper and consume larger prey, primarily peruvian anchovies *Engraulis ringens*, than do males (Zavalaga et al. 2007). However, such segregation may not be always observed: male and female Blue-footed Boobies, breeding on Isla San Ildefonso in the Gulf of California (Mexico), dive to similar depths (Weimerskirch et al. 2009a). In our study, females may dive deeper to catch different prey types or sizes due to differing nutritional requirements compared to males and/or to deliver different prey items to the chick. Although we were not able to collect prey samples here, dietary analyses of masked boobies breeding on Lord Howe Island (Priddel et al. 2005), approximately 900 km south-west of Phillip Island, and of birds breeding on Raine Island in the far northern Great Barrier Reef (Blaber et al. 1995), showed that these birds feed almost exclusively on flying fish (*Cheilopgon* spp. and Exocetidae, respectively), with fewer squid samples (Ommastrephidae). It is therefore reasonable to assume that masked boobies of Phillip Island feed on similar prey. Flying fish generally occur near the surface

(Cervigón et al. 1992), but it is unknown whether larger individuals occur at greater depths. The depth at which flying fish occur may further be influenced by the presence of subsurface predators such as tuna or dolphins, which drive them to the surface, where they become accessible to seabirds (Frimodt 1995, Ballance and Pitman 1999). Foraging in association with subsurface predators is an important foraging strategy in tropical seabirds (Ballance et al. 1997, Ballance and Pitman 1999), including masked boobies (e.g. Ballance et al. 1997, Mills 1998, Weimerskirch et al. 2008).

Conclusions

Our findings reveal that a combination of differences in individual body masses and parental roles (but the latter was not explicitly tested) influences the foraging behaviour of chick-rearing Masked Boobies. As such, individual characteristics, such as body mass, are as important as sex-specific foraging strategies. This underlines the need to account for intrinsic factors when examining the effects of extrinsic, environmental factors in sexually dimorphic species.

It has been shown in several species that parents adjust their foraging strategies according to changes in the availability and distribution of prey (e.g. Croxall et al. 1999, Burke and Montevecchi 2009, Garthe et al. 2011). However, despite such behavioural adjustments, changes in prey availability often lead to a dramatic decrease in reproductive success (e.g. by 50 % in Grey-headed Albatrosses *Diomedea chrysostoma* and by 90 % in Black-browed Albatrosses *D. melanophris* and Gentoo Penguins *Pygoscelis papua*; Croxall et al. 1999). This suggests that at least some individuals are restrictive in the increase of their parental effort. For example, the ability of Antarctic Petrels *Thalassoica antarctica* to adjust their parental effort depends upon their own body condition (Tveraa et al. 1998). Parents deserted the egg when their body mass reached some critical lower threshold (Tveraa et al. 1997). In this context, effects of changes in the temporal and spatial availability and distribution of prey could have different effects upon individuals of varying body masses within the same sex.

For example, in species exhibiting RSD and a division of labour, heavier individuals with a fixed breeding investment (*e.g.* male Masked and Brown Boobies) may be unable or unwilling to modify their time budgets at sea (*e.g.* spend more time in flight/flapping in search of food and less time resting) than their lighter counterparts. The latter, on the other hand, may have a lower critical body mass threshold. Conversely, individuals with a flexible breeding investment (*e.g.* female Masked and Brown Boobies) may cope better with changes in food availability. Nevertheless, they may be unable to maintain their role as the main parent provisioning the chick, once a critical lower body mass threshold is reached and/or males abandon offspring.

It is also important to emphasize, that a potential limitation of this study might be the relatively short study period (two and three weeks of each breeding season, respectively). Results shown should therefore be interpreted with caution and hypotheses confirmed in further long-term studies. Studies investigating the effects of individual body mass differences within a sex in species where no division of labour occurs would further help to disentangle the confounding effects of body mass and sex on foraging strategies.

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and in accordance with the principles and guidelines of the Animal ethics committee of the University of Tasmania.

Chapter 3 – Response of a marine predator, the Masked Booby, to spatial and temporal changes in the availability and distribution of prey

ABSTRACT

Marine resources are often patchily distributed, but shelf-edges and local upwelling promote the predictability and availability of prey to marine predators due to higher nutrient concentrations. Air-breathing marine predators often forage in dive bouts and both bout size and distances between dives within a bout have been related to the quality and density of prey patches, whereas distances between bouts reflect prey encounter rates. This study compared the diving behaviour and foraging movements of chick-rearing Masked Boobies *Sula dactylatra* at Phillip Island, Australia (South Pacific) over three study periods (early (*E1*) and late (*L1*) phase of the first breeding season and the following early season (*E2*)) under varying oceanographic conditions. Masked Boobies foraged in two distinct areas: over the nearby shallow shelf ('local foraging area') and over distant deeper waters ('distant foraging area'). Adults showed strong foraging site fidelity within the local foraging area between trips, but also between study periods. In this area, sea surface temperatures (SST) were overall lower and chlorophyll *a* concentrations (CHL) higher, suggesting permanent (or at least long-term) upwelling, providing predictable prey encounters. In *E1*, although CHL was relatively low, adults concentrated their foraging activities within the local area. In contrast, during *L1* (similar CHL as in *E1*, highest SST) and *E2* (highest CHL, similar SST as in *E1*), numerous long displacements into the distant foraging area were observed, indicating food scarcity, despite higher CHL, near the colony. Local foraging trips presumably ensure that chicks are fed more frequently, but the yield of these trips appears to be insufficient (except in *E1*) for adults to maintain their own body reserves while providing regular meals to the chicks, forcing adults to forage in more distant waters for self-feeding. In the distant foraging area, birds foraged in higher quality prey patches, as indicated by increased dive rate and bout size, but prey encounter rates, although similar between both foraging areas, were more variable, indicating less predictable prey encounters. Stable isotope analysis indicated that birds fed on higher trophic level prey items within the local foraging area, thereby covering the energetic requirements of both adults and chicks in *E1*, but not in *L1* and *E2*. This study revealed that, when food was scarce, birds experienced a trade-off between local foraging trips, where prey encounters were predictable but of lower

quality, in order to deliver more energy to the chick, and distant trips, presumably for self-feeding, where prey patch quality was higher, but prey encounters less predictable.

INTRODUCTION

Marine predator foraging behaviour depends largely on the distribution, abundance and reliability of their prey (Staniland et al. 2006), but also on intrinsic factors such as body mass and sex (*e.g.* Hindell et al. 1991, Kato et al. 2008). Marine food resources are generally distributed in patch hierarchies, with smaller-scale patches of high prey density nested within larger-scale patches of low density (Kotliar and Wiens 1990, Wu and Loucks 1995). Meso-scale oceanographic features, such as seamounts, fronts, shelf-edges, eddies or upwelling, determine the spatial distribution of primary productivity and are responsible for the transport and concentration of nutrients and plankton (Haury et al. 1978). This leads to a scale-dependent spatial pattern in the availability of resources to small pelagic schooling fish and krill, which in turn are prey for seabirds and other top marine predators (see review in Hunt and Schneider 1987 and Weimerskirch 2007; Boyd 1996, Harcourt et al. 2002). The influence of marine resource patchiness on predator foraging behaviour and ultimately life-history, and the ability of a predator to detect, feed and move optimally within and among prey patches, are central questions in ecology (Senft et al. 1987, Fauchald 1999).

Foraging site fidelity in marine animals is an indication that individuals are able to associate particular oceanographic features with predictable prey encounters (see Hunt et al. 1999 for review, Bradshaw et al. 2004, Weimerskirch 2007). The knowledge of such prey encounters, however, often decreases with distance and/or increasing spatial and temporal variation in resource distribution patterns (Fauchald 1999). Foraging site fidelity in central-place foragers, such as seabirds for instance, is related to the distance between the colony and the feeding grounds, with individuals being more faithful to nearby foraging sites and less faithful to more distant sites (Weimerskirch 2007). The longer it takes for an individual to return to the same foraging ground, the more likely that food resources may have moved (actively or passively) or been depleted (Weimerskirch 2007). However, long-ranging Wandering *Diomedea exulans* and Black-footed *Phoebastria nigripes* Albatrosses show high

foraging site fidelity to distant shelf-edges located more than thousands of kilometres from the colony, but not over distant oceanic waters (Weimerskirch 2007). This suggests that foraging site fidelity is also largely influenced by the type of meso-scale habitat that facilitates reliable prey encounters.

The quality of the foraging grounds (*e.g.* prey abundance) also plays an important role in the foraging decisions of animals. In seabirds, the alternation of short and long foraging trips during the high-energy demanding chick-rearing phase is generally associated with relatively resource-poor waters in close proximity to the colony (*e.g.* Chaurand and Weimerskirch 1994, Weimerskirch 1998, Weimerskirch and Cherel 1998). During short foraging trips, birds utilise these lower quality waters in order to maintain a high feeding frequency to the chick, generally at the expense of their own body condition. Longer foraging trips to more distant, but relatively productive, areas are used for self-provisioning (*e.g.* Granadeiro et al. 1998, Thalmann et al. 2009). In environments where resources are abundant, this alternation strategy disappears (Phillips et al. 2009).

Many marine predators forage in bouts (*e.g.* New Zealand Fur Seals *Arctocephalus forsteri* Harcourt et al. 2002, Cape Gannets *Morus capensis*, Ropert-Coudert et al. 2004, Peruvian Boobies *Sula variegata* and Guanay Cormorants *Phalacrocorax bougainvillii*, Weimerskirch et al. 2012) and both bout size (*e.g.* number of dives within a bout) and the distances between feeding events within a bout have been related to the quality and the density of prey patches (Boyd 1996, Mori 1998). Furthermore, distances between bouts, that is, the distance an animal has to travel to find the next available prey patch, can be used as a proxy for encounter rates, as the distances marine predators travel between prey patches should increase when prey patches are more dispersed (Boyd 1996). Consequently, inferences can be drawn about the quality, density and distribution of prey patches by investigating dive bout characteristics in air-breathing predators, while the predictability of prey encounters can be examined by studying foraging site fidelity.

We investigated this by analysing the foraging behaviour of Masked Boobies *Sula dactylatra* breeding at Phillip Island (Norfolk Island Group), Australia (South Pacific). Foraging movements of Masked Boobies vary considerably between populations (*e.g.* Weimerskirch

et al. 2009, Young et al. 2010), most likely due to differences in the availability of prey near the colonies, as was also found in other seabirds (*e.g.* Thick-billed Murres *Uria lomvia*, Falk et al. 2002; Wedge-tailed Shearwaters *Puffinus pacificus*, Peck and Congdon 2006). We determined:

- (I) The duration of foraging trips, foraging ranges and distances travelled during the energy demanding chick-rearing period to examine if foraging trips of varying trip length occur.
- (II) Bout size and dive rate as a proxy for prey patch quality in relation to the distance from the colony.
- (III) Distances between successive dives within a bout and distances between dive bouts as proxies for prey density within a patch and prey encounter rates, respectively, in relation to the distance from the colony.
- (IV) Individual foraging site fidelity between successive foraging trips.

In addition, we examined if prey encounter rates and quality of prey patches change between seasons. We used satellite images to assess whether foraging areas are static or change among seasons with respect to sea surface temperature and chlorophyll *a* concentration. Hereafter, 'prey encounter rates', as well as 'quality or density of prey patches' mentioned within the context of this study, refer to above defined diving parameters.

MATERIAL AND METHODS

Study site and species

Masked Boobies were studied on Phillip Island (29°02'S, 167°57'E) in the south-west Pacific Ocean. Phillip Island (190 ha) is part of the Norfolk Island Group, Australia, located approximately 1670 km north-east of Sydney, Australia and 1070 km north-west of Auckland, New Zealand. This group of islands lies on top of the Norfolk Island Ridge, where water depths range from only several meters to > 5000 meters (Williams et al. 2006). Masked Boobies are the largest of all boobies and exhibit strong reversed-sexual dimorphism (RSD, where females are larger than males, Nelson 1978). Females lay two eggs,

but generally only one chick is reared through obligate siblicide (Dorward 1962). The breeding season of Masked Boobies is protracted, with chicks hatching between early September and late March, although the majority of chicks hatch between October and December (Hermes et al. 1986, Priddel et al. 2010).

Birds were studied in three fieldtrips over two successive breeding seasons: (1) between 28 October 2009 and 07 November 2009, corresponding to the early phase/peak of the breeding season (hereafter *E1*), (2) between 12 February 2010 and 03 March 2010, corresponding to the late phase of the same breeding season (hereafter *L1*), and (3) between 27 October 2010 and 10 November 2010, corresponding to the early phase/peak of the following breeding season (hereafter *E2*).

Data devices and deployment

Three different types of GPS loggers were used to study the foraging movements of Masked Boobies: (1) CatTraQ GPS logger (44 x 27 x 13 mm, 22 g, Catnip Technologies, P.O. Box 383, Anderson, SC 29622, USA), (2) Sirtrack Micro GPS logger (64 x 33 x 14 mm, 18 g, Havelock North, New Zealand) and (3) Earth & Ocean GPS data loggers (46 x 32 mm, 20 g, Earth & Ocean Technologies, Kiel, Germany). CatTraQ loggers recorded time, latitude and longitude every 2 min, Sirtrack loggers every 5 min and Earth & Ocean loggers every 4 min. CatTraQ and Sirtrack loggers were only deployed during *E1*. Each CatTraQ unit was put in a heat-shrink tube for waterproofing. GPS loggers were attached on the top of three central tail feathers using waterproof adhesive TESA® tape (Beiersdorf AG, GmbH, Hamburg, Germany) to minimize the damage to the feathers (Wilson et al. 1997).

Cylindrical four channel depth-acceleration loggers (M190-D2GT, 12 bit resolution, 53 x 15 mm, 17 g, Little Leonardo, Tokyo, Japan) were used to study activity patterns of Masked Boobies in *L1* and *E2*, simultaneously recording depth (1 Hz), temperature (1 Hz) and acceleration (16 Hz) along two axes. The relative accuracy for the depth sensor was 0.1 m. The loggers contained an acceleration sensor measuring both dynamic (*e.g.* vibration) and static (*e.g.* gravity) accelerations. Loggers were attached underneath three central tail

feathers (in addition to GPS logger attached on the top) using TESA® tape to measure the surging acceleration along the longitudinal body axis and heaving acceleration dorso-ventrally (for details, see Watanuki et al. 2003, Ropert-Coudert et al. 2004).

Attachment weight, including tape, was 55 g (range 45 – 60 g, n = 49), corresponding to 2.3 % of female mean body mass (2436 g, range 2085 – 2870 g, n = 21) and 2.4 % of male mean body mass (2108 g, range 1685 – 2750 g, n = 28) (Phillips et al. 2003, Wilson and McMahon 2006, but see Vandenabeele et al. 2012). Either the female or the male within a pair was chosen randomly and captured with a noose-pole. Adults were sexed by voice (males have a distinctive higher pitched than females) and by measurements (males are smaller than females within a pair) (Nelson 1978). At first capture, birds were weighed using a spring balance (Pesola®, maximum deviation ± 0.3 % of load) and colour-marked on the breast with a green or blue sheep crayon for identification of the equipped individual in the field. Non-banded adults were banded with a metal leg band (Darvic®, Australian Birds and Bats Banding Scheme). After attachment of the loggers, adults were released onto their nests. All data loggers were retrieved after 1 – 4 days, recording 1 – 4 successive foraging trips. Upon retrieval, whole blood from a foot vein for stable isotope analysis was collected and stored in 70 % ethanol (storage in 70 % ethanol does not alter the isotopic composition of whole blood; Hobson et al. 1997). To minimize disturbance, only one individual in a pair was studied and individuals were never studied twice. No nests were deserted during the entire duration of the study and all loggers were retrieved successfully.

Data analysis

Foraging areas and site fidelity

Masked Boobies did not show a clear bimodal foraging trip distribution, as found in many other seabird species (e.g. Wedge-tailed shearwaters *Puffinus pacificus*, Congdon et al. 2005, Peck and Congdon 2005; Red-tailed Tropicbirds *Phaethon rubricauda*, Sommerfeld and Hennicke 2010; Little Penguins *Eudyptula minor*, Saraux et al. 2011). However, the frequency distribution of foraging trips was highly variable, with trips lasting only a few

hours, up to several hours or even days (Fig. 3.1). In order to investigate whether the diving behaviour differed between trips of varying duration and distance, trips were categorized into two distinctive types of trip: “local” vs. “distant”. This categorization was based on the median trip duration and diving location relative to the colony. Briefly, (I) individual foraging tracks and diving locations were plotted on a map and overlaid with 0.25 degree grid cells (each 0.25° grid cell corresponding to approximately 28 km²). (II) The median foraging trip duration was calculated: median trip duration was 4.92 h (n = 87). (III) The location of all dives in trips lasting < 5 h and > 5 h were plotted on the gridded map. (IV) The area of adjacent grid cells containing all dive locations of trips lasting < 5 hours was consequently defined as the “local foraging area”. This resulted in a local foraging area of approximately 250 km² (9 x 0.25° adjacent grid cells) located, except for one grid cell, to the south of Norfolk Island in *L1* and *E2* (Fig. 3.2). All trips within this area are consequently referred to as “local foraging trips”. The “distant foraging area” corresponded to the grid cells containing dives of trips > 5 h, which measured approximately 1150 km² in size (41 x 0.25° grid cells) (Fig. 3.2). All trips outside the local foraging area are referred to as ‘distant foraging trips’.

Foraging site fidelity was defined as the percentage of birds that dived within the same site from one foraging trip to the next, the location of at least one of the dives being within the same 0.25° grid cell as during the previous trip.

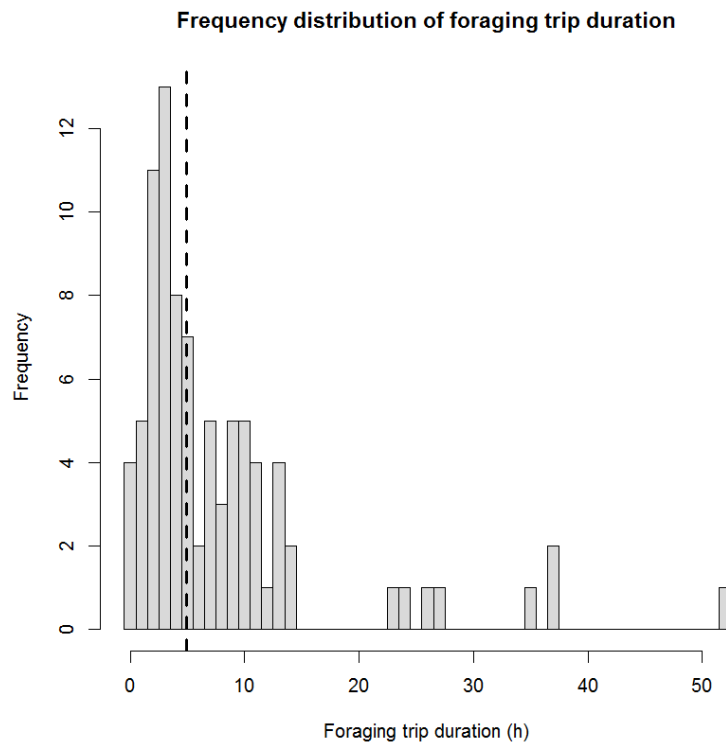


Figure 3.1. Frequency distribution of foraging trip duration (h) in Masked Boobies. Dashed line represents the median trip duration of 4.92 h.

Dive characteristics

Depth data were analysed using IGOR Pro 6.21 (Wavemetrics software, Portland USA). All dives < 0.2 m were excluded from the analyses. Dive bouts were determined using a bout ending criteria following Gentry and Kooyman (1986). Briefly, dives from all individuals were pooled and the dive bout ending criteria defined using the first inflection in a log-survivorship curve of post-dive intervals (Gentry and Kooyman 1986). This corresponded in Masked Boobies to an inflexion point of 780 s, allowing us to define discrete dive bouts. The start of a bout corresponded to the first dive, so that single dives corresponded to bouts of size '1' (taken to indicate the lowest prey patch quality). Dive rates corresponded to the total number of dives divided by the time spent at sea (excluding hours of darkness for overnight trips) within each 0.25° grid cell during each foraging trip. Distances between dives in a bout were calculated as the linear distance between two dive locations and used

as a proxy for prey density within a patch. Distances between bouts were calculated as the linear distance between the mean locations of two bouts and used as a proxy for prey encounter rates.

Environmental data and foraging habitat characteristics

Three different environmental variables downloaded from <http://coastwatch.pfeg.noaa.gov/erddap> were selected to characterize birds foraging habitat: (1) bathymetry, (2) sea surface temperature (SST) and (3) chlorophyll *a* concentration (CHL, as a proxy for primary productivity). Monthly composites of daytime SST and surface CHL were obtained from Aqua MODIS satellite images, provided at 0.05° spatial resolution. Bathymetry (Global topography, ETOPO1) was obtained at a 0.01° spatial resolution.

We described the foraging habitat of Masked Boobies in two steps: (1) at a broad-scale by contrasting SST and CHL between the maximum foraging ranges of the birds (obtained in this study) located to the south (*i.e.* latitudes between 29.0°S and 31.0°S) and north (*i.e.* latitudes between 27.0°N and 29.0°N) of Phillip Island among *E1*, *L1* and *E2*, and (2) at a fine-scale by contrasting CHL and bathymetry within and outside the local foraging area in *E1*, *L1* and *E2*. For comparing habitats, bathymetry, monthly SST and CHL values were averaged for each 0.25° grid cell.

Stable isotope analysis

Stable isotopes of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) in seabird tissue are derived from the isotopic values of their prey, providing an insight into the origin and type of prey consumed, although detailed information on prey taxa cannot be derived (Cherel et al. 2008). Carbon isotope values tend to increase from inshore to offshore (benthic vs. pelagic) in both tropical and temperate regions (Cherel et al. 2008). Nitrogen isotope values increase in a predictable manner with each trophic step, indicating the trophic position of a consumer (Vanderklift and Ponsard 2003). Avian erythrocytes, which we used to measure isotopic values, have a

lifespan of 28 to 45 days (Rodnan et al. 1957). Therefore, they most likely represent assimilated prey over the previous 4 to 6 weeks. As birds fed in both local and distant foraging areas within this time frame, we could not test for differences in the $\delta^{13}\text{C}$ and the $\delta^{15}\text{N}$ signature between foraging areas because isotope values would correspond to a mixture of the diets from both foraging habitats. Thus, we used stable isotope signatures to test for differences in the trophic levels consumed between the three study periods *E1*, *L1* and *E2*. Samples were analysed at the Research School of Biology Laboratory of the Australian National University in Canberra, Australia. Elemental precisions were 0.4 ‰ for both nitrogen and carbon.

Statistical analysis

All statistical analyses were performed using R 2.15.1 (R Development Core Team 2012). Generalized linear mixed models (GLMM, Faraway 2006), generalized linear models (GLM) and non-linear mixed models (LMM, Pinheiro and Bates 2000) were applied using the functions *glmer* and *glm* in R package *lme4* (Bates et al. 2011) and *lme* in R package *nlme* (Pinheiro and Bates 2000), respectively. To test for differences in the duration of foraging trips between seasons, we tested local and distant trips in two separate LMM with \log_{10} transformed trip duration as a response variable including season as a fixed effect and bird ID as a random factor to account for pseudo-replication. Bout size, total number of dives and the number of dive bouts per trip were included in the GLMM as response variables with a Poisson error distribution. Dive rates, distances between dives within a bout and distances between dive bouts were \log_{10} transformed and analysed in a GLMM with a normal error distribution. Foraging area (local vs. distant) and season were included as explanatory variables, with bird ID nested within each individual 0.25° grid cell as a random factor. To compare the variances in bout size, dive rate and distances between bouts, an *F* test was performed. To test for difference in the broad-scale foraging habitat, we fitted a linear model (LM) with \log_{10} transformed SST and CHL as response variables and respective study periods (*E1*, *L1* and *E2*) as fixed terms. We tested for significant differences in water depths between both foraging areas (fine-scale analysis) using a LMM with bathymetry as a

response variable, foraging area as a fixed effect and grid cell ID as a random effect. To test for differences in SST and CHL (response variables) between both foraging areas (fine-scale analysis) and among seasons, we included an interaction between the foraging areas and seasons in the model and used grid cell ID as a random effect. To analyse effects of study period (*E1*, *L1* and *E2*) on $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, we used a GLM as there was only one sample per bird. Model assumptions were checked following Crawley (2007). Correlations were calculated using Kendall's rank coefficient. All tests were two-tailed, with a significance level of $p < 0.05$. Mean ($\pm\text{SD}$) results are reported.

RESULTS

Foraging movements

Of the 49 equipped birds, eight made overnight trips. One male in *E1*, one female in *L1* and four males (with one spending two nights at sea) and two females in *E2*. Four of these foraging trips were excluded from the dive data analysis, three due to battery exhaustion in the depth-acceleration loggers before birds returned to the colony, and a further one as the male in *E1* had only a GPS attached with no depth recorder. The total number of equipped birds and foraging trips recorded with GPS and depth-acceleration loggers are summarized in Table 3.1. Due to low sample size, the effect of sex on foraging parameters could not be tested. Data of both sexes were therefore pooled.

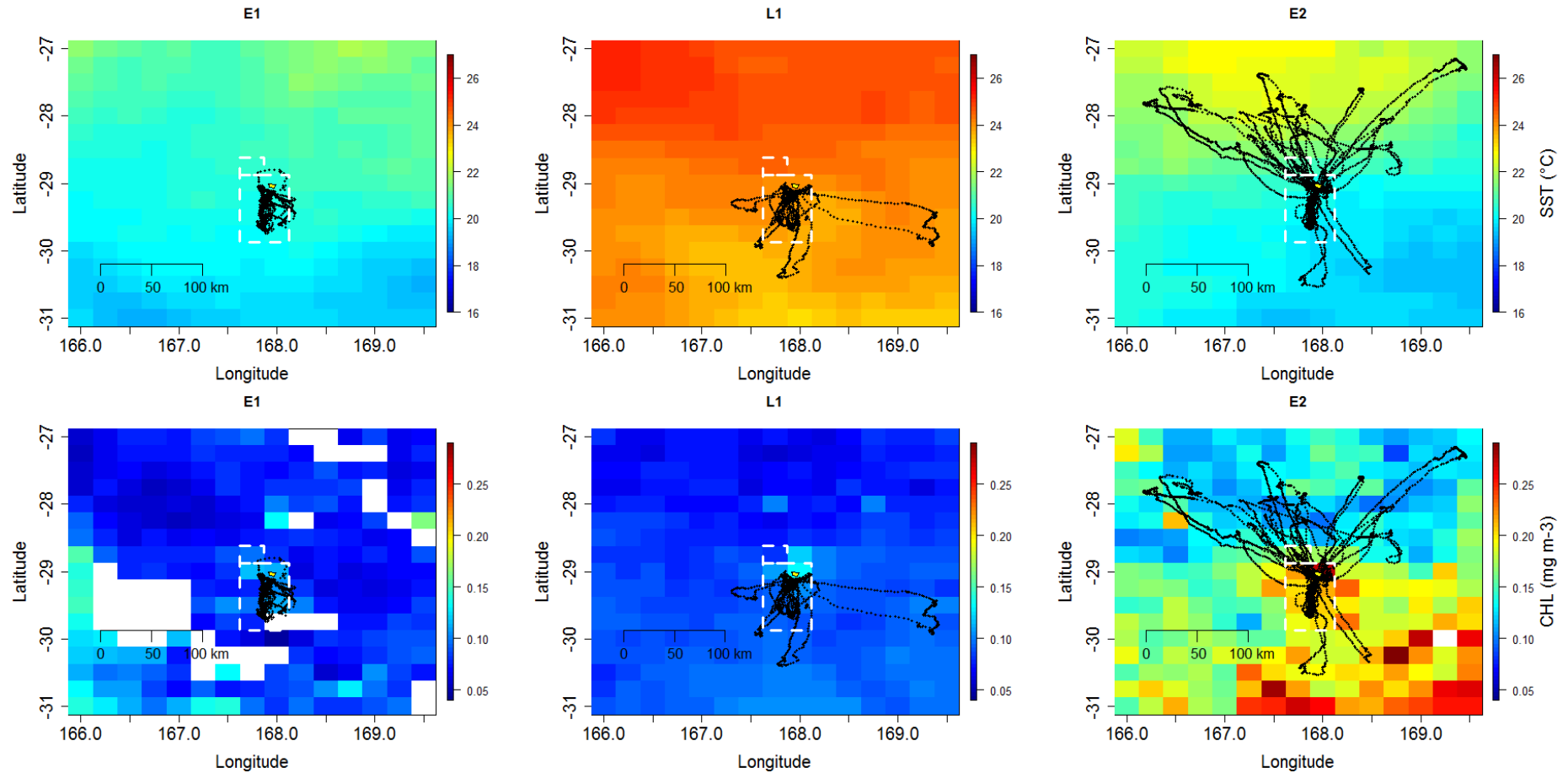


Figure 3.2. Foraging movements of Masked Boobies during early (*E1*) and late (*L1*) phase of the first breeding season and following early season (*E2*). Sea surface temperature (SST, top row) and chlorophyll *a* concentration (CHL, bottom row) are mean monthly values of each 0.25° grid cell. Local foraging area is represented by the white dashed line (note: one 0.25° grid cell is located north of Norfolk Island). White grid cells correspond to missing CHL values.

Masked Boobies concentrated their foraging activity almost exclusively within the local foraging area to the south of Norfolk Island in *E1*, whereas numerous long displacements took place to the south in *L1* and predominantly to the north in *E2* (Fig. 3.2). Irrespective of these very distinctive foraging movements, both types of trip (local vs. distant) were of similar durations across the three study periods (ANOVA $F_{2,25} = 2.35$, $p = 0.116$, $F_{2,25} = 1.17$, $p = 0.325$, respectively). Foraging trip duration was positively correlated with foraging range (Kendall $z = 9.56$, $p < 0.001$, $\tau = 0.70$, $n = 87$) and total distance travelled (Kendall $z = 10.42$, $p < 0.001$, $\tau = 0.76$, $n = 87$) (Fig. 3.3). Foraging ranges of trips within the local and distant foraging areas were similar between study periods (ANOVA $F_{2,25} = 0.31$, $p = 0.736$ and $F_{2,25} = 1.61$, $p = 0.220$, respectively), although the maximum foraging range in distant trips was almost four times greater in *E2* than in *E1* (Table 3.2). The total distance that the birds travelled did not differ significantly between study periods (ANOVA $F_{2,25} = 0.65$, $p = 0.531$ and $F_{2,25} = 2.02$, $p = 0.154$, respectively) (Table 3.2).

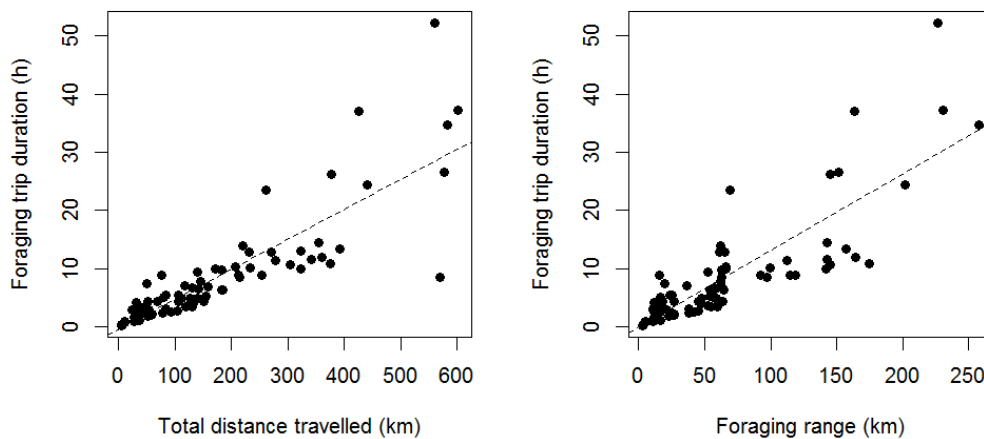


Figure 3.3. Relationship between foraging trip duration and total distance travelled and foraging range in Masked Boobies.

Breeding season	Device type	No. birds equipped	No. complete trips with position and dive data	No. complete trips with position data only
<i>E1</i>	CatTraQ + Sirtrack	21	0	23
<i>L1</i>	Earth & Ocean + DAC	15	23	3
<i>E2</i>	Earth & Ocean + DAC	13	33	5
Total	All devices	49	56	31

Table 3.1. Number of Masked Boobies equipped with GPS (CatTraQ, Sirtrack or Earth & Ocean) and depth-acceleration logger (DAC) and complete foraging trips recorded during early (*E1*) and late phase (*L1*) of the first breeding season and early phase of the following breeding season (*E2*).

Breeding season						
Foraging parameters	<i>E1</i>		<i>L1</i>		<i>E2</i>	
	Local trips (n = 17)	Distant trips (n = 6)	Local trips (n = 16)	Distant trips (n = 10)	Local trips (n = 11)	Distant trips (n = 27)
Trip duration (h)	2.7 ± 1.0 (0.2 – 4.3)	14.7 ± 5.3 (8.4 – 23.4)	3.3 ± 1.2 (0.6 – 4.9)	18.4 ± 13.5 (5.0 – 37.0)	3.8 ± 0.9 (0.3 – 4.8)	23.3 ± 15.2 (5.4 – 52.2)
Foraging range (km)	23.1 ± 18.3 (2.6 – 63.9)	64.5 ± 2.9 (61.5 – 69.3)	24.3 ± 18.7 (4.5 – 59.8)	74.7 ± 47.8 (16.5 – 163.4)	29.5 ± 17.5 (3.9 – 54.8)	115.8 ± 67.5 (15.7 – 258.)
Distance travelled (h)	53.3 ± 43.1 (4.6 – 151.7)	251.5 ± 43.2 (207.8 – 323.8)	58.4 ± 39.9 (10.4 – 139.2)	195.5 ± 116.1 (49.7 – 426.9)	72.7 ± 40.5 (7.7 – 132.8)	303.5 ± 167.2 (76.2 – 602.4)

Table 3.2. Foraging trip duration, range and total distance travelled of Masked Boobies during early (*E1*) and late phase (*L1*) of the first breeding season and early phase of the following season (*E2*). Values are given as mean ± SD. Ranges in parentheses. Sample size (n).

Foraging habitat characteristics

Broad-scale

Within the southern foraging range of Masked Boobies, SST was similar between both early breeding seasons (LM $b = 0.00$, $t = 1.11$, $p = 0.269$), but significantly higher during *L1* (LM $b = 0.07$, $t = 394.71$, $p < 0.001$) (Fig. 3.2, Table 3.3). Whereas north of the colony, SST was significantly higher in *E2* than in *E1* (LM $b = 0.02$, $t = 81.88$, $p < 0.001$), but highest in *L1* (LM $b = 0.07$, $t = 332.35$, $p < 0.001$) (Fig. 3.2, Table 3.3).

Chlorophyll *a* concentration was low overall in surrounding waters, averaging 0.11 ± 0.05 mg m^{-3} (range $0.04 - 0.29$ mg m^{-3}) (Fig. 3.2). South of the colony, CHL was highest in *E2* (LM $b = 0.07$, $t = 34.05$, $p < 0.001$), but similarly low in *E1* and *L1* (LM $b = 0.00$, $t = 0.71$, $p = 0.477$). The same pattern was observed north of the colony with the highest CHL in *E2* (LM $b = 0.04$, $t = 26.24$, $p < 0.001$) and similarly low CHL in *E1* and *L1* (LM $b = 0.00$, $t = 0.63$, $p = 0.530$) (Fig. 3.2, Table 3.3). There was a negative relationship between SST and CHL in all three study periods (*Kendall*, *E1*: $z = -30.96$, $p < 0.001$, $\tau = -0.17$, *L1*: $z = -101.87$, $p < 0.001$, $\tau = -0.51$, *E2*: $z = -112.26$, $p < 0.001$, $\tau = -0.56$).

Fine-scale

The local foraging area consisted of a zone of relatively shallow waters located mainly south of the colony over the shelf-edge of the Norfolk Island Ridge, with an average bathymetry of -579.3 ± 489.2 m (range -1466 to -38.1 m) (Fig. 3.4). The distant foraging area of Masked Boobies was characterized by significantly deeper waters (ANOVA $F_{1,253} = 77.64$, $p < 0.001$), reaching an average bathymetry of -2732.7 ± 765.6 m (range -4033.9 to -676.2 m). Sea-surface temperatures were similar between both foraging areas in *E1* and *L1*, but highest in *L1*. Whereas in *E2*, SST was significantly lower within the local foraging area than it was in the distant area, as indicated by the significant interaction between foraging areas and the three study periods (LMM $\chi^2 = 103318$, $df = 3$, $p < 0.001$) (Fig. 3.2, Table 3.3). Productivity was higher overall within the local foraging area, with similar CHL levels in *E1* and *L1* and the highest level observed in *E2* (Fig. 3.2, Table 3.3). In the distant foraging area, CHL was lower overall than in the local area, but again it was the highest in *E2* and relatively low in *E1* and

L1 (LMM $\chi^2 = 890.75$, $df = 3$, $p < 0.001$) (Fig. 3.2, Table 3.3). During all three study periods, the birds foraged within the local area of higher productivity and lower SST, but they did not travel to the higher CHL zones and cooler waters available within their southern foraging range in *E2*.

	South			North		
	<i>E1</i>	<i>L1</i>	<i>E2</i>	<i>E1</i>	<i>L1</i>	<i>E2</i>
SST (°C)	19.9 ± 0.9 (17.7 – 21.8)	23.8 ± 0.4 (22.5 – 25.0)	19.9 ± 0.5 (18.4 – 22.0)	20.8 ± 0.9 (19.2 – 22.9)	24.6 ± 0.4 (23.5 – 25.7)	21.7 ± 0.8 (19.6 – 25.4)
CHL (mg m ⁻³)	0.09 ± 0.02 (0.04 – 0.14)	0.09 ± 0.01 (0.08 – 0.13)	0.19 ± 0.03 (0.11 – 0.29)	0.07 ± 0.02 (0.05 – 0.16)	0.08 ± 0.01 (0.06 – 0.12)	0.13 ± 0.02 (0.08 – 0.21)
	Local foraging area			Distant foraging area		
	<i>E1</i>	<i>L1</i>	<i>E2</i>	<i>E1</i>	<i>L1</i>	<i>E2</i>
SST (°C)	20.3 ± 0.8 (19.2 – 21.8)	24.0 ± 0.3 (23.3 – 24.8)	20.2 ± 0.5 (19.2 – 21.7)	20.4 ± 0.9 (17.7 – 22.9)	24.2 ± 0.6 (22.5 – 25.7)	20.8 ± 1.2 (18.4 – 25.5)
CHL (mg m ⁻³)	0.10 ± 0.02 (0.08 – 0.12)	0.10 ± 0.01 (0.08 – 0.13)	0.21 ± 0.03 (0.17 – 0.27)	0.08 ± 0.02 (0.04 – 0.16)	0.08 ± 0.01 (0.06 – 0.11)	0.16 ± 0.04 (0.08 – 0.29)

Table 3.3. Broad-scale foraging habitat characteristics within the southern and northern foraging range of Masked Boobies of Phillip Island (South Pacific) and fine-scale habitat characteristics within the local and distant foraging areas during early (*E1*) and late phase (*L1*) of the first breeding season and early phase of the following season (*E2*). Sea surface temperature (SST), chlorophyll *a* concentration (CHL). Values are given as mean ± SD. Ranges in parentheses.

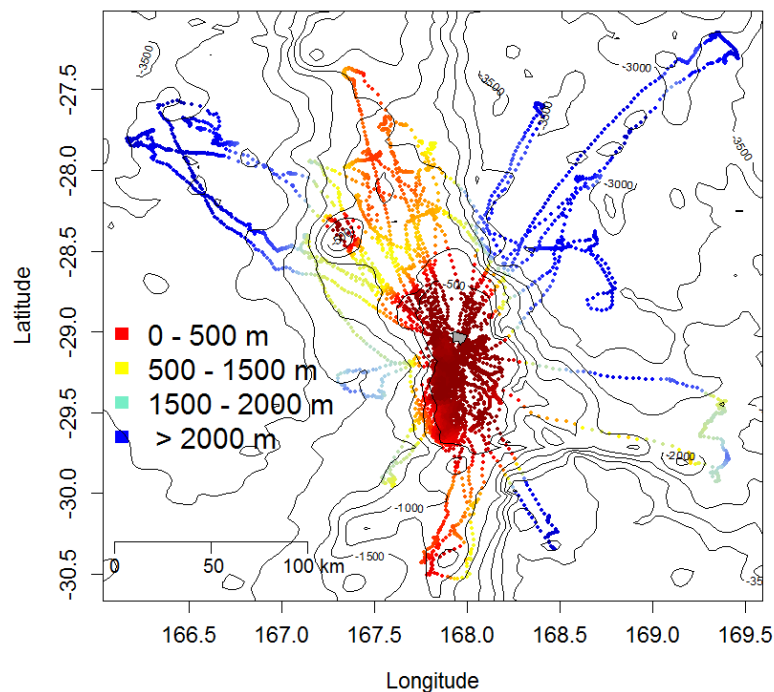


Figure 3.4. Foraging movements of Masked Boobies recorded over the three study periods, coloured by water depth. Bathymetry contours are represented by black solid lines; each line represents 500 m increase.

Dive characteristics

A total of 121 dives were recorded within the local foraging area and 623 dives within the distant area, corresponding respectively to 16.3 % and 83.7 % of the total number of dives recorded. In four foraging trips within the local foraging area (three males and one female), birds performed no dives; these trips lasted between 0.34 and 3.46 hours, with total distance travelled ranging from 7.72 to 188.84 km. Adults performed on average 4.84 ± 4.48 dives (range 0 – 18, $n = 25$) per trip within the local area and 20.10 ± 18.81 dives (range 1 – 73, $n = 31$) per trip in the distant area, which was significantly more often (GLMM $\chi^2 = 45.95$, $df = 1$, $p < 0.001$). Season had no effect on the number of dives (GLMM $\chi^2 = 2.17$, $df = 1$, $p = 0.141$).

Overall, dives were shallow (Table 3.4), with individuals diving to similar depths within and outside the local foraging area (GLMM $\chi^2 = 1.49$, $df = 1$, $p = 0.222$) and between seasons ($\chi^2 = -0.35$, $df = 1$, $p = 1.0$). Dive rates were significantly higher (GLMM $\chi^2 = 11.65$, $df = 1$, $p < 0.001$) and more variable (F-test $F_{67,62} = 0.50$, $p = 0.006$) outside the local foraging area, but did not change between the two seasons (GLMM $\chi^2 = 2.22$, $df = 1$, $p = 0.136$) (Table 3.4).

The average number of bouts per trip was 2.08 ± 1.61 (range 0 – 6, $n = 25$) within the local area, which was significantly lower (GLMM $\chi^2 = 36.37$, $df = 1$, $p < 0.001$) than the 6.84 ± 5.52 (range 1 – 27) recorded outside the local foraging area. However, the average number of bouts was similar between the two seasons (GLMM $\chi^2 = 1.16$, $df = 1$, $p = 0.281$). Dive bout size was significantly greater (GLMM $\chi^2 = 11.57$, $df = 1$, $p = 0.001$) and significantly more variable (F-test $F_{113,143} = 0.24$, $p < 0.001$) in the distant foraging area. In other words, Masked Boobies encountered prey patches that were on average of higher quality, although more variable, in deeper waters farther from the colony (Fig. 3.5, Table 3.4). Again, this did not change between *L1* and *E2* (GLMM $\chi^2 = 0.40$, $df = 1$, $p = 0.528$). Within the local foraging area, bout size did not differ between seasons (GLMM $\chi^2 = 1.53$, $df = 1$, $p = 0.216$).

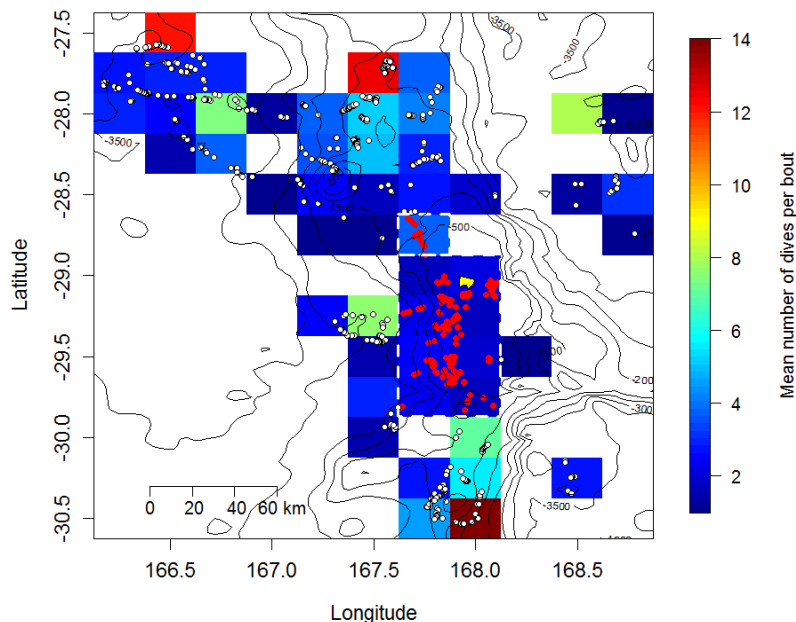


Figure 3.5. Mean number of dives per bout within each 0.25° grid cell. Red points are dives within the local foraging area (white-dashed line). White points with black contour are dives

outside the local foraging area. Bathymetry contours are represented by black solid lines; each line represents 500 m increase. Yellow area represents Norfolk Island.

The distances birds travelled between successive dives within a bout were similar in both foraging areas (GLMM $\chi^2 = 0.08$, $df = 1$, $p = 0.770$) and between the two seasons *L1* and *E2* ($\chi^2 = -1.92$, $df = 1$, $p = 1.000$) (Table 3.4), suggesting similar densities of prey within patches. Distances between dive bouts were also similar in both foraging areas (LMM $\chi^2 = 1.09$, $df = 1$, $p = 0.297$), but significantly more variable (F-test $F_{200,200} = 7.03$, $p < 0.001$) in the distant foraging area. The greatest distance between bouts recorded in the distant foraging area was, at 133.72 km, almost twice the maximum distance recorded inside the local foraging area (76.78 km) (Table 3.4). Season had no effect on the distances between dive bouts (GLMM $\chi^2 = 0.12$, $df = 1$, $p = 0.729$).

Foraging parameters	Foraging trips					
	Local foraging area	n	Distant foraging area	n	Statistics	P value
Dive depth (m)	2.35 \pm 1.51 (0.24 – 6.35)	246	2.77 \pm 1.31 (0.24 – 6.20)	498	GLMM	0.222
Dive rate	2.6 \pm 2.5 (0.22 – 12.08)	68	4.47 \pm 3.53 (0.16 – 18.09)	63	GLMM	< 0.001
Variance of dive rate	6.27	68	12.50	63	F test	0.006
Dive bout size	2.11 \pm 1.75 (1 – 9)	114	3.49 \pm 3.39 (1 – 23)	144	GLMM	0.001
Variance of dive bout size	3.06	114	12.89	144	F test	< 0.001
Distance between successive dives within a bout (km)	0.86 \pm 1.32 (0.01 – 7.34)	132	1.37 \pm 2.32 (0.01 – 22.42)	355	GLMM	0.770
Distance between dive bouts (km)	16.77 \pm 17.96 (0.26 – 76.78)	72	12.58 \pm 19.15 (0.18 – 133.72)	129	GLMM	0.250
Variance of the distance between bouts	322.5	72	366.8	129	F test	< 0.001

Table 3.4. Foraging parameters recorded in Masked Boobies with respect to foraging area (local vs. distant) and statistics. Values are given as mean \pm SD. Ranges in parentheses. Sample size (n). Generalized linear mixed models (GLMM).

Foraging site fidelity

In 14 out of 24 individuals (58 %) more than one foraging trip was recorded within the local foraging area ($n = 43$ foraging trips). Out of the 14 individuals, 10 (71 %) dived within 28 km (*i.e.* within the same 0.25° grid cell) of their previous dive location, while the remaining four individuals dived within 56 km of their previous location. Conversely, in only four out of 12 individuals (33 %) successive foraging trips were recorded outside the local foraging area. Of these four individuals, one adult had at least one dive within 28 km, one adult dived within 56 km and two adults dived within 112 km of their previous dive locations.

Stable isotopes

There were highly significant differences in $\delta^{15}\text{N}$ values between the three study periods. Mean $\delta^{15}\text{N}$ value of $12.6 \pm 0.3 \text{ ‰}$ in *E1* was significantly higher than the mean of $11.5 \pm 0.4 \text{ ‰}$ in *E2* (GLM $b = -1.19$, $t = -10.83$, $p < 0.001$) and the mean of $10.6 \pm 0.7 \text{ ‰}$ in *L1* (GLM $b = -1.06$, $t = -5.54$, $p < 0.001$), when $\delta^{15}\text{N}$ values were lowest (Fig. 3.6). Mean $\delta^{13}\text{C}$ values of $-17.9 \pm 0.2 \text{ ‰}$, $-18.0 \pm 0.6 \text{ ‰}$ and $-17.8 \pm 0.2 \text{ ‰}$, corresponding to *E1*, *L1* and *E2*, were not significantly different between *E1* and *L1* (GLM $b = -0.10$, $t = -0.75$, $p = 0.455$) and *E2* (GLM $b = 0.10$, $t = 0.67$, $p = 0.503$) (Fig. 3.6).

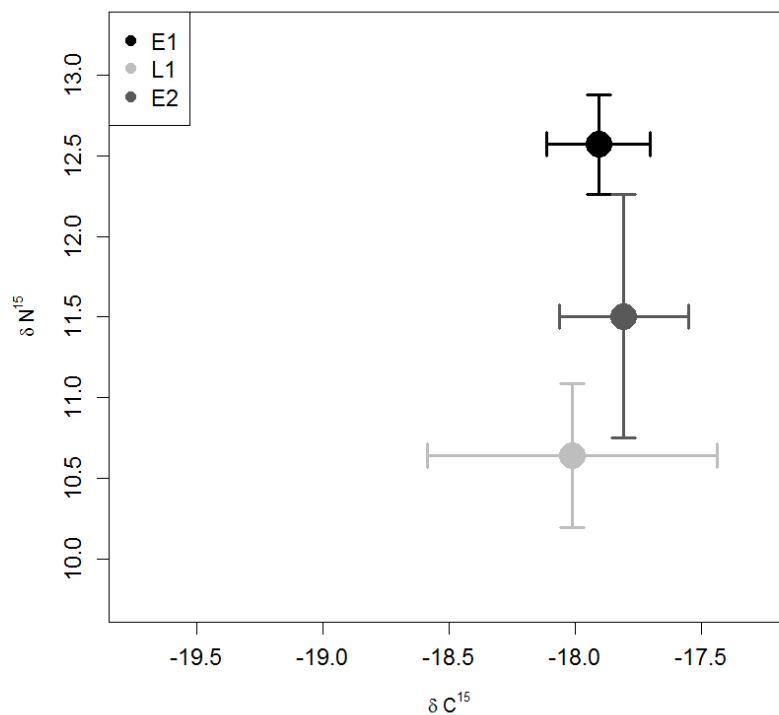


Figure 3.6. Stable carbon and nitrogen isotope values of chick-rearing Masked Boobies across three study periods. Early (*E1*) and late phase (*L1*) of the first breeding season and early phase (*E2*) of the following season.

DISCUSSION

In this study we demonstrated that Masked Boobies nesting at Phillip Island markedly changed their foraging movements within and between seasons. Individuals showed strong foraging site fidelity from one trip to the next within the local foraging area and also at the population level between study periods. The most surprising results of this study were, however, that prey patch quality was higher – yet more unpredictable – in more distant deeper waters than over the shallower shelf close to the colony, as inferred from the behaviour of the birds. In addition, mean distances travelled by adults between prey patches were considerably more variable in more distant deeper waters, indicating that prey encounters are less predictable.

The spatial and temporal predictability of prey modulates foraging site fidelity in marine predators (Weimerskirch 2007). Individuals learn where and when to find prey within their potential foraging range and return to the same feeding areas between trips or breeding seasons so as to maximize foraging efficiency (e.g. Great Cormorants *Phalacrocorax carbo* Grémillet et al. 1999; Northern Gannets, Hamer et al. 2001). Physical factors such as upwelling may locally increase primary production (Haury et al. 1978), thereby influencing the availability and predictability of prey for seabirds and other marine predators (Jaquemet et al. 2005). High CHL in combination with low SST within the local foraging area over the shallower shelf, located at the western edge of the plateau where prevailing currents meet shallow water, are indicative of a permanent, or at least long-term, upwelling (Williams et al. 2006). The repeated use of this area throughout the study period suggests that Masked Boobies associate this habitat feature with predictable prey encounters (see review in Hunt et al. 1999, Weimerskirch 2007). Foraging site fidelity in tropical species is rare (although studies investigating this remain scarce; Weimerskirch 2007) highlighting the importance of the nearby shallow shelf-edge for the foraging behaviour and life-history traits of this Masked Booby population.

In the conceptual framework of classical central-place foraging theory, travelling to more distant feeding grounds will incur increased costs in both time and energy (Orians and Pearson 1979, Stephens and Krebs 1986). These costs must therefore be compensated by increased net energy gain in the prey patches encountered (Orians and Pearson 1979, Stephens and Krebs 1986). This prediction was verified in Masked Boobies. The increased costs associated with travelling to distant foraging grounds are paid-off by foraging in higher quality prey patches and by a higher dive rate. Local foraging trips presumably ensure that chicks are fed more frequently, but the yield of these trips over the shallow shelf-edge are generally insufficient (except in *E1*, see below) for adults to maintain their own body reserves while providing regular meals to their chicks. As a consequence, adults undertake distant foraging trips to feed predominantly for themselves. Although we have no information on the changes in adult body mass after local and distant foraging trips, higher dive rates and greater bout sizes in the distant foraging area probably allow adults to restore body reserves which are then expended during subsequent local trips (but see

Weimerskirch et al. 2009 for differential parental roles in Masked Boobies). This has been reported in a range of species (*e.g.* Weimerskirch et al. 1994, Granadeiro et al. 1998, Peck and Congdon 2006, Paiva et al. 2010, Saraux et al. 2011). When food became scarce within the local foraging area, adults appeared to experience a trade-off between foraging trips over the shallow shelf, where prey encounters were predictable but of lower quality, in order to deliver more energy to the chick, and predominantly self-feeding distant foraging trips in deeper waters, where prey patch quality was on average higher, although more variable, and prey encounters less predictable. By undertaking distant foraging trips adults not only accept the associated increased costs, they also accept the risk of foraging in an environment where prey encounters are less predictable. In Wandering Albatrosses, distances between dive bouts were shorter over the nearby shelf and slopes than over deep oceanic waters, indicating that their prey, mainly squid, were more dispersed in deeper waters and thus less predictable (Weimerskirch et al. 2007), as was also found in this study.

In contrast to our observation of no seasonal differences in prey distribution between *L1* and *E2*, the time individual Fur Seals spent travelling between foraging bouts, which corresponded to the spacing of krill swarms measured during ship-based hydro acoustic surveys (Miller et al. 1993, Boyd 1996), varied between years, indicating inter-annual variability in the spatial distribution of prey (Boyd 1996).

Optimal foraging theory predicts that animals should forage so as to maximize net energy gain (MacArthur and Pianka 1966, Schoener 1971, Stephens and Krebs 1986) and distribute themselves so as to maximize foraging efficiency (Fretwell and Lucas 1970). Chick-rearing adults foraged exclusively within the local foraging area in *E1*, but alternated between both foraging areas in *L1* and *E2*. We propose three hypotheses, which may be non-mutually exclusive, for the observed changes in foraging movements between the three study periods.

(I) Intra- and interspecific competition for prey may have been higher in *L1* and in particular in *E2*, forcing adults to fly to more distant areas to find undisturbed fish schools. Masked Boobies may have undertaken long foraging trips to reach more distant foraging grounds to

avoid foraging in 'Ashmole's halo' (*i.e.* a zone near dense seabird colonies in which prey is less abundant due to high intra- and inter-specific competition; Ashmole and Ashmole 1967, Birt et al. 1987), in *L1* and *E2*, but not in *E1*. However, a change in the availability and abundance of prey nearby the colony due to prey depletion seems unlikely. Prey encounter rates and prey patch quality within the local foraging area were similar between *L1* and *E2*, *i.e.* between the late breeding season when considerably fewer birds are breeding and the early (peak) of the breeding season when bird numbers were the highest. Moreover, prey depletion near Philipp Island seems unlikely in such a relatively small population, since prey depletion near colony not even occurred in the world's largest Masked Booby colony on Clipperton Island (Weimerskirch et al. 2008). To the contrary, long foraging ranges were thought to be the result of direct intra-specific interference competition on patchy prey resources continuously moving with schools of tuna and dolphins (Weimerskirch et al. 2008).

(II) Prey patch quality may have been higher within the local foraging area in *E1*, enabling adults to feed the chick at regular intervals and maintain their own body mass, making it unnecessary to search for higher quality prey patches elsewhere. Unfortunately, this hypothesis cannot be proved or discarded because no data on dive bout characteristics are available for *E1*.

(III) Masked Boobies were feeding on different prey species in *L1* and *E2* than in *E1*. Isotopic differences in $\delta^{15}\text{N}$ between the three study periods indicated that Masked Boobies might have been feeding on different prey species. Higher values in $\delta^{15}\text{N}$ suggest that chick-rearing adults had access to higher trophic level prey items in *E1* than in *L1* and *E2*. The absence of these higher trophic prey items in *L1* and *E2* nearby the colony may have forced adults to forage in more distant, productive waters. However, we cannot exclude the possibility that adults were feeding on higher trophic level prey items over distant, deeper waters, and on lower trophic level prey items over the shallower shelf-slope as stable isotope values correspond to a mixture of both foraging areas. The intermediate $\delta^{15}\text{N}$ values recorded in *E2* could be a result of this. Observed differences in prey patch quality between both foraging areas could therefore reflect a different spatial distribution of different prey species. White-

chinned Petrels, for example, fed mainly on fish when foraging over a nearby shallow shelf and on a mixed diet of pelagic fish and Antarctic Krill *Euphausia superba*, when foraging over distant, deeper oceanic waters (Catard et al. 2000). Alternatively, adult Masked Boobies could be feeding on the same prey species in both foraging areas, but the prey distribution may have changed according to the habitat, as found in Wandering Albatrosses (Weimerskirch et al. 2007).

In chick-rearing Northern Gannets, inter-annual differences in foraging ranges and diving behaviour (birds were studied over two consecutive years) corresponded to changes in oceanic conditions and prey availability (Garthe et al. 2011). Warmer waters facilitated the dispersal of Atlantic Mackerel *Scomber scombrus* and Atlantic Saury *Scomberesox saurus*, resulting in greater foraging ranges and inter-dive distances for adults in the second year. In contrast, the smaller cold-water Capelin *Mallotus villosus* (*i.e.* the birds' main prey in the first year) was available within close range of the colony, but was found in more dispersed, low-density shoals (Garthe et al. 2011). Our observed changes in the foraging movements of Masked Boobies are therefore likely to reflect differences in prey species, which could be associated with the southward shift of warmer waters in *E2*, in addition to a possible higher prey patch quality in *E1* within the local foraging area. Unfortunately, we lack information on prey item isotope levels within the region, which would help improve the interpretation of our isotopic results. The diet of Masked Boobies worldwide consists largely of Flying Fish (Exocoetidae) and squid (Ommastrephidae), although there is considerable geographic and seasonal variability throughout their range (Schreiber and Clapp 1987 and references therein). Flying Fish generally form schools, which occur near the surface over both shallow and deep waters (Cervigón et al. 1992). Flying Fish are also preyed upon by swordfish, tuna and other large pelagic fishes (Frimodt 1995), which are known to drive Flying Fish to the surface where they become accessible to seabirds. It is therefore possible that the diet of Masked Boobies consisted largely of Flying Fish and/or other higher trophic level pelagic fish in *E1*, whereas in *L1* and *E2*, birds may have been feeding more on lower level trophic squid (just within the local foraging area or in both areas). Further analyses are required to confirm this.

We used CHL and SST to describe the foraging habitat of Masked Boobies. Both these parameters have been extensively used to map primary production in order to predict the location of possible foraging grounds and to describe the distribution and foraging movements of top marine predators such as sea turtles, marine mammals, predatory fish and seabirds (e.g. Polovina et al. 2004, Bailleul et al. 2005, Zainuddin et al. 2006, Paiva et al. 2010). The numerous distant foraging trips, mainly to the north of the colony, observed during the early phase of the second breeding season occurred when CHL was highest in both the local and distant foraging areas compared to both early and late phases of the first breeding season. Interestingly, birds did not forage within the relatively productive zones south of the colony during their distant trips in E2. A study investigating the link between primary productivity (higher CHL in combination with lower SST) obtained from satellite images and the distribution of Anchovies *Engraulis encrasicolus* and Sardines *Sardinops sagax*, the two main prey species of Cape Gannets foraging in the Benguela upwelling system (west coast of Africa), indicated a mismatch between the occurrence of these pelagic fish and the highly productive zones (Grémillet et al. 2008). While the lowest trophic level (phytoplankton) matched with the highest (top predator – here, Cape Gannets), it mismatched with the intermediate trophic levels (pelagic fish). Further, as in Masked Boobies, Cape Gannets breeding on Bird Island in South Africa's Western Cape Province foraged in significantly warmer and CHL poorer waters compared with birds of other colonies in the same region (Grémillet et al. 2008). These findings indicate that correlations between seabird distribution and indices of primary productivity measured by means of SST and CHL can be quite misleading, as seabirds are top predators that usually feed two to three trophic levels higher in the food chain (Grémillet et al. 2008, Grémillet and Boulinier 2009).

Conclusions

In the present study, we proposed that the quality and density of prey patches, as well as prey encounter rates, were reflected in the dive behaviour of Masked Boobies. The degree to which dive bouts reflect the true spatial and temporal distribution of prey remains to

some extent uncertain without direct observation of adults foraging at sea and *in-situ* information on the spatial and temporal distribution of prey. There is strong evidence, nonetheless, that the analysis of dive bouts in combination with foraging movements provides useful information about how marine predators respond to changing environmental conditions. This information may further be used as a proxy for prey availability and abundance (Boyd 1996, Harcourt et al. 2002).

Seabirds are capable of adapting their foraging behaviour to buffer a shift in the distribution of prey species or reduced availability of their preferred prey (Arcos and Oro 1996, Litzow et al. 2002), and of evolving life-history traits in response to environmental change (Erikstad et al. 1998). Numerous species further seem capable of modifying their diet when confronted with scarcity of their natural prey (*e.g.* Jaksic 2004, Wanless et al. 2007, Ainley and Blight 2009). However, a change in diet often had a negative effect on the birds' reproductive performance, indicating the importance of dietary specialisation in seabirds (Grémillet and Boulinier 2009). Moreover, there are clear eco-physiological limits to this plasticity, and below a certain threshold of prey availability, foraging is unprofitable (Enstipp et al. 2007), negatively affecting reproduction (Harding et al. 2007) and threatening adult survival (Grémillet and Boulinier 2009). This study showed that Masked Boobies experienced food scarcity (although the origin remains unclear) to which birds responded by searching for prey in more distant foraging grounds during the energy-demanding chick-rearing period. Fortunately for the birds, the prey patches encountered in distant foraging grounds were of higher quality (although less predictable), which enabled adults to forage efficiently. Results further indicate that adults might have modified their diet. However, it remains unknown how successful these adaptations were, as we lack data on their reproductive performance during this time. The influence of global warming and anthropogenic changes on oceanic processes, as well as the spatio-temporal availability of prey, is expected to increase over the next decades (Grémillet and Boulinier 2009). Further investigations combining analysis of the foraging behaviour, diet and reproductive success of adults, in association with biotic and abiotic environmental conditions, in particular prey availability/quality, are required to understand observed trends and to assess how Masked Boobies may cope with further changes in prey availability and distribution.

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Chapter 4 – Foraging parameters influencing the detection and interpretation of Area-restricted search behaviour in marine predators: a case study with the Masked Booby

ABSTRACT

Identification of Area-restricted search (ARS) behaviour is used to better understand foraging movements and strategies of marine predators. Track-based descriptive analyses are commonly used to detect ARS behaviour, but they may be biased by factors such as foraging trip duration, as well as non-foraging behaviours (*i.e.* resting on the water). Using first-passage time (FPT) analysis we tested the hypotheses that (I) daylight resting at the sea surface positions falsely increases the detection of ARS behaviour and (II) short foraging trips are less likely to include ARS behaviour in Masked Boobies *Sula dactylatra*. We further analysed whether ARS behaviour may be used as a proxy to identify important feeding areas in this species. Depth-acceleration and GPS loggers were simultaneously deployed on chick-rearing adults to (1) obtain location data every 4 min and (2) obtain detailed foraging activity such as diving rates time spent sitting on the water surface and in flight. In 82 % of 50 foraging trips, birds adopted ARS behaviour. In 19.3 % of 57 detected ARS zones, birds spent more than 70 % of total ARS duration resting on the water, suggesting that these ARS zones have been falsely detected through FPT analysis. Based on generalized linear mixed models, the probability of detecting false ARS zones was 80 %. False ARS zones mostly occurred during short foraging trips in close proximity to the colony, with very low or no diving activity. This clearly demonstrates the need to account for resting on the water surface positions in marine animals when determining ARS behaviour based on foraging locations. Dive rates were positively correlated with foraging trip duration and the probability of ARS behaviour increased with increasing number of dives, suggesting that the adoption of ARS behaviour in Masked Boobies is linked to enhanced foraging activity. We conclude that ARS behaviour may be used as a proxy to identify important feeding areas in this species. However, approximately 35 % of all dives occurred outside ARS zones, suggesting that Masked Boobies may forage opportunistically on isolated prey.

INTRODUCTION

Marine predators usually forage in an environment where food resources are patchily distributed in space and time (Fauchald 1999). Foraging success in marine predators

depends largely on the distribution of their prey and the search methods employed to find them (Staniland et al. 2006). It is generally assumed that animals should spend more time in areas where resources are relatively plentiful (Fauchald and Tveraa 2003). Accordingly, individuals are expected to adjust their travelling behaviour in response to prey density and maximise their prey encounters by increasing turning rates and reducing travel speeds (Kareiva and Odell 1987). This adaptive response to prey density is generally referred to as Area-restricted search (ARS) behaviour (Kareiva and Odell 1987).

Identifying ARS behaviour has been central to understanding how animals move through the environment in an effort to optimise their foraging success. In addition, understanding where and how animals allocate their time at sea is fundamental to predicting how animals may respond to changes in the marine environment (Ashmole 1971, McCafferty et al. 1998) and for management and conservation plans (*e.g.* Schofield et al. 2007, Costa et al. 2012). Several analytical methods have been developed in recent years to identify ARS behaviour in animals (*e.g.* Nams 1996, Fauchald and Tveraa 2003, Tremblay et al. 2007, Breed et al. 2009). First-passage time (FPT) analysis, by definition the time an animal requires to cross a circle of a given radius along its trajectory (Fauchald and Tveraa 2003), has been applied to identify ARS behaviour in studies investigating foraging movements in marine mammals, such as Elephant Seals *Mirounga leonina* (*e.g.* Thums et al. 2011, Dragon et al. 2012), as well as in numerous seabird studies across a wide range of species (*e.g.* Weimerskirch et al. 2007, Pinaud 2008, Hamer et al. 2009, Paiva et al. 2010). Another track-based descriptive analysis is the fractal landscape method, which is similar to FPT analysis, but uses fractal dimensions instead of time (Nams 1996, Tremblay et al. 2007). Finally, state-spaced models are also used to fit correlated random walks (Kareiva and Shigesada 1983, Marsh and Jones 1988) to animal tracking data (Anderson-Spreher and Ledolter 1991, Sibert et al. 2003, Breed et al. 2009). In all these different analytical approaches, travel speeds and turning rates play a key role in detecting areas in which animals increase their search effort (Benhamou and Bovet 1989, Bartumeus et al. 2008).

Many marine predators spend a significant proportion of their foraging time resting at the sea surface (*e.g.* Northern Fur Seals *Callorhinus ursinus*, Trillmich 1990; Gray Seals

Halichoerus grypus, Austin et al. 2006; Baltic Ringed Seals *Phoca hispida botnica*, Harkonen et al. 2008; Northern *Morus bassanus*, Votier et al. 2011, and Cape Gannets *M. capensis* Ropert-Coudert et al. 2004). These sea surface positions may, regardless of the analytical method employed, lead to inaccurate detections and interpretations of foraging movements in marine predators, including ARS behaviour. The reason behind this is that sea surface positions can rarely be properly quantified based solely on location. It is, for instance, very difficult if not impossible, to differentiate between plain roosting behaviour and potential in-water positions that may be associated with diving activity. This underlies the need to investigate foraging movements of marine predators in combination with time budgets. The detection of ARS behaviour can further be biased through foraging trip duration, because the shorter a foraging trip, the lower the number of locations available to identify ARS behaviour (Pinaud 2008).

Studies comparing ARS behaviour based on location data with known diving events or prey captures are still scarce in foraging ecology (but see Weimerskirch et al. 2007, Hamer et al. 2009, Thums et al. 2011, Dragon et al. 2012). In Wandering Albatross *Diomedea exulans*, no evidence was found that prey capture, measured by means of stomach-temperature loggers, was linked with ARS behaviour (Weimerskirch et al. 2007). However, a strong link between the adoption of ARS behaviour and increased dive rates has been found in Northern Gannets (Hamer et al. 2009), suggesting that, at least in some species, ARS behaviour is related to enhanced diving activity.

Masked Boobies *Sula dactylatra* are suitable marine predators to investigate this matter. Firstly, they forage mainly by plunge diving, which facilitates the detection of feeding events by means of pressure recording data devices. Secondly, trip duration in Masked Boobies is highly variable, with some trips lasting only a few hours, others several hours to days. This dichotomy makes it possible to address the influence of trip duration on the detection and accuracy of ARS behaviour. In addition, Masked Boobies have a relatively large body mass (range 1.7 – 2.9 kg; Marchant and Higgins 1990, this study). This allows simultaneous deployment of GPS and depth-acceleration loggers to investigate ARS behaviour in

combination with diving events, so as to precisely determine how birds allocate their time at sea.

This study therefore aimed to establish if ARS regions identified from the tracks of Masked Boobies were indicative of foraging. In particular,

(I) we investigated time budgets of individuals within detected ARS zones, including diving activity and time spent resting at the sea surface;

(II) we determined which factors influence the detection of ARS behaviour;

(III) we examined whether ARS behaviour can be used as a proxy to identify important feeding areas;

(IV) and, we developed a decision tree based on our findings to determine incorrectly-detected ARS zones resulting from high proportions of resting at the sea surface positions.

MATERIAL AND METHODS

Study site and species

The study was carried out on Phillip Island (29°02'S, 167°57'E) in the south-west Pacific Ocean. Phillip Island (190 ha) is part of the Norfolk Island Group (Australia), located approximately 1670 km north-east of Sydney, Australia and 1070 km north-west of Auckland, New Zealand. The Norfolk Island Group lies within the “Norfolk Island Seamounts area”, a unique marine ecosystem surrounded by a high number of seamounts (Williams et al. 2006). Fieldwork took place between 12 February 2010 and 03 March 2010, and between 27 October 2010 and 10 November 2010, corresponding to the late and early breeding seasons of Masked Boobies respectively.

Approximately 300 Masked Booby pairs breed on Phillip Island (Garnett et al. 2010, Priddel et al. 2010). Females lay two eggs, but generally only one chick is reared through obligate siblicide (Dorward 1962). All study animals were rearing chicks between 3 and 11 weeks of

age during February and March 2010 and between 2 and 7 weeks of age during October and November 2010.

Data devices and deployment

Foraging movements of Masked Boobies were studied using GPS data loggers (46 x 32 mm, 20 g, Earth & Ocean Technologies, Kiel, Germany) recording time, latitude and longitude every 4 min. GPS loggers were attached on the top of three central tail feathers using waterproof adhesive TESA® tape (Beiersdorf AG, GmbH, Hamburg, Germany), minimising the damage to the feathers upon retrieval (Wilson et al. 1997). The activity patterns of Masked Boobies were studied using cylindrical, four channel data loggers (M190-D2GT, 12 bit resolution, 53 x 15 mm, 17 g, Little Leonardo, Tokyo, Japan), which simultaneously recorded depth (1 Hz), temperature (1 Hz) and acceleration (16 Hz) along two axes. The relative accuracy for the depth sensor was 0.1 m. The loggers contain an acceleration sensor measuring both dynamic (vibration) and static accelerations (gravity). Depth-acceleration loggers were attached using TESA® tape underneath three central tail feathers (in addition to the GPS logger attached on the top) to measure acceleration along two axes: surging acceleration along the longitudinal body axis and heaving acceleration dorso-ventrally (for details, see Watanuki et al. 2003, Ropert-Coudert et al. 2004). Total attachment weight, including tape, was 55 g (range 45 – 60 g, n = 24), corresponding to 2.2 % of female mean body mass (2381 g, range 2120 – 2870 g, n = 9) and 2.7 % of male mean body mass (2072 g, range 1685 – 2465 g, n = 15), which is below the generally accepted 3 % body mass threshold (Phillips et al. 2003, Wilson and McMahon 2006, but also see Vandenabeele et al. 2012).

Chick-rearing adults (either the female or the male of a pair) were captured with a noose-pole and weighed using a spring balance (Pesola®, maximum deviation ± 0.3 % of load). Adults were sexed by voice and by measurements: males have a distinctive higher pitched voice than females and are smaller than females within a pair (Nelson 1978). Individuals were colour-marked on the breast with a green or blue sheep crayon for identification of the equipped individual in the field at first capture and, if non-banded, adults were banded with a metal leg band (Darvic®, Australian Birds and Bats Banding Scheme). Adults were

released immediately onto their nests after attachment of the loggers. Loggers were left on for 1 – 4 days before being retrieved. Only one adult per pair and nest was studied to minimise disturbance and individuals were never studied twice. No nests were deserted during the duration of the study.

First-passage time analysis

First-passage time analysis was conducted using R source code developed by D. Pinaud, CNRS, France (R Development Core Team 2012), with each track interpolated at 0.1 km (Pinaud 2008). First-passage time was then calculated at each interpolated location along the track for radii ranging from 0.1 to 25 km, incrementing at 0.1 km. By plotting the log-transformed variance as a function of the radius size (the log-transformation is required to ensure the variance is independent of the magnitude), ARS scales were identified for each individual foraging track as the maximum peak in the log-transformed variance (Fauchald and Tveraa 2003). With the function *lavielle* of R package *adehabitatLT* (Calenge 2012), foraging trips containing interpolated locations and FPT values were split into homogenous bouts (see Barraquand and Benhamou 2008). This function performs a non-parametric segmentation of a time series (here, the foraging track of the individual) using the penalised contrast method of Lavielle (Lavielle 1999, 2005, Calenge 2012). Next, we used the function *chooseseg* (*adehabitatLT*) to estimate the number of segments of each foraging track and the function *findpath* (*adehabitatLT*) to find the limits of the FPT segments (*i.e.* start and end of the segments). All segments of lower FPT values were then identified as “movement” and all higher segments were identified as ARS behaviour (see details in Calenge 2012).

Overnight foraging trips

Five individuals performed overnight foraging trips. Based on accelerometer information, these birds spent most of the night sitting on the water surface for long hours without any significant activity (Masked Boobies only dive during daylight hours). Accordingly, the

nocturnal portions of these trips were excluded because these resting positions may falsely increase the FPT variance (Weimerskirch et al. 2007). Potential resting at the sea surface positions occurring during daylight hours were not removed because (1) the primary intention here is to show to what extent the occurrence of ARS behaviour is affected by the amount of time individuals spend sitting on the water surface, and (2) because the removal of daylight in-water positions is likely to obscure diving events. Each day of an overnight trip was therefore treated as a separate foraging trip for FPT analysis and calculation of ARS behaviour.

Data analysis

Acceleration and dive data were analysed using IGOR Pro 6.21 (Wavemetrics software, Portland USA). The component of the gravity acceleration along the surging axis was firstly separated from the high-frequency component resulting from wing beat activity, using a low-pass filter (Tanaka et al. 2001). Then, the following types of behaviour were identified from the depth-acceleration logger signals: (1) on land, (2) take-off, (3) in flight (flapping/gliding), (4) sitting on the water surface and (5) plunge-diving. Diving threshold was set to 0.2 m. Flapping activity was identified as an oscillating pattern present simultaneously on both axes, with each propulsive stroke recorded on the heaving axis resulting in a forward acceleration recorded on the surging axis (see Watanuki et al. 2003, Ropert-Coudert et al. 2004). The absence of these distinctive oscillation patterns within a flight bout corresponded to gliding activity. The acceleration on the surging and heaving axes together with the body angle adopted by the birds allowed us to differentiate between plunge-dives or dives from the surface. On-land sections were excluded from the analysis.

Each foraging trip was divided into individually numbered sections based on presence or absence of ARS behaviour. For example, if a foraging trip had one ARS zone present along the track, the trip was divided into three sections of known duration: (1) ARS absent, (2) ARS present and (3) ARS absent. If a foraging trip had two ARS zones, the foraging trip was divided into five sections of known duration: (1) ARS absent, (2) ARS present, (3) ARS absent, (4) ARS present and (5) ARS absent. For each section of a foraging trip, the proportions of

time spent sitting on the water surface and in flight, as well as the total number of dives, were calculated.

Due to battery exhaustion of the depth-acceleration loggers, nine foraging trips were excluded from the data analysis and only complete foraging trips recorded by both GPS and depth-acceleration loggers are presented in the results section.

Decision tree for ARS behaviour

We used a classification tree to construct a decision tree in R (package *tree*, Ripley 2011) in order to identify ARS events in which birds spent a high proportion ($> 70\%$, see results) of the total ARS duration sitting on the water surface. Based on the analysis of the acceleration signals, such ARS events have a high probability of being falsely positive ARS zones. The decision tree was constructed to locate such *false* ARS zones in foraging trips of Masked Boobies for which only GPS information was available. ARS duration, scale of ARS zones (*i.e.* radius), mean distance of ARS zones from colony, as well as total foraging trip duration and total distance travelled (all parameters obtained through GPS devices) were used to classify *false* ARS. *Jack-knifing* (Quenouille 1949) was used to estimate the performance of the decision tree. Briefly, *Jack-knifing* is a re-sampling method systematically re-computing (here, 100 times) the sampling set by leaving out one observation at a time, and using the resultant model to predict the nature of the excluded record.

Statistical analysis

All statistical analyses were performed using R 2.15.0 (R Development Core Team 2012). Generalized linear mixed models (GLMM, Faraway 2006) were applied using the function *lmer* in R package *lme4* (Bates et al. 2011), with the occurrence or absence of ARS behaviour as a binomial response variable and the proportion of time birds spent sitting on the water surface (logit transformed), the number of dives, foraging trip duration and sex of the individual fixed effects, with individual “trip ID nested within season” included as a random effect to account for pseudo-replication. The GLMM used a binomial error distribution with

a logit-link function. Because the time adults spent sitting on the water surface was highly correlated with the time they spent in flight ($z = -7.397$, $p < 0.001$, $\tau = -0.405$, $n = 155$ *foraging trip sections*), the proportion of time adults spent in flight was excluded from the model. Prior to checking the fit of the model, model simplification and checking of model assumptions following Crawley (2007), we tested whether a nested random effect “trip ID within season” improved the fit of the model by comparing the change in deviance of the model using *anova* (chi-squared under one degree of freedom), including the nested random effect to a second model with same fixed effects, but with only trip ID as a random effect. As $p > 0.05$, we concluded that the nested random effect “trip ID within season” did not improve the fit of the model and used only individual trip ID as a random effect for further statistical testing. Bayesian inference from our simplified mixed model was obtained by applying the function *sim* of R package *arm* (Gelman et al. 2012) to draw 1000 random values from the joint posterior distribution of the model parameters, taking the correlation between the parameters into account. Correlations were calculated using Kendall’s rank coefficient. To test for differences between foraging trip durations with and without ARS zones, a Welch’s t-test was performed. All tests were 2-tailed, with a significance level of $p < 0.05$. Mean (\pm SD) results are reported.

RESULTS

Foraging trips

A total of 50 foraging trips from 26 individuals (10 females and 16 males) were recorded. Of the 26 individuals, 21 performed single-day foraging trips, while five adults (two females and three males) stayed overnight at sea, returning to the colony the next day. Masked Boobies had an averaged foraging trip duration of 6.52 ± 3.79 h (range 0.88 – 14.18 h, $n = 50$) and travelled on average a total distance of 160.74 ± 111.43 km (range 28.11 – 422.62 km, $n = 50$), at a mean maximum distance from colony of 74.41 ± 68.06 km (range 10.68 – 250.39 km, $n = 50$) (Table 4.1). Trip duration was positively correlated with total distance travelled

($z = 4.964$, $\tau = 0.54$, $p < 0.001$, $n = 50$) and maximum distance from colony ($z = 5.099$, $\tau = 0.554$, $p < 0.001$, $n = 50$).

Foraging parameters		n
Trip duration (h)	6.52 ± 3.79 (0.88 – 14.18)	50
Total distance travelled (km)	160.74 ± 111.43 (28.11 – 422.62)	50
Maximum distance from colony (km)	74.41 ± 68.06 (10.68 – 250.39)	50
Number of ARS per trip	1.1 ± 0.8 (0 – 4)	50
Duration of ARS (h)	2.22 ± 2.26 (0.04 – 11.38)	57
Scale of ARS (km)	3.51 ± 3.95 (0.3 – 16.9)	57
Distance of ARS from colony (km)	63.89 ± 62.77 (9.18 – 244.5)	57
% spent sitting on water within ARS	44.11 ± 26.14 (4.42 – 98.25)	57
Number of dives within ARS	8.3 ± 9.4 (0 – 36)	57

Table 4.1. Foraging parameters of Masked Boobies. Values are mean \pm SD. Ranges in parentheses. Sample size (n). Area-restricted search (ARS).

Characteristics of ARS zones

First-passage time analysis of the tracks revealed the presence of ARS behaviour in 41 out of the 50 foraging trips (82 %), while in the remaining nine foraging trips, no ARS behaviour was detected. Foraging trips with and without ARS zones lasted on average 6.71 ± 3.78 h (range 0.88 – 14.18 h, $n = 41$) and 5.67 ± 3.93 h (range 2.06 – 13.30 h, $n = 9$), respectively. The duration of foraging trips with and without the presence of ARS behaviour were not significantly different (*Welch's t-test* $t = -0.726$, $df = 11.48$, $p = 0.482$).

A total of 57 ARS events with an average of 1.1 ± 0.8 ARS zones per foraging trip (range 0 – 4 ARS, $n = 50$) were detected in Masked Boobies (Fig. 4.1). Average ARS duration was $2.22 \pm$

2.26 h (range 0.04 – 11.38 h, $n = 57$). The areas in which individuals increased their search effort were located at a mean distance of 63.89 ± 62.77 km (range 9.18 – 244.5 km, $n = 57$) from the colony and had a mean scale (radius) of 3.51 ± 3.95 km (range 0.3 – 16.9 km, $n = 57$) (Table 4.1). There was a significant positive correlation between mean distance of ARS zones from colony and scale of ARS ($Kendall\ z = 2.943$, $p = 0.003$, $\tau = 0.271$, $n = 57$). Mean distance of ARS zones from the colony was further positively correlated with trip duration ($z = 4.842$, $p < 0.001$, $\tau = 0.443$, $n = 57$) and duration of ARS behaviour ($z = 3.483$, $p < 0.001$, $\tau = 0.317$, $n = 57$).

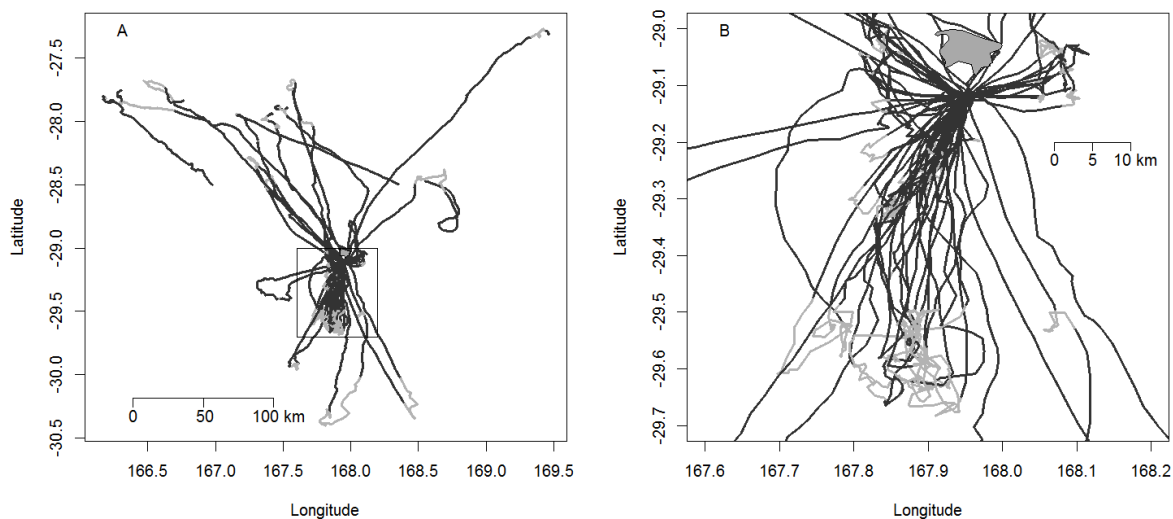


Figure 4.1. Foraging movements and Area-restricted search (ARS) behaviour of Masked Boobies recorded by GPS at 4 min intervals: (A) all foraging movements, and (B) foraging movements within close range of the colony. Light-grey lines correspond to ARS behaviour. Note: Foraging tracks ending or starting abruptly correspond to overnight foraging trips (see methods).

Time budget

A total of 537 dives were recorded, averaging 13.1 ± 13.0 dives per foraging trip (range 1 – 48, $n = 41$). Of all dives, 65.2 % ($n = 350$) occurred inside ARS zones, with a mean of 8.3 ± 9.4 dives being observed per ARS zone (range 0 – 36, $n = 57$). Outside ARS zones, birds dived an

average of 3.5 ± 6.1 times (range 0 – 29, $n = 98$). In 10 out of 57 ARS zones (17.5 %) no diving activity was recorded. All ARS events without dives were located less than 52 km from the colony, presented a smaller scale of ARS and were of shorter duration than ARS zones containing dives (Table 4.2). In addition, ARS behaviour with no diving activity was only observed during single day foraging trips.

The time birds spent sitting on the water surface within ARS zones represented on average 44.11 ± 26.14 % of the total ARS duration (range 4.42 – 98.25 %, $n = 57$), while outside ARS zones, birds spent a mean of 13.91 ± 21.46 % of their time sitting at the water surface (range 0.0 – 95.39 %, $n = 98$). Inside ARS zones, flight time accounted for a mean of 52.68 ± 25.63 % of the total ARS duration (range 1.31 – 93.59 %, $n = 57$), which was similar to the mean flight time outside ARS zones: 58.65 ± 38.10 % (range 1.29 – 100 %, $n = 98$).

	ARS without dives ($n = 10$)	ARS with dives ($n = 47$)
Trip duration (h)	4.52 ± 1.95 (2.26 – 6.57, $n = 7$ trips)	6.82 ± 3.82 (0.88 – 14.18, $n = 39$ trips)
ARS duration (h)	0.94 ± 1.01 (0.18 – 3.72)	2.49 ± 2.36 (0.04 – 11.38)
ARS scale (km)	1.44 ± 0.81 (0.5 – 3.0)	3.95 ± 4.21 (0.3 – 16.9)
Mean distance of ARS from colony (km)	18.45 ± 14.19 (9.18 – 51.63)	73.56 ± 64.91 (10.23 – 244.52)
Sitting on water surface (%)	63.19 ± 24.08 (31.11 – 94.31)	40.01 ± 24.95 (4.42 – 98.25)

Table 4.2. Foraging parameters of Area-restricted search (ARS) with respect to diving activity in Masked Boobies. Values are mean \pm SD. Ranges in parentheses. Sample size (n).

Factors influencing the detection of ARS behaviour

The probability of ARS behaviour occurrence did not differ between sexes (GLMM, $b = 0.478$, $z = 0.969$, $p = 0.332$), subsequently the term sex was dropped from the model. The probability of detecting ARS behaviour increased significantly with increasing time that adults spent sitting at the water surface (GLMM, $b = 1.214$, $z = 5.456$, $p < 0.001$) (Fig. 4.2)

and with increasing number of dives (GLMM, $b = 0.112$, $z = 2.487$, $p = 0.013$) (Fig. 4.2). A significant interaction between the proportion of time adults spent sitting on the water surface and the number of dives indicated that the longer adults sat on the water surface and the less they dived, the more likely it was that FPT analysis detected ARS behaviour (GLMM, $b = -0.084$, $z = -2.427$, $p = 0.015$). In contrast, a shorter time spent sitting on the water surface combined with a higher diving activity decreased the probability of detecting ARS behaviour. Surprisingly, the probability of an ARS event occurring decreased with increasing foraging trip duration (GLMM, $b = -0.261$, $z = -3.243$, $p = 0.001$) (Fig. 4.2).

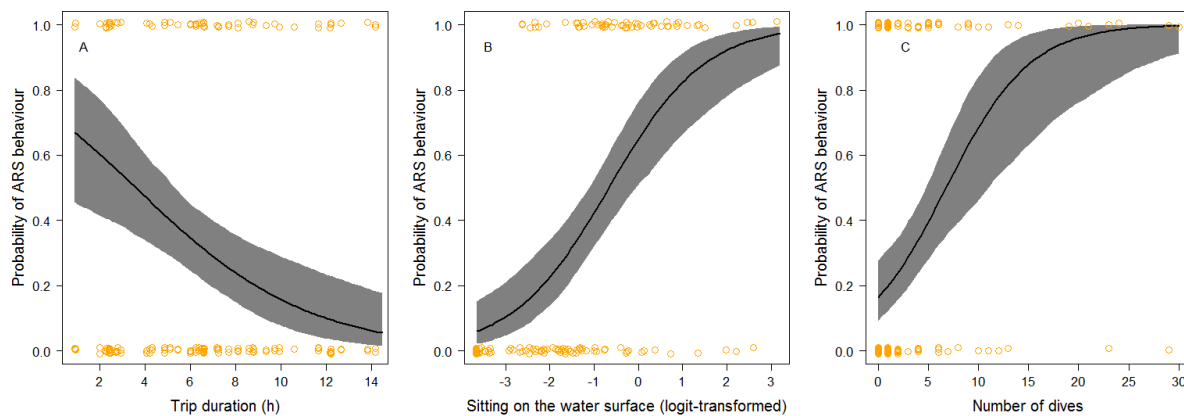


Figure 4.2. Predicted probability of Area-restricted search (ARS) behaviour in Masked Boobies in relation to: (A) foraging trip duration, (B) the logit-transformed proportion of time birds spent sitting on the water surface (a value of zero corresponds to 50 %) and, (C) the number of dives. Bold lines represent the regression lines of the GLMM. Grey shaded areas represent the predicted 95 % credible intervals. Orange circles are observed values.

Based on our model, the predicted probability of detecting ARS behaviour in birds spending 50 % of total ARS duration on the water surface was 0.65 (95 % credible interval: 0.51 – 0.76) and 0.8 for birds spending at least 70 % on the water surface (95 % credible interval: 0.65 – 0.90) (Fig. 4.2). That is, the probability of ARS behaviour to be detected was greater than 0.8, if individuals sat for more than 70 % of total ARS duration on the water surface, but less than 0.46 (95 % credible interval: 0.35 – 0.57), if individuals sat for less than 30 % of total ARS duration on the water surface (Fig. 4.2).

***False* ARS events and decision tree**

By visual inspection of Figure 4.2 and based on the high ARS detection probability of 0.8, we defined ARS events in which birds spend more than 70 % of the total ARS duration sitting on water as *falsely* positive ARS events. Therefore, 11 out of 57 ARS zones (19.3 %) were regarded as *false* (Table 4.3).

False ARS events were typically located at short distance from the colony, of short duration and small size (Table 4.3). Diving activity of birds was low overall within these *false* ARS zones and in 5 out of 11 ARS zones birds did not dive at all (Table 4.4). Out of the remaining 6 ARS zones containing dives, only one female (trip ID 363.3.1) (Table 4.4) undertook an overnight foraging trip. First-passage time analysis detected a *false* ARS behaviour in this female at a mean distance of 244.5 km from colony, with ARS duration of 5.27 hours and a total of 14 dives within an ARS zone. The remaining *false* detected ARS zones occurred in single day foragers, within less than 56.6 km from the colony and a much lower diving rate (Table 4.4).

	Sitting on water 0 – 70 % (n = 46 ARS)	Sitting on water 70 – 100 % (n = 11 ARS)
Trip duration (h)	6.51 ± 3.82 (0.88 – 14.88, n = 36 trips)	6.32 ± 3.51 (2.26 – 12.19, n = 9 trips)
Number of dives	7.09 ± 7.96 (1 – 30)	2.18 ± 4.19 (0 – 14)
ARS duration (h)	2.20 ± 2.23 (0.04 – 11.38)	2.28 ± 2.49 (0.39 – 6.85)
ARS scale (km)	3.97 ± 4.24 (0.3 – 16.9)	1.58 ± 1.27 (0.4 – 4.0)
Mean distance of ARS from colony (km)	69.78 ± 60.42 (10.26 – 225.32)	39.27 ± 69.37 (9.18 – 244.52)

Table 4.3. Foraging parameters of Masked Boobies with respect to the proportion spent sitting on the water surface within Area-restricted search (ARS) zones. Values are mean \pm SD. Ranges in parentheses. Sample size (n).

Based on the decision tree, *false* ARS events were likely to be detected in ARS zones with a spatial scale < 4.05 km, a total distance travelled < 284.4 km, a mean distance of ARS from colony < 25.14 km and a foraging trip duration > 6.0 hours (Fig. 4.3). If foraging trips lasted less than 6.0 hours, *false* ARS zones were likely to be detected if ARS duration was less than 0.90 hours (Fig. 4.3). Through *jack-knifing* (see methods), 15 out of 21 *false* ARS (71.4 %) and 76 out of 79 *true* ARS (96.2 %) were estimated correctly.

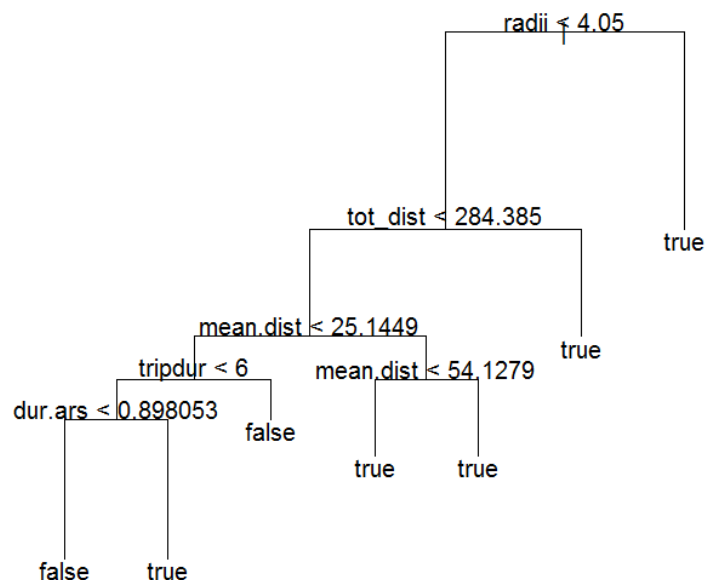


Figure 4.3. Classification tree for Area-restricted search (ARS) zones in Masked Boobies. ARS events in which birds spent more than 70 % of total ARS duration sitting on the water surface are regarded as *false*. ARS events in which birds spent less than 70 % on the water surface are regarded as *true*. Scale of ARS (radii), total distance travelled (tot_dist), mean distance of ARS from colony (mean.dist), foraging trip duration (tripdur) and duration of ARS behaviour (dur.ars). Distances and scale of ARS are given in km, duration in h.

Trip ID	Trip duration (h)	Max. distance from colony (km)	Total distance travelled (km)	ARS duration (h)	Mean distance ARS from colony (km)	ARS size (km)	Number of dives	% sitting on water	% in flight
18.2	2.92	11.0	36.49	0.68	9.18	0.6	0	92.3	7.7
70.2	8.74	15.71	68.53	6.85	14.69	4.0	1	76.4	21.9
70.3	6.57	36.64	113.84	1.41	15.34	0.8	1	71.3	26.3
70.3	6.57	36.64	113.84	1.07	10.28	0.8	0	71.4	26.3
272.1	9.73	65.92	168.74	1.63	56.62	0.4	1	98.3	1.3
275.1	4.87	16.29	121.82	0.46	14.46	0.5	0	94.3	4.6
285.1	7.17	19.38	44.16	6.09	18.81	1.4	5	95.2	3.5
287.1	2.39	16.58	37.62	0.82	11.53	1.4	0	72.3	26.5
287.1	2.39	16.58	37.62	0.40	11.45	1.4	0	83.6	14.3
290.2	2.26	37.77	77.76	0.45	25.13	2.3	2	81.3	17.5
363.3.1	12.19	250.39	275.19	5.27	244.52	3.8	14	80.5	17.7

Table 4.4. Individual foraging parameters of Masked Boobies spending > 70 % of the Area-restricted search (ARS) duration sitting on the water surface. Individual foraging trips (Trip ID). Note: Two distinct ARS zones were recorded in foraging trip “70.3” and “287.1

DISCUSSION

This study aimed to establish which foraging parameters influence the detection of ARS behaviour in foraging locations of Masked Boobies and whether ARS zones were indicative of foraging. Our results provide strong evidence that resting at the sea surface positions leads to an incorrect detection and interpretation of approximately 19 % of total ARS zones. This finding underlines the importance to account for resting at the sea surface positions when ARS behaviour is determined by means of foraging locations in marine predators and suggests that inferences should be drawn cautiously. In addition, we provide evidence that ARS behaviour is linked with enhanced diving activity, suggesting that ARS behaviour may be used as a proxy to identify important feeding areas in this species.

Characteristics of ARS zones

The adoption of ARS behaviour is expected to occur in patchy environments with high prey densities (Kareiva and Odell 1987). First-passage time analysis detected ARS behaviour in Masked Boobies in zones as close as 10 km from the colony but also in pelagic areas as far as 240 km from Phillip Island. The scale and duration of ARS behaviour increased with increasing foraging trip duration. In addition, the longer the foraging trip, the more remote the location of ARS behaviour from the colony, suggesting that adults searched greater areas for prey over distant pelagic waters, than when foraging closer to the colony during short trips. This further suggests that prey densities within close proximity of the colony may have been lower (birds presented lower diving activity), than over distant pelagic waters (higher diving activity; see below). A significant positive relationship between the mean distance of ARS zones from the colony and the mean scale of ARS zones, as it was found in Masked Boobies, was also found across a range of long-distance foragers, such as Yellow-nosed Albatrosses *Thalassarche carteri* (Pinaud and Weimerskirch 2005), Wandering Albatrosses (Pinaud and Weimerskirch 2007) and Antarctic Petrels *Thalassoica antarctica* (Fauchald and Tveraa 2006), but also in medium-ranging predators such as Northern Gannets (Hamer et al. 2009).

Time budget and factors influencing the detection of ARS behaviour

The model containing the number of dives, the amount of time that individuals spent sitting on the water surface, as well as foraging trip duration, best explained the detection of ARS behaviour in Masked Boobies. Higher dive rates within ARS zones suggest that the adoption of ARS behaviour in Masked Boobies is linked with enhanced foraging activity. Consequently, ARS behaviour may be used as a proxy to identify important feeding areas in this species, in particular during foraging trips of longer durations (see below). Although prey capture rates were not estimated in Masked Boobies, it is reasonable to assume that at least some dives resulted in prey capture, as it was observed Northern Gannets (Machovsky Capuska et al. 2011). In the latter, 43 % of short and shallow V-shaped dives, in which birds used only the momentum of their fall to gain depth, and 95 % of deep U-shaped dives, in which birds actively used their wings to reach greater depths and pursue prey, were associated with successful prey capture (Machovsky Capuska et al. 2011). Masked Boobies exhibited higher dive rates inside ARS zones than outside ARS zones. The lower probability of birds adopting ARS behaviour when the number of dives was low, suggest that dives outside ARS zones are most likely opportunistic foraging events on isolated prey along their trajectory (Weimerskirch et al. 2007). In addition, Masked Boobies may have quickly satisfied their energy requirements without adopting ARS behaviour, in particular during short foraging trips in close proximity to the colony (Hamer et al. 2009). A last possible explanation would be that the occurrence of dives outside ARS zones, are the result of unsuccessful dives. Foraging success in Southern Elephant Seals, inferred from *in situ* changes in relative body lipid content as derived from measured changes in buoyancy (Biuw et al. 2003), was positively related to the probability of being in ARS mode, but high foraging success was also observed when individuals were in transit (Thums et al. 2011). Outside these ARS zones, Elephant Seals moved quickly through areas without slowing down or increasing their turning rates (Thums et al. 2011). This pattern has also been observed in Gray Seals (Austin et al. 2006), Basking Sharks *Cetorhinus maximus* (Sims et al. 2006) and Wandering Albatrosses when foraging in flight (Weimerskirch et al. 2007). This suggests that successful foraging without the adoption of ARS behaviour could be a common foraging method in marine predators.

Foraging trip duration influenced the accuracy of FPT analysis in other species (Pinaud 2008). The shorter a foraging trip, the lower the number of locations available for FPT analysis and the detection of ARS behaviour. In this study, we expected short trip duration to have a negative effect on the probability of ARS behaviour, however the opposite was actually observed. A possible explanation for this might be that the shorter the trip duration, the higher the proportion of time adults spent sitting on the water surface. As the probability of ARS behaviour increased significantly with increasing time spent sitting on the water surface, the probability of ARS behaviour might thus be higher in short foraging trips.

***False* ARS events and decision tree**

First-passage time analysis cannot differentiate between areas in which individuals adopt slow travel speeds due to searching for prey or due to a resting pause at the sea surface. It is unlikely that Masked Boobies carried out surface-feeding events during these *false* ARS events, though such surface-feeding has been recorded in Cape and Northern Gannets (Ropert-Coudert et al. 2004a, 2009). All dives recorded by data loggers in this study were plunge-dives and not dives initiated from the water surface. In addition, Masked Boobies have often been observed plunge-diving within less than 100 m of Phillip Island, but were never seen diving from the water surface. We suggest that *false* ARS events occurred mainly within close range of the colony because birds may have rested at the water surface after opportunistic or single diving events, which typically occurred without the adoption of ARS behaviour (Hamer et al. 2009). In fact, birds dived within an hour (range 1 – 4 dives) prior to *false* ARS events in 7 out of the 10 *false* ARS zones.

Conclusions

Several analytical methods based on marine predators foraging movements have been developed (e.g. Nams 1996, Fauchald and Tveraa 2003, Breed et al. 2009, Tremblay et al. 2007) to provide information on the location of foraging and feeding areas, which are otherwise difficult, if not impossible, to obtain through direct observation. Such

comprehensive knowledge is ultimately needed to develop management and conservation plans for marine species and their habitats (*e.g.* Schofield et al. 2007, Costa et al. 2012).

We provide empirical evidence that the detection of ARS behaviour is highly influenced by the amount of time Masked Boobies spend sitting on the water surface during daylight hours, leading to an incorrect detection and interpretation of approximately 19 % of total determined ARS zones. Without the information on individuals' time budgets, we would have misleadingly assumed that the probability of ARS behaviour was higher during short foraging trips in the vicinity of the colony, than during long foraging trips at greater distances. This clearly demonstrates the need to account for time budgets during daily foraging movements in order to correctly identify ARS behaviour in marine predators. Nevertheless, although approximately 35 % of the dives occurred outside ARS zones, the probability for ARS behaviour to occur was strongly linked with increased dive rates, which in turn were negatively correlated with the time spent resting on the water surface by adults. This suggests that ARS behaviour may be used as a proxy to identify important feeding areas in this aerial marine predator. This study was developed on foraging data of Masked Boobies, but the methods employed and our findings have implications for the detection and interpretation of ARS behaviour in other marine predators.

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carried out under permission of Norfolk Islands National Park and in accordance with the principles and guidelines of the Animal Ethics Committee of the University of Tasmania.

GENERAL DISCUSSION

The foraging ecology of marine predators is often described as a function of the surrounding habitat influencing prey availability (Staniland et al. 2006). The presence of particular oceanographic features, such as shelf-edges, frontal zones or upwelling, in addition to intra- and inter-seasonal changes in prey abundance due to environmental variability (*e.g.* increased SST) influences the spatial distribution and foraging ecology of polar (Boyd et al. 1994, Kirkwood and Robertson 1997, Hunt et al. 1999), temperate (Hyrenbach et al. 2002, Garthe et al. 2007) and tropical species (Spear et al. 2001, Le Corre et al. 2003). However, several studies show that a range of intrinsic factors are just as important factors in shaping predator foraging ecology (Hindell et al. 1991, Beck et al. 2003, Kato et al. 2008).

Central-place foragers, such as seabirds, are constrained in their foraging range due to the need to return to the colony and finding an optimal balance between chick-provisioning and self-feeding (Orians and Pearson 1979). In addition, tropical seabirds experience unique foraging challenges (Ashmole 1971), because tropical waters are less productive, less structured, and have a more patchy distribution of food resources than temperate and polar waters (Longhurst and Pauly 1987, Nybakken 2001, Weimerskirch 2007). Tropical seabirds should, therefore, have evolved to maximise energy intake in face of these lower feeding opportunities (Ainley 1977, Au and Pitman 1986, Ballance and Pitman 1999, Weimerskirch et al. 2008) and their foraging ecology is expected to contrast that of temperate-polar species.

This thesis examined the effects of differences in body mass and size within sexes on key foraging parameters in chick-rearing Masked Boobies. Differences in diving behaviour and foraging movements of adults during the chick-rearing period were determined, and relationships between these parameters and changes in dive bout size and dive rates, used as proxies for prey availability and distribution in a tropical marine environment, assessed. This thesis further analysed the accuracy of FPT analysis to determine ARS behaviour, a method that has been increasingly used in a variety of studies across a range of marine species.

The findings reported in the second chapter of this thesis indicated that a combination of differences in body mass within sexes and differential parental roles influenced the foraging behaviour of chick-rearing adults. Results reported in the third chapter revealed that this species adjusts its foraging movements and diving behaviour according to the availability of prey, in addition to a possible modification in diet, most likely driven by environmental variability. In the fourth chapter, results showed that at sea surface positions due to resting led to false detection, and consequently wrong interpretation, of ARS zones.

The findings reported in this thesis highlight the need to consider both intrinsic and extrinsic, environmental factors in combination in order to understand the underlying mechanisms of predator foraging ecology. The findings also highlight that track-based analytical methods used to determine important foraging areas in seabirds, and possibly in other marine species, need to take into account the influence of locations derived from non-foraging behaviour, such as resting on the water.

The results were interpreted in their own particular context at the end of each chapter. This chapter incorporates the findings of this thesis in a comparative overview of the foraging ecology of temperate-polar and tropical seabird species during the energy-demanding chick-rearing period with respect to foraging movements and behaviour, foraging habitat and site-fidelity, as well as foraging strategies with an emphasis on tropical species.

Foraging movements of chick-rearing seabirds

When local resources are poor, many central-place foragers alternate between short foraging trips for chick-provisioning in nearby, relatively resource poor waters and self-feeding trips in more distant, productive waters (Weimerskirch et al. 1993, 1994). This bimodal foraging pattern might further be related to sex-specific foraging and provisioning strategies (*e.g.* Peck and Congdon 2006, Weimerskirch et al. 2009). Both these strategies are generally attributed to sexual dimorphism (*e.g.* Beck et al. 2003, but see Lewis et al. 2002 for sex-specific foraging strategies in a monomorphic species) and can be particularly useful when local prey resources are scarce. As an illustration, chick-rearing Wandering Albatrosses

Diomedea exulans from the Crozet Islands adjust their foraging movements throughout the breeding season (Weimerskirch et al. 1993). During chick-brooding, larger males mainly foraged at the edge of the continental shelf, whereas the smaller females tended to forage over more pelagic waters off the shelf. When chicks were larger and left unattended, adults alternated between short trips over the shelf edge and long trips over distant pelagic waters 117 and 1534 km from the colony. Trips lasted 2.4 and 11.6 days respectively, with females foraging over more northerly waters than males (Weimerskirch et al. 1993). During the short trips, individuals of both sexes lost body mass, but they gained mass during long trips, suggesting lower resource availability over the shelf edge than over more distant, deeper waters (Weimerskirch et al. 1993, 1994). In addition, males spent a greater proportion of their time foraging during short trips than did females and fed the chick more often, indicating that this species exhibits a sex-specific parental investment (Weimerskirch et al. 1997).

Wedge-tailed Shearwaters *Puffinus pacificus* also alternate short and long trips during the chick-rearing phase (Congdon et al. 2005, Peck and Congdon 2005). However, this was found to be colony-specific and related to prey availability near the colony (Congdon et al. 2005, Peck and Congdon 2005). Birds breeding on Heron Island in the tropical south-western Pacific Ocean performed successive short trips lasting between 1 to 4 days followed by a single long trip of approximately 8 days. However, alternations between short and long trips were primarily driven by the duration of the foraging trip of the partner rather than body mass (Peck and Congdon 2005), as is commonly the case (Weimerskirch et al. 1993, 1994). While one adult is on a long foraging trip, the partner at the nest performs short trips until the mate returns. The attendant bird then leaves for a long trip and the returning mate switches to short trips (Peck and Congdon 2005). Conversely, the population from Lord Howe Island, also located in the south-western Pacific, used a unimodal foraging strategy with an average trip length of 1.75 days due to higher prey availability near the colony (Peck and Congdon 2005, 2006). In this population, trip duration was significantly longer and provisioning rates lower in females. Inter-sexual competition at the foraging grounds provided the most parsimonious explanation for the sex-specific differences in this monomorphic species (Peck and Congdon 2006).

Boobies differ in their foraging movements from most other tropical or temperate-polar species, by typically returning to the colony every day (with the exception of Masked Boobies, see below). This implies that either adults are able to find sufficient prey within their limited foraging range or are reluctant to spend the night at sea (Weimerskirch et al. 2005). Maximum foraging ranges recorded in Red-footed Boobies, a species with RSD, breeding on Palmyra Atoll in the central Pacific Ocean were 67.52 km for trips lasting on average 8.67 h, which was more than twice the maximum foraging range and trip duration recorded in Masked Boobies of the same Atoll (29.35 km and 2.84 h, respectively) during the same study period (Young et al. 2010). An explanation for the observed differences between the two species might be a feeding niche segregation to avoid competition for the same resources (Young et al. 2010). Red-footed boobies may forage at greater distances from the colony to avoid competing with the larger Masked Boobies for prey. Such spatial feeding niche segregation is common in sympatric species. For instance, a study on Sooty Terns *Sterna fuscata*, White-tailed Tropicbirds *Phaethon lepturus*, Red-footed Boobies and Great *Fregata minor* and Lesser Frigatebirds *F. ariel* breeding on Europa Island revealed a spatial feeding niche segregation between these species (Cherel et al. 2008). One distinct foraging area was used by Sooty Terns and White-tailed Tropicbirds, another niche was solely used by Red-footed Boobies and both frigatebirds (Cherel et al. 2008).

Interestingly, Red-footed but not Masked Boobies showed a bimodal foraging pattern on Palmyra Atoll, which is surrounded by oligotrophic waters, with both sexes alternating between short and long trips (Young et al. 2010). Such bimodal pattern cannot be explained by feeding niche segregation. Physiological differences between species could explain this difference: Masked Boobies have higher wing loadings than Red-footed Boobies, which result in faster flight speeds and shorter travel times when soaring, but also incur increased flight costs (Brewer and Hertel 2007, Young et al. 2010). Thus, the smaller and more agile Red-footed Booby might be able to forage at greater distances from the colony, possibly in higher productive waters, due to its lower flight costs. However, foraging ranges and trip durations reported in this thesis, as well as in the population from Clipperton Island (Weimerskirch et al. 2008, 2009), showed that both male and female Masked Boobies are physiologically capable of travelling twice as far as individuals from Palmyra, and are even

able to spend the night at sea during the chick-rearing period. This suggests that factors other than flight costs or lower prey abundance near the atoll (Red-footed and Masked Boobies feed predominantly on Flying Fish (Exocetidae) and squid (Ommastrephidae), Young et al. 2010) may have led Red-footed but not Masked Boobies to alternate between short and long trips. In addition, no division of labour was found in chick-rearing Masked Boobies on Palmyra. It was suggested that this was because a division of labour may only be possible in a high-productivity environment, where the higher availability of prey permits greater flexibility in parental roles when provisioning offspring (Young et al. 2010). Considering the findings of this thesis with respect to the effects of body mass on adults' trip durations and time budgets, it would be interesting to test how differences in body mass within sexes influences the foraging behaviour of Masked Boobies on Palmyra Atoll. Table 5.1 in the Appendix provides an overview of the foraging parameters and diet of several Masked and Red-footed Booby populations, and of Northern Gannets.

Within the Sulidae, foraging ranges of chick-rearing Masked Boobies are only exceeded by Northern Gannets *Morus bassanus*, with maximum foraging ranges of 540 km (mean 232 km) for trips lasting 13 to 84 h (Hamer et al. 2000). Foraging movements and trip durations during the chick-rearing phase are also highly variable between colonies (see Table 5.1 in the Appendix). This has been directly linked to differences in prey caught (small forage fish vs. large pelagic fish) and the geographical location of the two colonies (offshore vs. inshore) (Garthe et al. 2007). In addition, Cape and Northern Gannets use a bimodal foraging strategy (Adams and Klages 1999, Garthe et al. 2003, Ropert-Coudert et al. 2004). In both species, the bimodal distribution coincided with a partitioning of trips into 1- and 2-day trips. In the former, adults were thought to perform 2-day foraging trips because they were unsuccessful during the first day of the trip (Adams and Klages 1999, Ropert-Coudert et al. 2004) and not because birds were alternating between shorter chick-provisioning and longer self-feeding trips.

The varying foraging movements reported in this thesis and other Masked Booby populations most likely reflect differences in prey availability (Gibbs et al. 1987, Anderson 1989, Jahncke and Goya 2000, Priddel et al. 2005). For example, Masked Boobies nesting on

Lobos de Tierra Island feed extensively on Peruvian Anchovies *Engraulis ringens*, available in nearby coastal waters. During El Niño years they switch to oceanic prey species in response to the absence of Peruvian Anchovies (Jahncke and Goya 2000). This indicates that birds not only modify their diet, but also that they switch from foraging in nearby coastal to distant oceanic waters when their preferred prey becomes scarce, as reported in this thesis. In contrast, the diet of Masked Boobies breeding on Lord Howe Island, approximately 900 km south-west of the Norfolk Island Group, almost exclusively consisted of Flying Fish (*Cheilopgon* spp.) during the early phase of the breeding season. During the late phase of the same breeding season when reproductive failure was high, their diet contained more squid, indicating that other prey species became scarce during the course of the season and that birds were unable to adapt accordingly (Priddel et al. 2005). However, foraging trip duration and ranges were not analysed in the Lord Howe Island population. It thus remains unknown whether adults were unable to adjust their foraging movements, so as to forage in more distant, more productive waters, and consequently suffered breeding failure, or whether there simply were no high quality prey patches available within their distant foraging ranges.

Foraging habitat characteristics and site fidelity

Prey is often aggregated in patches in the marine environment. The spatial pattern of prey patches changes with time due to the mobility, migration and passive transport of nutrients and lower trophic order organisms, with smaller scale structures changing faster than larger scale structures (Haury et al. 1978). At larger scales, prey patches are often linked to meso-scale (100–1000 km) oceanographic features such as upwelling zones, shelves, eddies or fronts (*e.g.* Murphy et al. 1988, Maravelias et al. 1996). Within these meso-scale features, small pelagic fish and other smaller species (*e.g.* squid and crustacea) may form scattered, high-density patches of schools and swarms at smaller scales (Fauchald et al. 2000). The spatial distribution of the prey of seabirds can thus be described by a hierarchical spatial patch structure where prey patches at smaller scales are nested within patches at larger scales (Murphy et al. 1988, Kotliar and Wiens 1990, Russell et al. 1992).

The spatial and temporal predictability of prey modulates foraging site fidelity. In order to maximise foraging efficiency, individuals learn where and when to find prey within their potential foraging range and return to the same feeding areas from one trip to the next or from one breeding season to the next (*e.g.* Great Cormorants *Phalacrocorax carbo*, Grémillet et al. 1999; Northern Gannets, Hamer et al. 2001), but the degree of such site fidelity, that is the degree of predictable prey encounters, is temporal-, scale- and habitat-dependent (Wiens 1989, Weimerskirch 2007).

Temperate-polar species often show strong site fidelity over shelf edges or productive fronts (*e.g.* Black-legged Kittiwakes *Rissa tridactyla*, Irons 1998; Adélie Penguins *Pygoscelis adeliae*, Watanuki et al. 2003a). Black-browed Albatrosses *Thalassarche melanophris* from Kerguelen Islands travel to the same foraging site over the shelf-break from one trip to the next as well as year after year (Weimerskirch et al. 1997a). In this population, a moderately constant high breeding success indicates highly predictable prey encounters over long time lags. Whereas the breeding success of Black-browed Albatrosses from Campbell Island, where adults repeatedly forage over the distant polar front during long trips, is lower and more variable than that in the Kerguelen Islands (Waugh et al. 1999, 1999a, Weimerskirch 2007). These findings indicate a link between the predictability of prey in relation to different oceanographic features and variability in breeding success (Weimerskirch 2007).

In tropical waters, the association of seabirds with particular oceanographic features is far less common than in temperate-polar waters (except for upwelling zones). It is generally assumed that this difference results from the overall lower productivity of tropical waters and consequently a lower spatial and temporal predictability of resources (Christian and Murtugudde 2003, Weimerskirch 2007). Indeed, one of the most striking differences between the foraging strategies of temperate-polar seabirds and those from tropical waters is that only non-tropical species have been shown to exhibit foraging site fidelity at a coarse-scale (1–100 km), although studies investigating this in tropical species are scarce and foraging ranges of examined species were limited to 40–300 km (Weimerskirch 2007).

Thus, the strong foraging site fidelity over the shallower shelf at a coarse-scale in Masked Boobies is unusual for a low-latitude species. This strong site fidelity as well as the inter-

seasonal use of the local foraging area by the population implies that the nearby shallow shelf provides highly predictable prey encounters at a coarse-scale over long periods. The prey patches however, appear to be of low quality in some seasons. These findings demonstrate that foraging site fidelity in association with a particular oceanographic feature does occur in a tropical environment and further confirms that the predictability of prey is highly scale and habitat dependent. The presence of this shallow shelf-edge within close range of the colony has, beyond doubt, important ramifications for the Masked Booby population and life history strategies, and presumably also for other seabirds and marine species in this region.

Masked Boobies from Clipperton did not show any foraging-site fidelity (Weimerskirch et al. 2008). The absence of a distinctive oceanographic feature such as a shelf edge or other physical processes concentrating prey within the foraging range might explain why individuals do not return to the same foraging area between trips. In addition, this population is thought to rely almost exclusively on associations with tuna and dolphins for feeding (the waters surrounding Clipperton Island are home to one of the world's largest tuna fishing industries), which are highly mobile predators, indicating that prey encounters are not predictable at a smaller scale (Weimerskirch et al. 2008).

Foraging strategies of tropical seabirds

How animals locate and capture prey is a central question in foraging ecology. Tropical seabirds use a variety of strategies to locate and capture prey, which are non-mutually exclusive and which can also be present in non-tropical species. Boobies, tropicbirds and gannets are plunge-divers, which plummet from height into the water and primarily use the momentum of their fall to attain depth (Ashmole 1971, Nelson 1978). Brown Boobies differ from other plunging boobies by entering the water at a low angle (Schreiber and Norton 2002). Whereas, Red-tailed Tropicbirds and Red-footed Boobies appear to occasionally use their wings or feet under water to reach greater depths (Le Corre 1997, Sommerfeld and Hennenke 2010, but see Weimerskirch et al. 2006 for dive depths attained by Red-footed Boobies). This behaviour has also been recorded in Blue-footed Boobies foraging in

subtropical waters (Zavalaga et al. 2007). In gannets, the use of wing flapping underwater to reach greater depths is a common technique (Ropert-Coudert et al. 2004, 2009). Dive depths of Masked Boobies reported in this thesis, as well as in other studies (Weimerskirch et al. 2008, 2009a), indicate that individuals capture prey within the first six meters of the water column and that they do not plunge-dive from the surface or make use of wing flapping underwater.

Other prey capture techniques found in tropical species involve pursuit-diving (e.g. Wedge-tailed and Audubon's Shearwater *P. ilherminieri*, Burger 2001), surface-plunging (e.g. Red-tailed Tropicbirds, Ashmole 1971; Red-footed-Boobies, Weimerskirch et al. 2006), surface-seizing (e.g. Flesh-footed Shearwater, Brown et al. 1978; frigatebirds, Nelson 2005), kleptoparasitism (e.g. frigatebirds *Fregata* spp., Nelson 2005) and aerial feeding (e.g. Red-footed Boobies, Nelson 1978, 2005; Sooty Terns *Sterna fuscata*, Flint and Nagy 1984; frigatebirds, Nelson 2005). The latter being a prey capture technique unique to tropical seabirds (Ballance and Pitman 1999).

Most tropical seabirds are therefore restricted to prey that either occurs within the first few meters of the water column or that are chased to the surface by subsurface predators. Subsurface predators include fish, cetaceans (e.g. Davoren et al. 2010) and pinnipeds, but in the tropics, tuna are likely the single most dominant group (Ashmole and Ashmole 1967, Harrison and Seki 1987, Au and Pitman 1988). With the presence of subsurface predators, prey becomes accessible for seabirds from the air, because the water surface acts as a boundary from which most prey cannot escape (Ballance et al. 2001). Flying Fish and squid, which comprise a substantial proportion of the diet of tropical seabirds (Ashmole and Ashmole 1967 Harrison et al. 1983), including Masked Boobies (Priddel et al. 2005, Weimerskirch et al. 2008, 2009, Young et al. 2010, 2010a), have evolved a flight escape response, presumably as a result of predator pressure from below (Ballance and Pitman 1999). While flight has made them less vulnerable to predation from below, it has increased their vulnerability to seabirds (Ballance et al. 2001). Foraging in association with subsurface predators, which has also been documented in non-tropical species (Obst and Hunt 1990,

Grebmeir and Harrison 1992), is therefore considered to be one of the most important prey capture strategies in the tropics.

Another important strategy is feeding in flocks. Although feeding flocks can merely be the result of passive aggregation of individuals at a shared resource, there is evidence that seabirds benefit by feeding in the presence of other individuals (Ballance et al. 1997). For example, individual fish in a school become disoriented and more vulnerable when attacked by increasing numbers of birds in a flock (Götmark et al. 1986). Intra- and inter-specific feeding flocks commonly occur in association with subsurface predators (Au and Pitman 1988, Ballance et al. 1997) and both the presence of subsurface predators as well as feeding flocks signals the location of prey to other individuals (Hoffman et al. 1981).

In the eastern tropical Pacific, Masked Boobies have been observed feeding in multi-species flocks in close proximity to their breeding islands in association with dolphins, mainly Spotted and Spinner Dolphins *Stenella attenuata* and *S. longirostris*, respectively, as well as with Yellowfin Tuna *Thunnus albacares* (Ballance et al. 1997, Mills 1998, Weimerskirch et al. 2008). Masked Boobies breeding within the Norfolk Island Group are often observed feeding in flocks (sometimes > 20 Masked Boobies) and in association with Yellowfin Tuna and dolphins (D. Bigg, pers.comm.). The extent to which this population relies on subsurface predators to capture prey and whether the presence of subsurface predators varies between foraging habitats (nearby shallow shelf vs. distant, deeper waters) is unknown and requires further investigation.

Another strategy to forage in habitats that differ in structure and/or where prey availability varies at a range of spatial scales is to adjust the search patterns accordingly. Individuals often increase their search effort in response to a specific habitat or in response to prey encounters, by increasing their turning rate and decreasing their travel speed, a behaviour termed ARS behaviour (Fauchald 1999, Fauchald and Tveraa 2003, 2006). It is suggested that the adoption of larger scale ARS zones may occur in response to areas where prey availability is predictable, such as over shelf-edges or fronts. The adoption of ARS behaviour at smaller spatial scales (often nested within these larger scales) however, could be a

function of immediate prey encounters (Hunt et al. 1999, Pinaud and Weimerskirch 2005, Pinaud and Weimerskirch 2007).

Studies investigating ARS behaviour in tropical species are still scarce (but see Weimerskirch et al. 2008, 2009a, Young et al. 2010, this thesis). In Masked Boobies from Clipperton, the areas in which individuals increased their search effort were evenly distributed around the colony with no particular hotspot (Weimerskirch et al. 2008, 2009a). Based on the findings of this thesis, it is likely that some of these ARS zones, in particular those located closer to the colony, were falsely detected by FPT analysis due to the inclusion of locations where birds rested on the water. Nonetheless, the absence of strong physical processes in the area surrounding Clipperton (Weimerskirch et al. 2008) suggests that adults most likely adopted ARS behaviour in response to immediate prey encounters. This thesis has not analysed if ARS behaviour occurred at different spatial scales, but it is possible that Masked Boobies adjusted their search effort at a larger scale when reaching the shallow shelf-edge and then at a smaller scale when birds detected prey. This is certainly an important aspect of the foraging strategies of Masked Boobies that should be addressed in future investigations.

Conclusions and perspectives

Understanding the factors that determine marine predator foraging ecology is crucial to assess how populations respond to environmental variability (Ashmole 1971, McCafferty et al. 1998) and heterogeneity (Pinaud and Weimerskirch 2007), and for the development of management and conservation plans (Schofield et al. 2007, Costa et al. 2012). In particular the latter has received increased attention in recent years, as seabirds and many other marine species are now threatened on a world-wide scale (see Powles et al. 2000, Butchart et al. 2004). Marine predators are susceptible to multiple threats (*e.g.* global warming, bycatch, pollution, oil-spill and over-exploitation of fish stocks) within their foraging grounds and migratory routes (Anderson et al. 2003, Hooker and Gerber 2004, James et al. 2005, Burger and Shaffer 2008). There is consequently an increasing demand for defining marine conservation plans, in particular the design of Marine Protected Areas (MPAs). It is generally

agreed that seabirds, as well as many other marine predators and smaller organisms, will greatly benefit from these protective areas (Grémillet and Boulinier 2009).

The role of bio-logging has been increasingly recognised as a valuable tool for conservation planning and monitoring (Hyrenbach et al. 2006, Burger and Shaffer 2008, Chilvers 2008). Foraging movements and time budgets derived from data loggers and track-descriptive analytical methods are used to define important foraging areas, and consequently design MPAs (Schofield et al. 2007, Block et al. 2011, Maxwell et al. 2011). However, defining these areas is challenging because factors influencing predator foraging ecology are wide-ranging, as demonstrated in this thesis, and because marine ecosystems are highly variable on a spatio-temporal scale (Hyrenbach et al. 2000).

The results reported in this thesis emphasize the importance of long-term studies in order to design MPAs. Central-place foragers, such as seabirds, should be tracked over several breeding seasons, as their foraging movements can vary markedly within a breeding season or from one season to the next due to changes in prey availability. At the same time, this study demonstrates how the distribution of a pelagic species is influenced by the predictability of prey, which in turn is associated with a specific oceanographic habitat feature. The amount of time such habitat features provide predictable prey encounters, the prey patch quality they provide, and how much its extent varies in time and space will determine the feasibility of MPAs (Hyrenbach et al. 2000). The biological importance of the shallow shelf-edge located south of the Norfolk Island Group for marine predators should most certainly be further investigated and evaluated.

Two of the most important findings of this thesis are that differences in body mass within sexes influence adults' foraging behaviour and that the extent of these effects varies between sexes, most likely due to sexual dimorphism and different parental roles. Consequently, studies investigating foraging behaviour, in particular studies of dimorphic seabirds, should consider these factors, as a sample size biased towards heavier or lighter individuals of one or both sexes may not be representative of a population. However, studies investigating these effects are still rare (but see Kato et al. 2008, Zimmer et al. 2011), often due to logistical constraints.

Finally, results reported in this thesis highlight that track-based analytical methods used to identify important foraging areas with the aim of marine conservation (*e.g.* Block et al. 2011) need to take into account the effects of resting at the sea surface positions to avoid false detection and incorrect interpretation of ARS zones. This is particularly important when the design of MPAs is constrained by the need to balance the requirements of marine megafauna and human activities (Harris et al. 2007, Pichegru et al. 2009).

This thesis evaluated some of the intrinsic and extrinsic, environmental factors influencing the foraging ecology of a central-place forager, but many gaps still need to be addressed. A better understanding of the functioning of oceanographic processes and structures is crucial to improve our knowledge of the foraging ecology of top predators (Burger and Shaffer 2008). Moreover, the reproductive performance and survival rates of a population, in addition to information on prey species, should be assessed whenever possible to evaluate if and how a species copes with environmental variability or change, and whether protective measures are successful. As a final point, one of the major challenges in marine conservation is to study the foraging ecology of non-breeding predators (Grémillet and Boulinier 2009). Many species spend a large proportion of their life-time at sea, travelling from hundreds to thousands of kilometres within days, and do not recognise political boundaries (Ballance et al. 2001, Costa et al. 2012). Studies simultaneously tracking the foraging movements and time budgets of marine predators (ideally of both sexes while accounting for differences in body mass within and between sexes), as well as assessing their diet will help fill some of the existing gaps.

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APPENDIX

Breeding site	Trip duration (h)	Foraging range (km)	Total distance travelled (km)	n	Diet	n	Reference
Phillip Island (MB)	6.52 ± 3.79 (0.88 – 14.18)	74.4 ± 68.0 (10.7 – 250.4)	160.7 ± 111.4 (28.1 – 422.6)	50	-		this study (Chapter 4)
Phillip Island (MB)	7.03 ± 8.16 ^M (0.15– 41.79)	57.9 ± 54.9 ^M (2.2 – 226.7)	148.6 ± 143.4 ^M (3.2 – 577.7)	41 ^a , 39 ^b	-	-	this study (Chapter 2)
	8.18 ± 7.61 ^F (0.52 – 37.19)	77.6 ± 64.4 ^F (4.5 – 230.8)	213.9 ± 174.0 ^F (10.4 – 602.3)	20 ^a , 19 ^b			
Lord Howe Island (MB)	-	-	-	-	<i>Cheilopgon</i> sp. (86 %) Squid (14 %)	21	Priddel et al. 2005
Raine Island (MB)	-	-	-	-	Exocetidae (40.8 %) <i>Hirundichthys</i> sp. (23.7 %) <i>Cypselurus</i> sp. (15.8 %) <i>Sthenoteuthis</i> sp. (6.7 %) <i>Cheilopgon</i> sp. (2.6 %) <i>Exocoetus volitans</i> (2.6 %)	76	Blaber et al. 1995
Clipperton Island (MB)	8.9 ± 4.5 (0.87 – 12)	103.1 ± 65.6 (5 – 245)	-	62	Exocetidae (60.8 %), Hemiramphidae (27.3 %) Coryphaenidae (6.1 %) other fish (4.1 %) Ommastrephidae (1.4 %).	30*	Weimerskirch et al. 2008
Clipperton Island (MB)	8.9 ± 3.8 ^M	90.9 ± 72.3 ^M	-	21 ^M	Exocetidae (^M 77.8, ^F 79 %) Hemiramphidae (^M 11.1, ^F 9.7 %) Scombridae (^M 5.5, ^F 6.4 %) Coryphaenidae (^M 4.9, ^F 3.2 %) Ommastrephidae (^M 4.9, ^F 3.4 %)	112 ^M , 98 ^F 16 ^M , 12 ^F 8 ^M , 2 ^F 7 ^M , 4 ^F 7 ^M , 4 ^F	Weimerskirch et al. 2009
	7.3 ± 3.1 ^F	109.4 ± 44.3 ^F	-	17 ^F			

(Table. 5.1 continued)

Breeding site	Trip duration (h)	Foraging range (km)	Total distance travelled (km)	n	Diet	n	Reference
Palmyra Atoll (MB)	2.84 ± 1.52	29.35 ± 11.50	89.41 ± 38.39	34 ^c	Exocetidae (70 %) Squid: mainly Ommastrephidae	14 ^d	Young et al. 2010
Latham Island (MB)	105 ± 35 (71 – 166)	315 ± 79 (171 – 389)	1125 ± 833 (405 – 2896)	7**	Exocetidae (90 %)	49	Asseid et al. 2006
	85 ± 42 (30 – 163)	221 ± 101 (56 – 367)	516 ± 275 (116 – 1018)	9***			
Lobos de Tierra Island (MB)	-	-	-	-	<i>Engraulis ringens</i> (64.1 %) <i>Scomberesox saurus scombroides</i> (25.2 %) <i>Scomber japonicus</i> (10.71 %)	8 ^g	Jahncke and Goya 2000
					<i>Engraulis ringens</i> (27.3 %) Exocetidae (25.5 %) <i>Mugil cephalus</i> (21.4 %) <i>Scomber japonicus</i> (9.1 %) <i>Katsuwonus pelamis</i> (7.5 %) <i>Merluccius gayi peruanus</i> (2.7 %) not determined (6.4 %)	11 ^h	
					<i>Scomber japonicus</i> (50.3 %) Exocetidae (21.5 %) <i>Scomberesox saurus scombroides</i> (8.3 %) <i>Anchoa nasus</i> (10.7 %) <i>Katsuwonus pelamis</i> (8.1 %) Loliginidae (0.86 %) <i>Sardinops sagax sagax</i> (0.22 %)	12 ^j	
Palmyra Atoll (RFBO)	8.67 ± 5.30	67.5 ± 44.2	195.6 ± 125.4	54	Exocetidae (70 %) Squid: mainly Ommastrephidae	34 ^d	Young et al. 2010
Europa Island (RFBO)	10.1 ± 1.9 ^e (4.8 – 12.5)	67.2 ± 34.0 (12 – 148)	169.6 ± 82.2	46	-	-	Weimerskirch et al. 2005
	5.0 ± 2.0 ^f (1.1 – 7.3)	39.2 ± 28.5 (10 – 114)	117.3 ± 65.5				

(Table. 5.1 continued)

Breeding site	Trip duration (h)	Foraging range (km)	Total distance travelled (km)	n	Diet	n	Reference
Bass Rock (Gannets)	32.2 ± 13.2 (13.1 – 84.0)	232 ± 100 (39 – 540)	-	72	<i>Scomber scombrus</i> (31.6 %) <i>Clupea harengus</i> (21.5) <i>Ammodytes marinus</i> (29.3 %) <i>Sprattus sprattus</i> (23.0 %) Gadidae (15.0 %) Others (3.7 %)	266 ⁱ	Hamer et al. 2000
Funk Island (Gannets)	14.9 (3.8 – 25.9)	62 (51 – 92)	177 (108 – 264)	14,11,11	<i>Mallotus villosus</i> (89 %) <i>Salmo salar</i> (6 %) <i>Clupea harengus</i> (3 %) <i>Scomber scombrus</i> (1 %)	-	Garthe et al. 2007
Bonaventure (Gannets)	28.0 (5.9 – 138.5)	132 (8 – 225)	432 (30 – 1292)	20,15,15	<i>Scomber scombrus</i> (50 %) <i>Clupea harengus</i> (33 %) <i>Mallotus villosus</i> (10 %) <i>Ammodytes</i> sp. (5 %) <i>Illex loligo</i> (2 %)	-	Garthe et al. 2007

Table 5.1. Foraging parameters and diet of Masked Boobies *Sula dactylatra* (MB), Red-footed Boobies *Sula sula* (RFBO) and Northern Gannets *Morus bassanus* (Gannets). Mean values ± standard deviations are given, with ranges in parentheses. Diets are given as percentages of total prey samples collected, unless otherwise noted. Sample size (n).

*Prey samples collected from 27 breeding adults and 3 chicks

** Seven foraging trips of one none-breeding adult

*** Nine foraging trips of one breeding adult

^M Values recorded in male Masked Boobies

^F Values recorded in female Masked Boobies

^a Sample size corresponds to trip duration

^b Sample size corresponds to foraging range and distance travelled

^c Data were collected from 25 chick-rearing and 9 incubating adults

^d Sample size corresponds to the stomach contents of 14 breeding Masked Boobies and 34 breeding Red-footed Boobies, respectively

^e Data obtained from incubating and ^fchick-rearing adults

^{g, h, i} Prey samples were collected in 1996, 1997 and 1998, respectively

ⁱ Sample size corresponds to 266 regurgitates